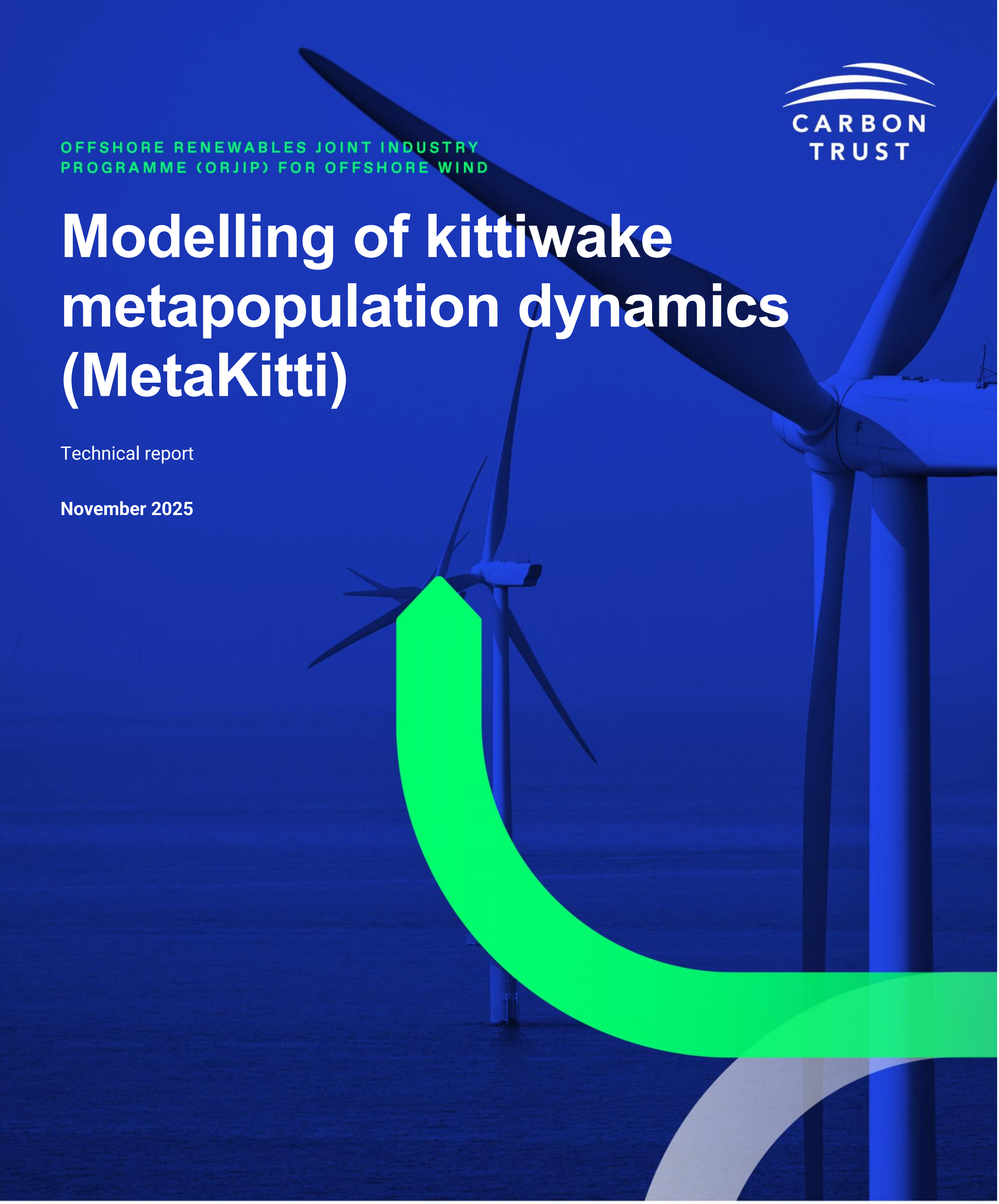

CARBON TRUST

OFFSHORE RENEWABLES JOINT INDUSTRY PROGRAMME (ORJIP) FOR OFFSHORE WIND

Modelling of kittiwake metapopulation dynamics (MetaKitti)

Technical report

November 2025

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working to accelerate offshore consenting

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- 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.

The programme pools resources from the private sector and public sector bodies to fund projects that provide empirical data to support consenting authorities in evaluating the environmental risk of offshore wind. Projects are prioritised and informed by the ORJIP Advisory Network which includes key stakeholders, including statutory nature conservation bodies, academics, non-governmental organisations and others.

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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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Contents

Modelling of kittiwake metapopulation dynamics (ORJIP MetaKitti project).

Jason Matthiopoulos, Jana Jeglinski, Julie Miller & Robert W. Furness

2025-10-03

Abstract

Background: The extensive spatial configurations of breeding seabirds are increasingly understood as metapopulations, comprising connected subpopulations, each with its unique demography, population dynamics and exposure to risk. However, until now, the viability of each subpopulations has been treated in isolation from other neighbouring subpopulations, and under assumptions of density independence, made for simplicity and generally considered both parsimonious and precautionary. However, both connectivity and density dependence are widespread in nature and it is unclear whether ignoring such well-documented mechanisms leads to unbiased population assessments. This issue is of particular concern for the black-legged kittiwake (*Rissa tridactyla*, hereafter kittiwake) metapopulation, a red-listed species in the UK, which is assessed as being in decline. Conservation to date has focused on individual Special Protection Areas (SPAs) which enclose subpopulations of interest, but it is not clear how these are connected within the network of all kittiwake colonies, if non-SPA colonies supplement or drain SPA colonies and how the whole system of kittiwake colonies is responding to disturbance. **Objectives**: Here, we tested the assumptions of parsimony and precaution by developing the first seabird metapopulation model to contain connectivity, three hypothesised forms of density dependence and the existence of floater birds that can act as buffers to population perturbations. We aimed to fit this sophisticated model to all available kittiwake data in the UK and Ireland, hence examining the role played by density dependence and connectivity. Using kittiwakes as an example, we also aimed to develop the next-generation fast and realistic metapopulation PVA for seabirds and explore the need for global and localised mitigation and compensation measures. **Data Collation**: We collated all available relevant data, compiling the most complete and up-to-date data set on kittiwake demography and population sizes across the Britain and Ireland. We highlight limitations and assumptions and propose approaches to the treatment of spatial subdivisions of the kittiwake metapopulation network. The dataset encompasses both SPA and non-SPA colonies, covering population size surveys from 1985 to 2023, data surveys on breeding success, survival of adults and immatures, and observations and ringing data on dispersal. **Model development**: Our modelling approach aimed to achieve 1) A biologically realistic representation of demography by incorporating time-varying demographic rates (with potential to include environmental covariates) and density dependence of three types (Allee effect, crowding at colonies and scramble competition at sea), 2) A metapopulation structure of sufficient detail, incorporating 89 colonies (a mixture of 33 SPA and 56 non-SPA locations), 3) Integrated use of multiple sources of data, including population sizes together with survival and breeding success data, along with dedicated sub-modelling used to extract the most informative priors possible. We examined the performance of three models. Model 1 (regional summaries model) allowed each colony to have independent time series of survival and breeding success. Model 2 (regional dynamics model) aggregated demographic performance (survival and breeding) into six spatial regions (NW,NE,W,E,SW,SE points of the compass). Model 3 (regional trends model) was the same as model 2, but with the addition of time trends in demographic performance. The three models were fitted to successful convergence to the complete colony network and available data. A crucial limitation in the process were the lack of any direct or indirect information on the localised carrying capacities of breeding colonies. The models produced adequate fits, but with extensive associated levels of uncertainty on the strength of density dependence. The fitted models presented similar patterns, indicating that only the middle and eastern part of the British isles is characterised by persistent populations. **Forecasts and counterfactuals**: Using the most parsimonious model 2, we generated forecasts of population trends. All colonies in the metapopulation are predicted to tend towards extinction over a period of 50 years. Geographically, there are no clear patterns in the speed with which populations are declining. Running the model with connectivity switched off shows that connectivity does not make much difference to these trends since the entire metapopulation comprises sink populations. To understand possible mitigation/compensation options, we explored the level of improvements needed in demographic rates for the decline to be reversed. We considered combinations of incremental improvements and deteriorations for four demographic rates: Breeding success, Adult survival, Pre-breeder survival and Floater survival. The most important demographic rate, by far, was found to be adult survival. We also investigated possible mitigating effects of artifical nesting structures (ANS). Our approach illustrates how the positioning and benefits of ANS can be investigated. We illustrate a practical approach investigating positioning and benefits of ANS as mitigating conservation management action. For assessing the feasibility of such recovery strategies the features of connectivity and density dependence examined here are highly relevant, especially the Allee form of density dependence that refers to colonies whose size is well below their carrying capacity. **Conclusions**: For a declining population in which all subpopulations are sinks, we conclude that the advanced metapopulation PVA developed here adds very little in predicting the time to extirpation of each subpopulation. This is mainly because the levels of donations between subpopulations are not greatly affecting their fate. However, because covariates are not included it is unclear how the metapopulation may redistribute in response to environmental change, and how this may change local and national persistence. We illustrate a practical approach investigating positioning and benefits of ANS as mitigating conservation management action. For assessing the feasibility of such recovery strategies the features of connectivity and density dependence examined here are highly relevant, especially the Allee form of density dependence that refers to colonies whose size is well below their carrying capacity.

1 Background

1.1 Connectivity in seabird metapopulations

The stable and distinct arrangement of some seabird breeding colony networks means that, during their breeding season, they are naturally modelled as *metapopulations* (Jason Matthiopoulos, Harwood, and Thomas 2005; Klomp and Furness 1992; E. Cam et al. 2004; Coulson 2011; Votier et al. 2011) whose overall dynamics are affected by connectivity, the net transfer of individuals from one sub-population to another (Levins 1969; Hanski and Gilpin 1997). In seabirds, connectivity results from the capability for wide, dispersive movements by prospecting and recruiting sub-adults (Coulson 2016). This ability of seabirds to disperse widely after fledgling (Bicknell et al. 2012; Genovart et al. 2013) combined with the large geographical extent of available colonies, implies high mark-recapture effort for direct estimation of pairwise connectivity between colonies. The difficulty in quantifying connectivity directly (Furness 2015), has led to legislation that treats each Special Protection Area (SPA) as closed to possible subsidies of new recruits from other colonies. However, the broadly assumed precautionary nature of the *closedness* assumption has never been validated, and it is certainly not biologically realistic: In metapopulations, the observed rate at which any colony grows, or declines may be confounded by subsidies from other colonies. These may become confounded with the effects of crowding and resource depletion (see next section) and a multitude of environmental variables and anthropogenic disturbances (Pulliam 1988; Oro and Ruxton 2001; Oro et al. 2004; Seward et al. 2019; Dugger et al. 2010). Because sub-populations may vary in their carrying capacities, one way in which such networks operate may be by a net emigration in one sub-population whilst another experiences growth from net immigration. *Source* populations, defined as those whose intrinsic growth rate is positive (births exceed deaths), may be essential for the persistence of *sink* populations, whose intrinsic growth rate is negative in the absence of immigration (Thomas and Kunin 1999). Identification of source and sink populations is therefore important for assessments of the impact of disturbances in SPAs, but may not even be measurable as the balance of observed mortality and fecundity in a population. For instance, *pseudosink* populations may exhibit a negative balance of local births and deaths but only because their breeding success is suppressed by immigration from a nearby source population (Holt 1985; Watkinson and Sutherland 1995). Immigrants may come from one or more source sub-population within the network. Sub-populations that become extinct may, in time, become recolonised (Hanski and Gilpin 1997). Ultimately, resilience against extinction across a metapopulation is subject to contributing influences from regulation (i.e., environmental and demographic stochasticity) (Foley 1994) combined with immigration of (mainly) pre-breeder dispersal in seabirds. The empirical study of species dispersal and recruitment in population ecology is complicated, particularly in the presence of demographic and environmental stochasticity, and confounded by density-dependent processes. The main premise behind the present work is that the effects of such intricately connected forces can only be teased apart once viewed from a holistic and quantitative perspective, by use of integrated metapopulation modelling. However, there are only few instances where seabird dynamics have been formalised by metapopulation models (Seward et al. 2019; Inchausti and Weimerskirch 2002) and even fewer examples of such models fitted to real population and demographic data (Miller et al. 2019; Jeglinski et al. 2023). With regard to connectivity, our aim in this project is to use both direct (i.e., ring-resighting) and indirect (i.e., population count) data to quantify connectivity across a computationally feasible but realistic representation of the kittiwake breeding metapopulation.

1.2 Density dependence in seabird breeding colonies

The future risks to populations in SPAs are usually evaluated with the aid of Population Viability Analyses (PVAs). These models may include some form of environmental and demographic stochasticity (Searle et al. 2019) and their vital rates may be formulated either as density-independent parameters or as density-dependent functions. Although there is clear evidence for the effects of environmental stochasticity and density dependent regulation in seabirds (Miller et al. 2019; Catharine Horswill and Robinson 2015), the magnitude and form of these important regulatory forces have been considered difficult to quantify and therefore are often omitted from PVAs. Density independence, in particular, is considered a more precautionary assumption based on the following rationale: If empirical estimates of vital rates are affected by underlying processes of density dependence, then they are likely to be underestimates of the population's true potential. As such, any PVA based on these empirical estimates will exaggerate risk. However, the opposite view is rarely considered. If indeed the estimates of vital rates are unbiased or upwardly biased (because they have been based on small, increasing populations far below their carrying capacity, or because they include subsidies from proximate source populations), then the assumption of density independence may underestimate long-term risk by relying on these high growth rates being sustainable (Merrall et al. 2024).

Taken together, the two factors of connectivity and density dependence can easily lead us to deceptive (non-precautionary) conclusions about viability. For instance, a large colony close to its carrying capacity may act as a source to several smaller protected subpopulations, but this effect will neither be known, nor directly measurable if connectivity is achieved by immigration of surplus sub-adults (*floaters*, see below) from the source colony. Anthropogenic disturbance of this complex of colonies would lead to a double jeopardy for the smaller colonies, affecting their own growth capacity, and depriving them of their subsidies, due to reduced surplus production in the source. If considered outside their true metapopulation and density-dependent context, such effects may appear as direct mortality induced by Offshore Wind Farm (OWF) developments on the smaller colonies and thus lead to gross overestimation of OWF impact.

Density dependence may operate at a local and regional scale, influence different demographic rates and have different strength at different parts of the metapopulation network (Jeglinski et al. 2023; Merrall et al. 2024; Cat Horswill, O'Brien, and Robinson 2017). For instance, recruitment into the breeding population may depend on local environmental features, determining the number of suitable sites/nest locations in each colony - a number that may differ from one colony to another. This colony-specific form of density dependence will be driven by the size of the breeding population of a colony as demonstrated for kittiwakes at colonies in the UK (Furness and Birkhead 1984). Alternatively, breeding success may depend on the availability of marine resources for chick provisioning. This regional form of density dependence will be determined by the breeding populations of all colonies that could potentially compete for resources in a particular part of the marine environment. Both forms exist in synergy, but the driving form of density dependence will simply be the one that exerts a stronger influence on the focal colony at a given point in time.

An additional form of density dependence, one that affects colonies well below their carrying capacity is the *Allee effect*, otherwise known as *depensatory* density dependence (Courchamp, Clutton-Brock, and Grenfell 1999; Stephens and Sutherland 1999; Merrall et al. 2024; Cat Horswill, O'Brien, and Robinson 2017). The term describes a rate of population growth disproportionately low compared to population size for small populations and implies that newly founded populations cannot grow unassisted when their size is below a certain threshold (a form of demographic "critical mass"), or conversely, that declining populations that drop below this threshold will go extinct. This form of density dependence is not generally considered in seabird PVAs (Schippers et al. 2011), but may be very important, particularly for seabird species of conservation concern due to their declining population size.

1.3 The importance of floaters

Floaters are birds that do not form part of the breeding population, including pre-breeders who are approximately old enough to start breeding, but also birds that are older than the average breeding age that were either widowed, or decided to take a year out from breeding (sabbaticals). Floaters are a population component that is invisible to breeding population surveys, which try to actively exclude non-breeding individuals (Ainley et al. 2024), and this component is exceedingly hard to count and quantify. As a class of individuals floaters constitute a buffer whose size may determine localised subsidies, encouragement of founding of new colonies and potential population resilience to catastrophic events, such as major weather events and disease outbreaks.

For seabird population models and data, floater individuals are a form of “ecological dark matter”, having important and, possibly, unexpected effects on metapopulation dynamics, without being directly countable. For instance, the viability of a population may not purely depend on its size, but also, on whether the population has recently been changing or been stable. An increasing population probably has been experiencing high recruitment and therefore may have a low reserve of floaters. A decreasing population probably has a low breeding success or a high adult mortality, meaning that reserves of floaters are also likely to be low. In contrast, a stable population close to the carrying capacity, experiences comparatively lower recruitment and may therefore have surplus individuals. In the event of an extreme failure in survival or fecundity, we would therefore expect previously changing populations to be more vulnerable than similarly sized, previously stable populations. The interplay between metapopulation dynamics and the unknown ways in which floater individuals may buffer their native, or adopted colonies makes this a more complicated situation. In the metapopulation context, the importance of floaters may depend on the level of synchrony between the dynamics of different colonies. If the metapopulation is decreasing or increasing as a whole it may be more exposed to lack of buffering, compared to a scenario where different colonies are following different trajectories, or one where all colonies are at carrying capacity.

However, the size of the floater class, and the rate of accumulation of new floaters can only be deduced by proxy, via the augmentation impact they have on the size of breeding colonies within the metapopulation. It is therefore essential that this non-breeding class is modelled and monitored within model fitting as a latent population component. The demographic attributes of these birds are known to differ from breeders’ (O’Hanlon et al. 2021) so they need to be estimated as separate parameters in the model (e.g., their capability to recruit at particular colonies and their survival probability compared to pre-breeders, or breeding adults).

2 Project Objectives

The project objectives were adjusted during the life of the project in response to the developing results about the declining dynamics of the UK metapopulation and detailed insights into data availability for covariates. Hence, the examination of covariates, source-sink dynamics have assumed a smaller role than initially anticipated, allowing us to focus instead on the magnitude of necessary population-wide or localised mitigation/compensation measures.

2.1 Objective 1: Estimate connectivity and density dependence between kittiwake colonies.

Work under this objective sought to adapt and expand on previous models on metapopulation connectivity by deriving an appropriate distance- and density-dependent model for direct and indirect forms of connectivity. These two forms of connectivity are identifiable because direct connectivity (due to prospecting immatures) affects rates of migration and density-dependent recruitment at lags of 4 years, whereas indirect connectivity (due to competing provisioning adults) affects density dependent breeding success in the current year. This connectivity model was embedded into the demographic long-term dynamics of the metapopulation and fitted to a collated data base of diverse data types (population, age structure, breeding success, survival, movement, natural and anthropogenic covariates), within a Bayesian state-space framework. Originally, it was envisaged that the computational demands of fitting a complex metapopulation model to the entire network of kittiwakes would be prohibitive, but this was overcome, so the model was fitted to the entirety of the data and spatiotemporal extent (i.e. 89 colonies over 39 years).

2.2 Objective 2: Produce next-generation PVA and use it to forecast kittiwake dynamics.

The fitted metapopulation model was turned to the task of forecasting, hence functioning as a high-grade Population Viability Analysis. Uniquely, this PVA approach included features on three types of density dependence (Allee effect and crowding for recruits, as well as scramble competition between provisioning adults), and two types of connectivity (distance-dependent exchange of recruits between colonies and distance dependent food competition between colonies). Furthermore, the model was fully stochastic and also accounted for the important class of floater birds. Different versions of the model examined spatial clustering in the fluctuations of vital rates (fecundity and survival) across the colony network.

2.3 Objective 3: Predict population responses in closed vs. open systems.

We examined the net fluxes of individuals between colonies and also compared predictions of the population trajectories from models with and without connectivity, to investigate source and sink properties.

2.4 Objective 4: Investigate population-level and localised mitigation/compensation measures.

We carried out an exhaustive exploration of detrimental perturbations and beneficial mitigation on four demographic parameters simultaneously (breeding success and adult, immature and floater survivals). The detrimental effects were quantified, but not causally defined (i.e., we did not associate survival effects on OWF or catastrophic weather events). Further, we examined the likely beneficial impact of localised source populations (such as those that might be generated by artificial nesting sites).

2.5 Objective 5: Provide recommendations for the use of developed models, including in other regions.

We considered recommendations based on the findings from the above objectives, highlighting the degree of disturbance than can be tolerated by a focal colony, and the collection of future data aiming at maximum precision gains for long-term predictions.

3 Data availability and collation

3.1 Colony census counts

Kittiwakes build substantial nests of mud, seaweed and grass, that are plastered onto narrow ledges. Most kittiwakes nest in distinct colonies but nests tend to be patchily distributed with high numbers on suitable ledges. Kittiwake colonies tend to be towards the lower part of high cliffs, which makes counting nests from clifftops particularly difficult at colonies with high cliffs. Some nest within caves, under overhangs, or in narrow cliff "geos" which can make counting from land extremely difficult. Some nest on artificial structures such as coastal buildings or on offshore gas platforms (Christensen-Dalsgaard, Langset, and Anker-Nilssen 2020; O. D. O. Wind 2023). Most colonies on terrestrial artificial sites such as buildings can be counted accurately, but the numbers nesting on offshore platforms in UK waters are not well known, and this nesting habitat was excluded from the latest national census (Burnell et al. 2023) so that the total population size including those nesting offshore has been underestimated by an uncertain amount. However, apart from the colonies on gas platforms, the locations of kittiwake colonies in Britain and Ireland are well known and kittiwakes are considered one of the easiest species of seabird to census because of their high visibility and spacing between nests (Walsh et al. 1995). Some colonies require counting of kittiwakes from the sea rather than from clifftops, or a hybrid with some counts from land and a check by boat of areas not visible from land (Burnell et al. 2023). The recommended census method (Walsh et al. 1995) is for counts of Apparently Occupied Nests (AONs) during a preferred survey period of 24 May to 14 June or as close to that seasonal window as possible.

Numbers of AONs cannot be easily translated into numbers of breeding pairs, although it is often assumed that the two metrics are essentially identical. Some AONs are occupied by immature birds that will not breed but will most likely fully recruit into the breeding population the next year. Some kittiwake nests in which eggs are laid are lost from the colony relatively early in the breeding season, often as a result of extreme weather, intra-specific competition and fighting, avian predators, or inter-specific competition for nesting sites. Some late-breeding birds may complete a nest long after some of those losses have occurred, and some birds that lose eggs early during incubation (but usually only about 50% of those) can lay a replacement clutch about two weeks later (Coulson 2011). As a result, the number of AONs at a colony will change from day to day, tending to increase to a peak in early incubation (around late May) then decline. Changes in the numbers of AONs tend to be small during the optimal census window, which is why that window has been defined, and probably correspond well to the number of breeding pairs. However, colonies that are increasing will most likely have a higher proportion of AONs occupied by immature birds than at colonies where numbers are decreasing, which may introduce a systematic bias. Most counts at kittiwake colonies follow the census guidance and are likely to be accurate (Burnell et al. 2023). However, there can be errors resulting from inappropriate seasonal timing of counts or from "corrections" made to count totals to allow for parts of the colony not visible to be censused. The latter is problematic where a count is only from land so that some of the colony cannot be viewed. Some counts present the numbers of AONs observed, so represent a minimum number whereas others estimate how much of the colony was not seen and adjust the total to allow for likely numbers in the unobserved area. For a problematic count at Flamborough-Bempton, we followed Coulson (2011) in replacing the estimate of 83,000 pairs in the 1980s by 41,500 pairs as the evidence suggests that the higher count was expressed as the number of breeding adults rather than the number of breeding pairs.

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. Locating data requires filtering by count type (colony), species (kittiwake), years (1986 to 2024) and site. Searching by site can be performed using the SPA name, but in many cases there are multiple entries by site name so that the correct case needs to be entered. For example, there are 54 different pages of data for Hoy, of which Hoy SPA contains the kittiwake census data. Once located, the census data may be provided as the number of AONs in the whole SPA in a particular year, but in many cases the data are provided for defined subunits of the SPA and so need to be totalled for the whole SPA. Care also needs to be taken as some data are presented in non-standard units (for example numbers of individuals rather than AONs). The database provides the date of the count in some cases, allowing checking that the count was made during the recommended survey window. For example, all of the count data for Rum SPA in 1999 were collected on dates outwith the recommended count window, whereas counts in 2016 were within the count window. Out-of-window counts have not been excluded because they are given in the JNCC SMP database at face value, and in many cases the date of the count is not given, which further constrains evaluating the reliability of the data. The identity of the counter is also omitted from the database, so that may not be easy to infer likely reliability of the count based on the expertise of the counter.

Data for kittiwake AON counts at the 33 SPA colonies in the UK where breeding kittiwake is a feature (Burnell et al. 2023) were extracted from the SMP database and listed in an Excel spreadsheet for use in the modelling. The geographical coordinate of a point close to the central part of each SPA is included in the tabulation, derived from Google maps. As a sense check, the counts for these sites in the national censuses of 1998-2002 and 2015-2021 were also extracted from Burnell et al. (2023). Data for "Tyne" are also included as that site is monitored in detail and holds large numbers of breeding kittiwakes, although the site consists of predominantly birds nesting on buildings and is not an SPA. The Excel sheet is named "SPA colony count data JNCC SMP".

A separate spreadsheet tab "counts by area" lists the regional administrative areas in GB, the number of "colonies" (defined by JNCC) within each of those areas in 2015-21 and the total number of AONs in that area in 2015-21. It also lists which SPA site is within each area and by subtracting the number of AONs in each SPA from the area totals it computes the numbers of kittiwake AONs in each area that are in colonies that are not SPAs with breeding kittiwake as a feature. The same calculations are tabulated for the national census data for 1998-2002 (Seabird 2000) and for 1985-87 (Seabird Colony Register). This permits inclusion of non-SPA kittiwake numbers in the model (which in 2015-21 represented 21.7% of the total population in GB, 22.4% in 1998-2002). It would be preferable to use data for each individual non-SPA colony, but those data are not published, and the data associated with the Seabirds Count survey (2015-2021) seem not to match up clearly between maps and tables in Burnell et al. (2023) and the JNCC SMP database. For example, the database only lists counts for seven sites in Tyne & Wear in 2015-2021 (all for 2015) despite there being published counts in every one of those years, whereas the book has a map showing only three dots for kittiwake in Tyne & Wear, and a data table stating that there were nine kittiwake colonies in Tyne & Wear in 2015-2021. It appears that the JNCC SMP database does not hold all the data used in preparing Seabirds Count, and that the presentation of data on colony numbers in Burnell et al. (2023) uses a different definition of site or colony from that used in the database (which splits Tyne Bridge into two separate sites but amalgamates all colonies in Newcastle Quayside (including colonies on different buildings and on a nearby railway bridge) as a single data entry. These issues would be challenging to resolve and so, for non-SPA sites, we have had to use pooled data for administrative regions as the only practical way to compare between national survey data sets (see section Treatment of Space, below).

3.2 Breeding success

Kittiwake breeding success is monitored at many colonies throughout Britain and Ireland following two recommended methods (Walsh et al. 1995). Method 1 involves mapping individual nests during incubation, revisiting the site several times through the breeding season, and counting the number of chicks on each visit. This labour-intensive method is rarely used and at most sites productivity is monitored using Method 2 (comparison of nest and chick counts). Method 2 uses a count of AONs in a defined area (either the whole colony or a defined sub-plot) followed by a count of the total number of chicks in each of three size classes (small, medium, large) around 15-20 July. The method assumes that all large and medium sized chicks will fledge and that half of the small chicks will fledge. In practice, it is unclear whether all fieldworkers who use Method 2 make the correction based on a 50% survival of small chicks, and in some cases all those chicks may be included in the estimate of breeding success. However, in most colonies in most years a count around 15-20 July is likely to find very few small chicks, so this correction may not be very influential. Walsh et al. (1995) suggest that Method 2 probably overestimates actual productivity by about 10-20% but does not present evidence to support that suggestion. Data in the JNCC SMP database on kittiwake productivity at SPA colonies where breeding kittiwake is a feature were extracted and entered into an Excel spreadsheet. Data are presented as the total number of chicks (correction not specified) in relation to the total number of AONs, allowing productivity to be computed as the mean number of chicks per AON for comparison among years or colonies. In some cases the data are provided as a single count for the colony and year, but in many monitored colonies there are several separate monitoring plots, and the data are generally presented by individual plot – in these cases data of individual plots were summarised where that is the case. This then requires summing of data over multiple within-colony plots to obtain a value for the colony. The Excel tab is named "SPA productivity JNCC SMP". Additional productivity data are available for some non-SPA colonies (sources see below). Those data have not been extracted from the JNCC SMP database. However, 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. Those were collected before the official guidance on methodology was drawn up and presented in Walsh et al. (1995) but since these earlier studies tended to use almost identical methods to the recommended Method 2, so the data are comparable. Data for artificial nest sites at the Tyne from 2001 to 2023 have been published as annual monitoring reports (Turner 2023). The annual summary of those data is provided in the Excel sheet "Tyne Turner data". Data for North Shields from 1954 to 1990 have been published in Coulson (2011) as have data for Marsden for some years from 1954 to 2010 and for Foula (Shetland) from 1971 to 2009. However, the data in Coulson (2011) have been provided as mean numbers of chicks per AON without the sample size being reported. Those data are provided in the Excel sheet "Coulson 2011". Data for Foula are available from 1971 to 2023 and are listed in the Excel sheet "Foula productivity data". Where these overlap with the JNCC SMP database the data match, but the Foula data are for a much longer time series than represented by the JNCC

SMP database.

3.3 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, mostly based on resightings of individually colour-ringed adults. In Brittany, France, survival was estimated to average 0.795 (SD 0.065) from 1980 to 1994 (E. Cam et al. 1998). In that study it was also estimated that survival of sabbatical birds was lower than the survival of breeding birds, and the authors inferred that the individuals taking a year off from breeding were therefore of lower fitness. In Denmark, adult survival at the main colony of Bulbjerg from 1992 to 2010 averaged 0.82 (SE 0.02) with very little annual variation (Lerche-Jørgensen, Pedersen, and Frederiksen 2012). At Foula, Shetland, adult survival averaged 0.80 from 1986 to 1997, but annual values varied from 0.53 (SD 0.08) to 0.98 (SD 0.01) and were affected both by sandeel stock biomass and by the impact of predation by great skuas (Oro and Furness 2002). At Fair Isle, Shetland, adult survival between 1986 and 1997 averaged 0.83 (SD 0.12) (Rothery et al. 2002). At Hornøya, north Norway, adult survival between 1989 and 2003 averaged 0.88 (SD 0.1) (Sandvik et al. 2005). The Isle of May kittiwake survival rate declined from 0.99 in 1986 to 0.83 in 1996 but averaged 0.882 over those years (M. P. Harris, Wanless, and Rothery 2000). However, annual survival rates of kittiwakes are very strongly correlated with measured annual return rates (M. P. Harris, Wanless, and Rothery 2000) and at the Isle of May, east Scotland, breeding adult annual return rate varied between 62.9% and 96% from 1987 to 2019 (JNCC 2024). The sightings data on which these return rates are based are being re-analysed at present to derive survival rate (Searle et al. in prep.). Kittiwake adult survival at the Isle of May between 1986 and 2002 was influenced by sandeel fishing in the area and by sea temperature effects on the food web, being lower when sandeel fishing was occurring and lower when sea temperature in winter was higher (Frederiksen et al. 2004). At Skomer, Wales, kittiwake survival rate between 1986 and 2018 varied from 0.7 to 0.96 (S. J. Harris et al. 2024). Despite the likely relevance of sandeel stock biomass for kittiwake adult survival, data on Shetland sandeel stock biomass are only available for the years 1976 to 2004 as the fishery at Shetland closed when the stock collapsed, and no fishery-independent monitoring continued. For the ICES sandeel areas 1r (Dogger Bank region) and 4 (off east Scotland) data are available from 1983 to 2023 (SA1r) and from 1993 to 2023 (SA4). These are included in tab “sandeel abundance covariates” in the Excel spreadsheet. The longest time-series of annual survival or mortality of individually-marked breeding adult kittiwakes is for birds at Tyne colonies (Coulson and Strowger 1999) for every year from 1955 to 1996. We have excluded data from that study for 1997 and 1998 for two reasons; firstly the birds were apparently affected by an exceptional local red tide toxin mortality outbreak in those two years (Coulson 2011), and secondly the estimation of survival becomes less reliable in the last two years of a long-term study as a result of some missing marked birds that are still alive and may reappear after a year or two. The British Trust for Ornithology (BTO) runs the Re-trapping Adults for Survival (RAS) scheme, which has included several studies of individually ringed breeding kittiwakes, at a range of colonies around the UK. Those include Claremont Pier Lowestoft, Saltmeadows Tower Gateshead, site 137 Puffin Island Anglesey, site 314 Rinsey Cliffs and Trewavas Head Cornwall, site 432 Canna Highlands, site 481 Yorkshire and possibly some others. Sites can be added or lost from the RAS scheme and so the number of sites included and their geographical representation can vary from year to year. Data from the BTO RAS scheme are published for years 2000 to 2022 (BTO 2024. Retrapping adults for survival. https://www.bto.org/get-involved/volunteer/projects/bird-ringing-scheme/ringing-surveys/retrapping-adults-survival) and have been presented also in annual Ringing Reports (Walker et al. 2018, 2021, 2023; Walker, Robinson, Barimore, Blackburn, Barber, McCambridge, et al. 2020; Walker, Robinson, Barimore, Blackburn, Barber, Bugg, et al. 2020). Unfortunately the data in the annual Ringing Reports differs substantially from the data presented online on the RAS web page and it is unclear why that is the case. However, mean survival estimated from the RAS data is around 0.82 which is similar to published estimates for single-site studies. Although adult survival is for birds that have established as breeders at a study colony, it was suggested that survival is likely to be similar for immatures more than one year old (Coulson 2011) and indeed, despite being less experienced and so possibly at greater risk than breeding adults, survival of immatures might possibly be slightly higher than that of breeding adults as immature kittiwakes are not subject to the same levels of competition in the vicinity of the colony (Porter and Coulson 1987). Annual estimates of adult kittiwake mortality were taken from Coulson and Strowger (1999) and listed in Excel sheet “Tyne adult annual mortality”. Estimates of annual return rates of adult kittiwakes at the Isle of May, and annual survival rates of adult kittiwakes at Skomer and Foula were listed in Excel sheet “adult return or survival”. Annual estimates of survival data from the BTO RAS studies of adult kittiwakes are provided in the Excel sheet “BTO RAS”.

3.4 Nonbreeding by established adults (sabbaticals)

At two colonies in Brittany, France, the proportion of adults missing breeding each year was around 5 to 15% in different years and in colonies differing in dynamics (Danchin and Monnat 1992). At the North Shields study colony, a breeding season was missed by about 5% of adult males and about 10% of adult females (Coulson 2011). There was also some variation among time periods, especially among females, with a suggestion that fewer birds missed a breeding season when competition was lower (Coulson 2011). E. Cam et al. (1998) found that in most years at a study colony in Brittany, France, about 6% of adults chose not to breed in a particular year, but that increased to 25% in one year (when breeding was unusually late). E. Cam et al. (1998) found evidence that sabbatical birds were of lower quality and had lower survival than birds that nested every year. This further emphasises that the proportion of adults that choose not to breed in a particular year is likely to be influenced by environmental conditions and in particular the level of competition (density dependence), with poorer quality birds refraining from breeding in increasing numbers as competition increases. M. P. Harris, Wanless, and Rothery (2000) estimated that non-breeding by established adult kittiwakes occurred at the Isle of May only in some years, but could be substantial in some of those years, which is consistent with the suggestion that non-breeding is a facultative response to environmental deterioration. Birds that have been established breeders but take a sabbatical will probably not build a nest that season and so will be missing from the colony census of AONs.

3.5 Adult dispersal

Most breeding adults return to exactly the same nest site year after year (Coulson 2011) but a few will move to another colony, usually as a consequence of breeding failure suggesting that a move may be to seek a higher quality nest site (Danchin and Monnat 1992). Based on data in Danchin and Monnat (1992), Catharine Horswill and Robinson (2015) estimated that between 1% (in an increasing population) and 6% (in a decreasing population) of adult kittiwakes may show breeding dispersal each year. There are several examples of kittiwakes abandoning particular colonies that were subject to extreme breeding failure, or predation impact, or exclusion from nest sites by human

Table 1: The age at first breeding of male and female kittiwakes which had been ringed as chicks and later nested at North Shields (from Coulson 2011)

Period	No males	Age 1st breeding	SD	No females	Age 1st breeding	SD
1961-70	64	4.59	0.12	17	4.22	0.26
1971-80	69	4.42	0.12	15	4.25	0.29
1981-90	77	3.69	0.1	21	3.61	0.22

actions such as putting up exclusion netting, and moving to a nearby safer nesting area (Coulson 2011). For example, a colour-ringed breeding adult that had been part of a RAS study and which nested each year from 2017 to 2020 at a colony in Cornwall moved to Skellig Michael, Co. Kerry in 2023 after the Cornish colony declined dramatically in numbers, in part due to predation of many of the chicks by peregrine falcon (*Falco peregrinus*) (https://cornishringing.blogspot.com/). However, where kittiwakes achieve moderate to high breeding success such movements seem to be rare (Porter and Coulson 1987).

3.6 Age at first breeding

Catharine Horswill and Robinson (2015) note that age of first breeding in kittiwakes is typically four years old, although this may vary among individuals and range from two to seven years (Wooller and Coulson 1977). Coulson (2011) noted statistically significant differences in mean ages of first breeding between the sexes (being younger in females) and among time periods at the North Shields colony (Table 1). However, these data are all for philopatric individuals (birds that were born at North Shields and also nested there) and there is no evidence on age of first breeding of individuals that emigrated or immigrated. It is likely that age of first breeding will be influenced by competition, so will show density-dependence with earlier breeding where competition is low due to numbers being below carrying capacity [Porter and Coulson 1987; Furness (2015)].

At study colonies in France, age of first breeding was 3.9 years (SD 0.83) at a flourishing colony, 3.71 at a declining colony, 4.17 at other nearby colonies (Danchin and Monnat 1992), so overall similar to that reported at North Shields (Table 1). Danchin and Monnat (1992) also noted a mean of 5.4 years at colonies elsewhere in Brittany but noted that that value was too high due to a lower intensity of observation at those sites; this emphasises the difficulty of obtaining accurate estimates of the age of first breeding as noted also by Coulson (2011). However, Porter and Coulson (1987) concluded that age of first breeding decreased as adult mortality increased, and that this density-dependent response, together with an increase in immigration, compensated for the change in adult mortality.

3.7 Immature (pre-breeder) survival

From ring recovery data, Coulson and White (1959) estimated pre-breeder survival to be 0.79 up to age one year old. 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. It could be lower because individuals are still relatively inexperienced, or it could be higher because there are fewer threats to kittiwakes in pelagic environments than there are at colonies.

3.8 Natal dispersal

There is a pool of potential recruits (immature kittiwakes) from which new recruits into the breeding population are drawn (Porter and Coulson 1987). At North Shields, NE England, about 11% of each cohort returned to breed in their natal colony, whereas the vast majority of the cohort appear to emigrate to breed elsewhere (Porter and Coulson 1987). However, most of the birds that returned to breed at their natal colony were males, and most females dispersed to breed at another colony. This sex difference implies that the mean or median natal dispersal distance of males will be much less than that of females, but the natal dispersal distances measured from ring recovery data cannot be allocated to sex because plumages of male and female kittiwakes are identical. Small (new) colonies of kittiwakes cannot produce enough young during their first 70 years of existence and are sustained by immigration (Porter and Coulson 1987). At North Shields where all chicks reared at the colony were ringed every year, the proportion of male recruits that had been ringed as chicks at North Shields increased from close to zero in 1956 to a peak of 50% in the early 1970s, then fell to around 20% in the 1980s (Porter and Coulson 1987). The proportion of female recruits that had been ringed as chicks at North Shields was zero from 1956 until 1963, then increased slowly to a peak of 15% in the late 1960s, then fell to around 5% in the late 1970s and early 1980s (Porter and Coulson 1987). Overall, Coulson (2011) calculated that 64% of male recruits to North Shields were immigrants (430 immigrants out of 677 male recruits) as were 91% of female recruits (550 out of 603). Porter and Coulson (1987) concluded that the pool of potential recruits and especially the large numbers of immigrants from other colonies provide an important buffering system to kittiwake colony dynamics. They concluded that control of recruitment to the colony from the pool of potential breeders is density-dependent and is the main factor determining the pattern of growth of kittiwake colonies. How far do immigrants travel? In some cases it is clear that both male and female kittiwakes that form new colonies remote from established colonies must have immigrated over a considerable distance. New kittiwake colonies in Denmark and Spain were established more than 500 km from the nearest existing colony and so the birds founding those new colonies must have shown natal dispersal in excess of 500 km (Coulson 2011). Indeed, four kittiwakes ringed as chicks at colonies in the UK have been found as adults in the main Danish kittiwake colony of Bulbjerg (The Danish Bird Migration Atlas). Ringing of kittiwake chicks at a variety of colonies has shown the origin of some breeding adults; a chick ringed at the Farne Islands, NE England, subsequently nested at the Scilly Isles (Coulson 2011) about 700 km away by direct line overland, but about 1100 km away by the shortest sea route. However, longer natal dispersal distances have been recorded, including two birds ringed as chicks in Sweden that nested in France at a distance of over 1200 km (Rickeard unpublished), and a kittiwake ringed as a chick on Utsira, Norway seen at a nest at Croix Island, France, (Tveit, Mobakken, and Bryne 2004) a natal dispersal of 1300 km. Straight-line (including overland) minimum natal dispersal distances of 14 individuals ringed as chicks but caught as breeding adults at the colony in Boulogne (Rickeard unpublished) were 1200, 1200, 900, 670, 550, 550, 550, 550, 530, 500, 490, 200, 200, and 200 km. At the Rinsey Cliffs and Trewavas Head kittiwake colonies which have been a BTO RAS site since 2012, although only 52 adults were colour ringed at that site between 2012 and 2015, some 22 sightings of kittiwakes that had been colour ringed as chicks at colonies in France were made over the same period, suggesting a high rate of immigration of French-born kittiwakes to Cornwall (https://cornishringing.blogspot.com/). BTO ring recovery data for kittiwake accumulated up until 1990 were analysed by Coulson and

DeMenergnies (1992) to determine the pattern of natal dispersal. They only considered kittiwakes that had been ringed as chicks and were recovered at least four years later (so were of breeding age) during the breeding season (defined as April to July). This gave a sample of 145 recoveries which showed a bimodal distribution of natal dispersal distances, with most distances less than 50 km but with a smaller peak of movements at 400 to 1000 km (Coulson 2011), 17.5% of movements falling into this second peak. More recent analysis of the BTO ring recovery data (Wernham et al. 2002) found that 112 recoveries of kittiwakes ringed as chicks but recovered in the breeding season when at least three years old were within 20 km of the colony of birth, whereas 165 were more than 20 km from the colony of birth (Wernham et al. 2002), and included movements to Norway, Sweden, and even Greenland and Canada. While there is no confirmed evidence of kittiwakes ringed as chicks in Britain and Ireland breeding in colonies in Greenland or Canada, there is confirmed evidence of breeding birds showing natal dispersal between Britain and Norway, Sweden, Denmark, Germany and France (Wernham et al. 2002), suggesting that while natal dispersal is often over only a few km, a substantial fraction of kittiwakes move tens or hundreds of km from their natal colony to where they recruit. Many of the kittiwakes caught as adults on nests have been caught where the species breeds on “artificial” sites such as the Saltmeadows Tower, Gateshead, and various buildings. There is therefore a tendency for a high proportion of the confirmed cases of natal dispersal to involve kittiwakes ringed as chicks that recruited to breed in urban/artificial colonies, although this may be an observational artifact of the fact that some urban structures are more accessible to survey. Nevertheless, there is no evidence to suggest that such birds are atypical in terms of their natal dispersal distances. In order to update the analysis of natal dispersal distances of kittiwakes using the method developed by Coulson and DeMenergnies (1992) ring recovery data (recoveries anywhere of kittiwakes ringed in Britain and Ireland, and recoveries in Britain and Ireland of kittiwakes ringed abroad) held by the BTO were requested. The BTO provided these as a spreadsheet in late June on payment of a commercial fee and after checking that there were no objections from individual ringers responsible for a significant proportion of the ringing of kittiwakes in Britain and Ireland to the data being provided.

4 Modelling approach

4.1 Bayesian integrated metapopulation modelling

Although the ORJIP-funded project is nominally focusing on the kittiwake we have prioritised the development of an approach that can lead, more broadly, to the next generation of Population Viability Analyses for seabirds. The three overarching advancements required to achieve this approach were:

1. **A biologically realistic representation of demography.** Demographic processes do not develop at constant rates since they are affected by environmental covariates and various forms of density dependence. Environmental covariates may be influential at the location of the colonies (e.g., physical environment available for nesting, weather events, or general exposure to weather) or in the seas around each colony (e.g., prey abundance, sediment type forming prey habitat, existence of anthropogenic structures). Density dependence is rarely examined in seabird PVA analyses, under the notion that ignoring density dependence results in a precautionary approach to risk. We have identified three forms of density dependence that have never previously been examined simultaneously in population models and, only rarely been individually incorporated into seabird risk assessments (Merrall et al. 2024): 1)

Depensatory density dependence (the Allee effect), representing the difficulty faced by nascent colonies to increase in size (Porter and Coulson 1987), 2) Compensatory density dependence (crowding at colonies), 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.

2. **A metapopulation structure of sufficient detail.** Kittiwake colonies tend to receive attention if they are large and have been designated Special Protection Area (SPA) status. Disaggregating large colonies to subunits is not computationally prudent, especially if these aggregations of birds behave as a connected whole. On the other hand, ignoring smaller colonies with no SPA status may be bypassing important stepping stones in connectivity. Connectivity between colonies may play a role at multiple points. We have identified two such points in the demographic model. First, recruitment of individuals born in one colony into the breeding population of another may be described via a distance-dependence function. The flux of such immigrants will depend on the number of emigrants from the source colonies so, crowding and the Allee effect need to be quantified while controlling for the size of neighbouring colonies. Second, competition for marine resources (a process possibly affecting breeding success) will be intensified in the proximity of other colonies, especially if they are large. So, marine density dependence needs to account for the size of neighbouring colonies, again via a distance-dependent kernel. The operative word in both of these statements is “neighbouring”. 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.

3. **Integrated use of multiple sources of data.** The availability of data for this study spans observations on population size, demographic rates, but also information from ringing data on connectivity. Dedicated modelling analyses are often required to extract priors for some of the components of the model, since not all data are suitable for direct incorporation into the metapopulation model’s likelihood. The use of priors via a Bayesian approach is done purely from the pragmatic perspective, enabling us to incorporate disconnected pieces of supporting information. However, wherever integrated analysis is possible (e.g., including population sizes together with survival and breeding success data into the model’s likelihood structure), it is preferable.

Rather than being parameterised informally (by provision of parameter values or ranges), the metapopulation model is fitted to the multiplicity of available data directly, within a Bayesian state-space modelling (SSM) framework. A state-space framework (Buckland et al. 2004, 2007; Auger-Méthé et al. 2021) 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. Much more than simply modelling several colonies simultaneously (effectively using “colony” as a random effect), it is required that colonies are coupled by connectivity functions, whose parameters are to be estimated at the same time as the demographic aspects of the model. 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.

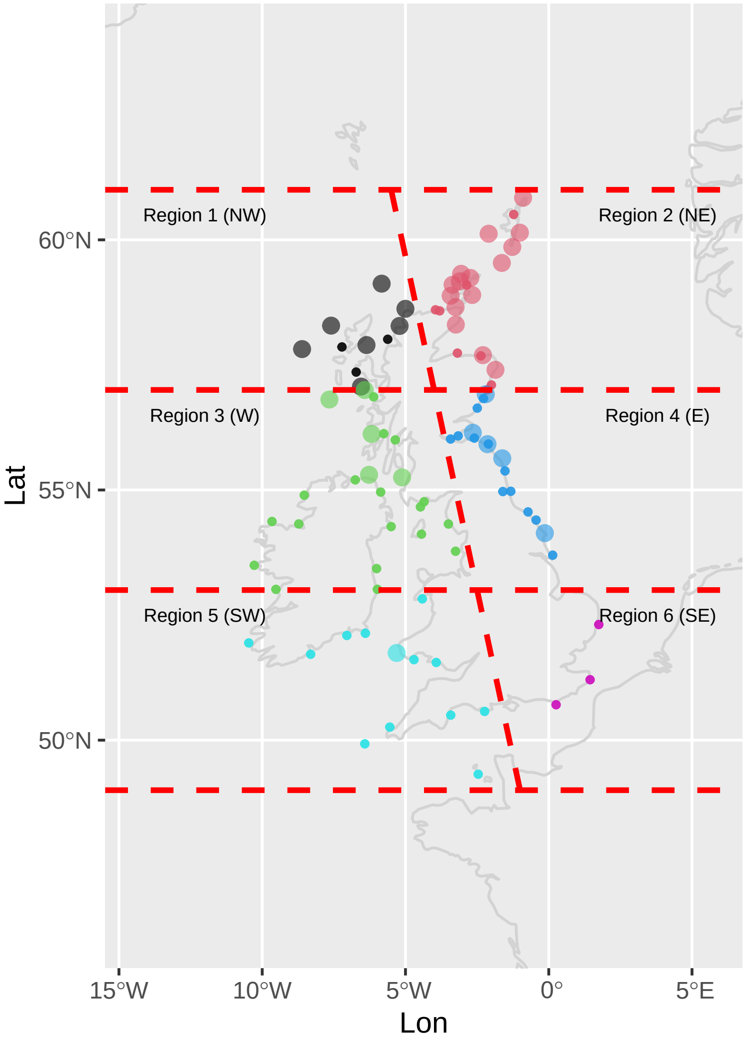


Figure 1: The network of SPAs (large circles) and approximate management areas (small circles) corresponding to named administrative regions. The six regions defined by the dashed red lines were used for further analyses of aggregate population trends and demography.

4.2 Treatment of space

Throughout the modelling it was essential to safeguard the statistical power of the available data. A key area where this was a risk related to the level of spatial disaggregation of colonies (e.g., by further resolving colony locations around important SPAs, or adding Site of Special Scientific Interest (SSSI) locations to the SPA and non-SPA network). Adding more colonies can quickly exhaust the information in the data, particularly since they rarely come with substantial additional data. Indeed, the most important colonies (both in terms of size and available data) are already considered in the SPA list, and increasing their number further adds minimal information via the location of additional points as stepping stones for relatively small fluxes of bird numbers.

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. These 56 non-SPA areas have been consistently used in the national seabird censuses, the most recent being Burnell et al. (2023) containing the 2015-2021 data. Like previous books, it uses local government administrative regions so those are clearly defined but obviously not all have the same sizes. We have assigned exact coordinates to the SPAs and approximate coordinates to the administrative regions (Fig. 1). The centroid locations of the admin regions were determined approximately as follows:

1. The name of the administrative region was used to determine its boundary on Google earth.
2. Visual comparison with the JNCC report by Mitchell et al. (2004) providing graphical locations of kittiwake colonies indicated the locations of the non-SPA colonies.
3. The representative location for the region (small dots in Fig. 1) was placed manually along the coast at a location in-between the JNCC locations.

Despite their large number (there are >10 non-SPA colonies for every single SPA), non-SPA colonies constitute a small proportion (~22%) of the total kittiwake metapopulation, and only come with up to three population counts across the entire time period of observation. Representing each of these minor colonies individually, would draw more computational and statistical power to reconstruct their detailed dynamics than the benefits we may conceivably gain from a more resolved representation of their geographic locations.

The non-SPA regions are treated by the model as locations that hold breeding pairs and potential recruits. These locations were used in two ways, first to determine the likelihood of recruits settling into those areas, and second, to determine the level of competition for marine resources between neighbouring SPA and non-SPA populations. Ideally, we would have expert information on the maximum number of birds each site can hold, but this information was not available.

We considered whether colonies that are SSSIs with kittiwake features should also be considered alongside SPAs as priorities for the network rather than being reduced to regional representation. There is considerable overlap between SPAs and SSSIs because all SPAs designated for breeding seabirds are underpinned by SSSI designation. However, some SPAs contain several separate SSSIs and so if the SSSI was taken as the modelled unit it would be necessary to split SPA populations into their constituent SSSI components. That would seem to gain little in terms of the science, provide an impractical approach for conservation management, and additionally increase modelling time by increasing the number of colonies. We therefore took the view that the SPAs were the most appropriate unit for this project. The administrative regions provide a suitable "catch-all" for the relatively small part of the population that is not contained in SPAs, although we recognise two important exceptions, Tyne and Lowestoft, where breeding numbers are large but those sites are neither SPAs nor SSSIs for breeding kittiwakes. They presumably do not qualify for SSSI designation because birds are nesting on non-natural habitat, and perhaps because numbers were not considered large enough for SSSI designation in the past, but have increased since. Given the importance of those colonies in terms of numbers and in terms of their focus in new compensation projects for OWF impacts, we can see a reason to treat those two non-SPA sites as special cases in future modelling efforts.

Non-SPA colonies are almost a quarter of the total metapopulation. This non-SPA network of 56 colonies corresponds to 63% of the total spatial network in the model. To put this into perspective, the computational cost of the model increases to the second power of the number of colonies used. Therefore, our extended network increases running times by a factor of 7.27: An SPA model that would take a day to run, now takes about a week, so as to capture regional dynamics of less than a quarter of the population.

To enable the investigation of spatial patterns across the metapopulation's range, we opted to subdivide space into a small number of regions. As suggested by the steering group, we investigated the existence of previously established spatial subdivisions of the full UK range (e.g., in the Seabirds Count book). However, these subdivisions (e.g., Olin et al. (2020)) were neither in common use, nor sufficiently spatially expansive to cover our complete kittiwake network. Therefore, we divided into regions corresponding to six compass points (correspondingly: Region 1-NW, 2-NE, 3-W, 4-E, 5-SW, 6-SE), shown in 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.

4.3 Treatment of time

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. Of course, important components of adult survival are determined in the overwintering year, outside of the breeding season, when the birds experience environmental conditions at regions far away from the breeding colonies. The penalty of focusing exclusively on the breeding season, as nearly all seabird modelling and conservation studies do, is that we cannot directly correlate overwintering conditions experienced by a mixture of breeders in overwintering areas, to colony-specific survival probabilities.

Because of its spatial and demographic structure, the model needs to be able to deal with data missing at multiple times. For instance, our data do not contain complete population or demographic time series for all colonies. Some of those time series may start later than our designated first year (1985), finish before our designated final year (2023), or have several consecutive years missing in the middle. In particular, time series of breeding and survival for most colonies are completely absent. Our model deals with these varying degrees of latency by treating every such missing state as a model parameter, to be estimated (imputed) on the basis of the surrounding information.

Hind-casting to years before 1985 is treated in the same way, by imputation, but initial years require priors for population size, which are unavoidably arbitrary and can unduly influence parameter estimation if they are inadvertently too restrictive or mis-specified and hence if they contradict the earliest years of population counts. For this reason, we set up the model to hind-cast population sizes a decade before the start of observations so that population size priors refer to 1975 and hence are not so close to the start of the data. Forecasting is also dealt with imputation into future states, but there is the additional option to simulate future trajectories by drawing parameterisations from the joint posterior of the fitted model.

5 Development of 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, because these processes do not operate in isolation. The overview of the model is shown in Fig. 2. In that diagram, we distinguish between state variables (the circles) and dynamical processes (the rectangles). Not all causal arrows shown in Fig. 2 operate on an annual cycle and not all processes are affected by the same external/internal influences. Four types of regulators can be distinguished (see also Background sections, above), which are designated with coloured dots.

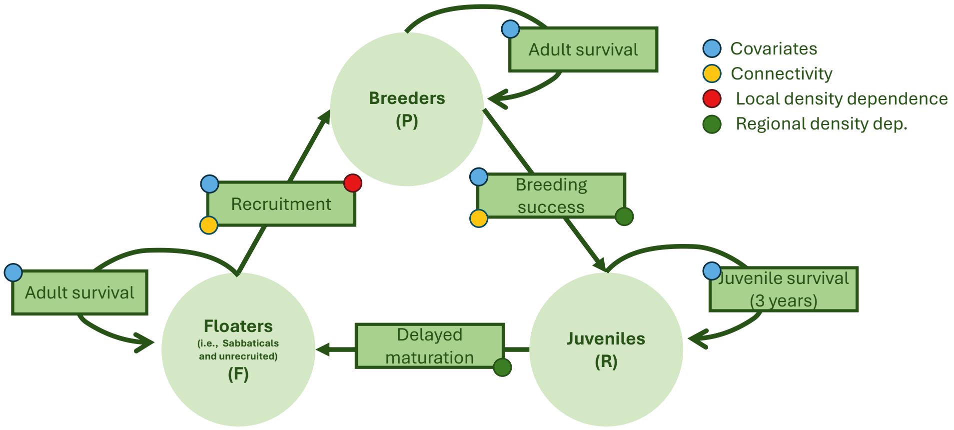


Figure 2: Overview of the model structure. Large circles enclose state variables of the model. Rectangles enclose demographic processes that determine the fluxes between state variables. The coloured dots at the apexes of the rectangles indicate different regulators that may affect each demographic process.

5.1 General form and state variables

All mathematical notation used in this report is collected in Appendix I. The model functions in discrete time t measured in annual units, and tracks the breeding population $P_{i,t}$ of the i^{th} colony (in units of breeding pairs, or alternatively, it can be thought of as tracking the female population). The metapopulation's state with regard to breeders is therefore described by the vector $\mathbf{P}_t$. The second state variable $F_{i,t}$ records the number of floaters associated with each colony. These may be birds that are trying to recruit into the breeding population for the first time, surviving birds that failed to recruit in previous years, or sabbatical breeders. The third state variable in Fig. 2 is $R_{i,t}$, the pre-breeding birds that were originally born at the i^{th} colony. The update equations for the breeders and floaters, in deterministic form (for presentational simplicity), are as follows:

$$\begin{aligned} P_{i,t+1} &= s_{a,i,t}(P_{i,t} + q_{i,t}F_{i,t}) \\ F_{i,t+1} &= s_{f,i,t}(1 - q_{i,t})F_{i,t} + \Psi_{i,t} \end{aligned} \tag{1}$$

where, $s_{a,i,t}$ represents adult survival at the i^{th} colony in year t, $s_{f,i,t}$ is the survival of floaters associated with the i^{th} colony in year t, $q_{i,t}$ is the net recruitment of floaters into the breeding population and $\Psi_{i,t}$ is the number of prebreeders entering the pool of floaters (colony- and year-specific) as a function of the available pre-breeders $R_{i,t}$ from all colonies.

Animals entering into the floater class may come from anywhere in the population depending on past breeding success.The number of individuals contributed by each colony j to the floater population are the chicks born in year $t-3$, that have survived to the present and that will be maturing in year $t+1$ (an average age-to-maturity of four years):

$$R_{i,t} = b_{i,t-3}P_{i,t-3}\prod_{k=0}^{3} s_{r,i,t-k} \tag{2}$$

$s_{r,i,t}$ is the survival of chicks and pre-breeders, and $b_{i,t}$ is the breeding success of adults. The influx of candidate recruits into the floater population occurs according to a transition probability ($\pi_{j\to i}$). Overall:

$$\Psi_{i,t} = \sum_{j=1}^{I} \pi_{j\to i}R_{j,t} \tag{3}$$

The constituent terms of the above deterministic equations are, in fact, implemented as stochastic processes for the purposes of both simulation and statistical inference. In the following sections, we examine these, divided into four categories of processes, by considering combinations of recruitment v demography and internal v external processes to individual colonies.

5.2 Approach to systematic stochasticity

Demographic events are often modelled via canonical stochastic processes. Death and recruitment processes are conceptualised as binomial and birth processes are often treated by some generalisation of a Poisson (e.g., a gamma Poisson i.e., negative binomial). In the process of developing the model, attempting to introduce such multiple intermediary stochastic nodes for the different demographic components of the model led to computational issues (pre-convergence numerical conflicts with the observations, or slowing down of computation). Running times of such fully compartmentalised and stochastic models extended to two weeks or more. We therefore took a more pragmatic approach, where the intermediate numbers born, dying, recruiting etc. were modelled deterministically, but the final update equations (eqs (1)) for breeders and floaters were equipped with overdispersed (gamma-Poisson) likelihoods. The overdispersion parameter for these processes was estimated as part of model inference. We also note that additional sources of overdispersion existed in the linear predictors of the demographic processes, in the form of colony- and year-specific random effects.

As will be seen in later sections, in this work we have explored three distinct model structures, differing in their treatment of stochasticity in the demographic rates (breeding success and survivals). Model 1, the **regional summaries model** allowed independent time series for each colony in the network, but summarised those as averages across the six geographic regions of Fig. 1. Model 2, the **regional dynamics model**, and the one that we subjected to more extensive investigation, allowed independent time series for the six geographic regions of Fig. 1, hence assuming that all colonies within each region followed common demographic trajectories. Finally, Model 3, the **regional trends model** included temporal trends in each region, in addition to annual fluctuations.

The regional summaries model (model 1) only had a universal baseline value across all colonies. In contrast, within the regional dynamics and regional trends models (i.e., model 2 and 3), each region was characterised by its own baseline for each demographic rate. The estimates of the baselines for each region (and indeed, the reconstructions of demographic rate fluctuations) were driven by the entirety of data for that region. This includes population size counts, survival estimates and breeding success data where available. Demographic rates are not only informed by a single data source (e.g., breeding success does not purely rely on breeding counts). The other data types contribute information indirectly. For instance, the model uses population size data to verify whether the estimated breeding rates are corroborated by observed population declines or increases. Having said this, direct data availability on a demographic rate will be more informative for that rate. Given that this information tends to be more abundant for SPAs and also given that SPAs have more frequent and resolved counts, it is likely that demographic estimates are influenced more by SPA, than non-SPA colonies.

5.3 Within-colony demography: Survival ($s_{a,i,t}$, $s_{f,i,t}$, $s_{r,i,t}$)

The survivors of any population class each year are a proportion of the class size at start of year. For instance, the adult survivors in-between two successive years are

$$s(P_{i,t}) = s_{a,i,t}P_{i,t} \tag{4}$$

In general, we implement survival processes for any given class ($\star = \{a, f, r\}$) as inverse-logit functions of corresponding linear predictors $S_{\star,i,t}$:

$$\begin{aligned} s_{\star,i,t} &= logit^{-1}(S_{\star,i,t}) \\ S_{\star,i,t} &= \sigma_{\star,0} + \sum_{m=1}^{M} \sigma_{\star,m}X_{m,i,t} + \varepsilon_{i,t} \\ \varepsilon_{i,t} &\sim N(0, \sigma_{\varepsilon}) \end{aligned} \tag{5}$$

where survival may be determined by the prevailing values of M covariates $X_{m,i,t}$ (such as anthropogenic and natural disturbance), with associated coefficients $\sigma_{*,m}$. Baseline survival (when covariates are zero) is determined by the intercept $\sigma_{*,0}$. The stochastic random effect $\varepsilon_{i,t}$ generates extra dispersion. Depending on the version of the model examined, different colonies or different regions were allowed to have different demographic rates. Assuming complete independence between the $\varepsilon_{i,t}$ terms can lead to too much flexibility and, possibly, lack of model convergence at fitting. We consider three solutions to this problem:

1. The random effect terms can be constrained by using a prior with a low dispersion (parameter σ_ε).
2. As covariates are included in this analysis, and future implementations of the model, it is hoped that they will absorb some of the variability represented by $\varepsilon_{i,t}$. However, in general this may not happen, e.g., because the available covariates may have no explanatory power.
3. Spatio-temporal patterns may be explored by connecting the random effects via a random walk (time dependence) or a spatial correlation structure in the form of a Gaussian random field (spatial dependence).

Our core model implemented a simplified version of the third of these approaches, clustering the breeding success and survival processes into the six regions of the map in Fig. 1.

5.4 Survival priors

Adult breeder survival for kittiwakes is reported to vary greatly annually, in the range 0.67-0.93 (see recent review by O'Hanlon et al. 2021). Overall mean reported values are 0.82. These variations include the effects of environmental influences, whether captured in our model by covariates or by the colony and year-specific random effects. We therefore sought to specify priors for $\sigma_{a,0}$ and σ_ε in a way that these variations would be captured. We assumed that uncertainty in $\sigma_{a,0}$, the mean survival, is lower than annual variability, as defined by σ_ε. An appropriate set of priors is

$$\begin{aligned} \sigma_{a,0} &\sim N(1.5, 0.1) \\ \sigma_\varepsilon &\sim Beta(1, 5) \end{aligned} \tag{6}$$

This expression for σ_ε has a high concentration of probability density close to zero, so it applies a precautionary (shrinkage) approach to the variability in the iid random effects $\varepsilon_{i,t}$. Non-breeding individuals have lower survival, with similar dispersion and a mean value of 0.76 (O'Hanlon et al. 2021). We therefore modified the non-breeder survival via the prior $\sigma_{f,0} \sim N(1.15, 0.1)$. pre-breeder and immature survival are lower, in the range 0.5-0.85 (O'Hanlon et al. 2021). We used the prior $\sigma_{r,0} \sim N(0.7, 0.1)$.

5.5 Within colony recruitment: Local density dependence on recruitment ($q_{i,t}$)

Given a pool of potential recruits ($F_{i,t}$) at the i^{th} colony, to determine the number of successful recruitment events ($q(F_{i,t})$), we need to quantify the probability of recruitment $q_{i,t}$. We express this as a proportional process on an inverse-logit-transformed linear predictor

$$\begin{aligned} Q_{i,t} &= \rho_0 + \rho_{A,i} P_{i,t} - \rho_{C,i} P_{i,t}^2 \\ q_{i,t} &= logit^{-1}(Q_{i,t}) \\ q(F_{i,t}) &= q_{i,t} F_{i,t} \end{aligned} \tag{7}$$

The quadratic expression in the linear predictor encodes two types of density dependence. The coefficient $\rho_{A,i}$ represents the strength of the Allee effect (depensatory density dependence - or how recruitment probability initially increases with population size) while the coefficient $\rho_{C,i}$ represents crowding (compensatory density dependence - or how crowding eventually dominates a growing population and slows down growth).

5.6 Local density dependence priors

The parameters ρ_0, ρ_A, ρ_C provide us with flexibility to formulate the two types of density dependence, but they present us with two challenges. First, they have no direct meaning in terms of the critical population sizes that they are meant to encode and second, if allowed to be unconstrained (both in their individual values and in the values of one relative to the others) they may introduce an unacceptable level of volatility in model fitting.

We therefore need to connect these parameters to characteristic adult population sizes $P_A, P_{C,i}$. P_A represents the population size above which the colony can become established and grow without external subsidies (the Allee effect threshold size). We will assume that this is a species-wide characteristic, describing behavioural responses to low densities. The population size $P_{C,i}$ represents the carrying capacity of the i^{th} colony, a property of the colony's location determined by the physical availability of suitable nesting sites. In Appendix II, we derive the following relationships between the ρ parameters and the critical values $P_A, P_{C,i}$.

$$\begin{aligned}
\rho_{A,i} &= (Q_E - \rho_0)\frac{(P_A + P_{C,i})}{P_A P_{C,i}} \\
\rho_{C,i} &= (Q_E - \rho_0)\frac{1}{P_A P_{C,i}} \\
\rho_0 &< Q_E
\end{aligned} \tag{8}$$

$$Q_E = \text{logit}\left(\frac{(1-s_a)(1-s_f)}{b s_a s_r - s_f + s_a s_f}\right)$$

The behaviour implied by this model for the recruitment curve is seen in Fig. 3.

It is now possible to set priors directly for the biologically interpretable parameters. We set the independent prior $P_A \sim \Gamma(1, 0.1)$ which has a mean of ~100 AOS (standard deviation ~30AOS). To ensure that the other two parameters adhered to the requirements of eqs ((8)) the remaining two priors were set as follows:

$$\begin{aligned}
\Delta P_{C,i} &\sim \Gamma(1, 0.0001) \\
P_{C,i} &= P_A + \Delta P_{C,i} \\
\\
\Delta\rho_0 &\sim \Gamma(1, 10) \\
\rho_0 &= Q_E - \Delta\rho_0
\end{aligned} \tag{9}$$

Looking ahead at how these parameters will be estimated, there are two possible sources of information that the model can rely on: Either explicit, informative priors from expert opinion, or population data that come from newly-funded populations, or populations at carrying capacity. Both of these two sources of information are rare, so despite its capability, in-principle, to obtain posterior distributions for these parameters, the model was expected to face difficulty with them.

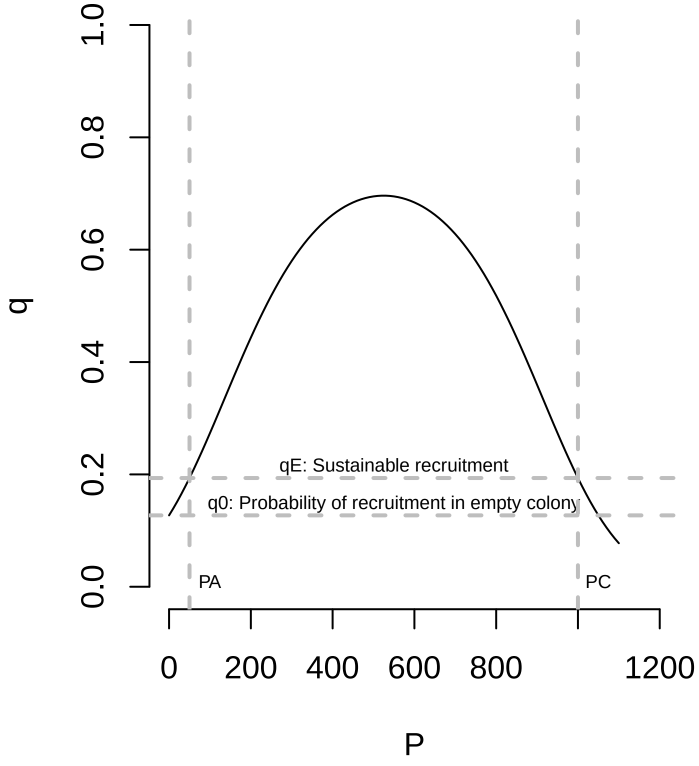


Figure 3: The reqruitment probability with two types of density dependence. The baseline demographic parameters used in this example are s_a=0.8, b=1.125, s_f=0.7, s_r=0.5, P_A=50, P_C=1000. The value of q_E, which represents the recruitment that exactly counterbalances net losses in the population for these demographic rates is 0.194. The probability q_0 that a new bird establishes at an empty colony is 0.127. The colony will continue growing as long as the population is between the values P_A and P_C.

5.7 Between-colony demography: Regional density dependence on breeding success ($b_{i,t}$)

Breeders reproduce according to a colony- and year-specific per-capita rate $b_{i,t}$. This is likely to depend on the ability of adults to find resources to build up condition and feed their chicks. Therefore, any density dependent effects on breeding will be in response to regional depletion by all colonies in the vicinity, depending on their size. We therefore express breeding success as a log-linear, per-capita rate and we model the number of births in the population as an overdispersed rate, the overdispersion coming from a random effect $\psi_{i,t}$ in the linear predictor

$$\begin{aligned} b(P_{i,t}) &= b_{i,t}P_{i,t} \\ b_{i,t} &= \exp\left(\beta_0 - \beta_D \sum_{j=1}^{I} \varphi_{j\to i} P_{j,t} + \psi_{i,t}\right) \\ \psi_{i,t} &\sim N(0, \beta) \end{aligned} \tag{10}$$

where $\varphi_{i\to j}$ is the strength of density dependence (e.g., via scramble competition for fish) of the j^{th} colony on the breeding success of the j^{th} colony. We will express this in terms of d_{ij}, the at-sea distance between the two colonies. The kernel function φ was modelled as a distance-decay whose rate of decrease was determined by a parameter $\delta_\varphi > 0$:

$$\varphi_{j\to i} = \exp(-\delta_\varphi d_{ij}) \tag{11}$$

Note that the collective density dependence strength experienced by the i^{th} colony, includes scramble competition from competitors in the i^{th} colony itself. Using this fact, we can interpret the coefficient $\beta_D > 0$ as the density dependence experienced by the breeders of a colony when all the other colonies are very far away (i.e., the case where $b_{i,t} = \exp(\beta_0 - \beta_D P_{i,t} + \psi_{i,t})$).

5.8 Regional density dependence priors and breeding

Breeding success and variations therein are well informed by the supplementary data to which the model is also being fitted. We used a rescaled beta prior with values ranging between 0.3 and 0.36 corresponding to a baseline value of 0.33 female chicks per nest (O'Hanlon et al. 2021).

There is scant evidence of density dependence in breeding success in kittiwakes Merrall et al. (2024). The present analysis represents considerably higher analytical power, given that it examines the phenomenon as a resultant from the competition of multiple, dynamically changing colonies. The prior for the strength of this regional density dependence was set to $\beta_D \sim \Gamma(1, 50000)$. For an effective density of 5000 kittiwakes competing at sea, this is capable of giving values of density dependence in the range of 0-1.5 which has comparable magnitude to the mean prior value of $log(b_0) = -1.11$. Therefore, this parameter prior for β_D ensured that the effect of competition for resources was allowed to be from negligible to strong, without assuming values so high that they could consistently eliminate breeding success and become non-identifiable under model fitting.

Similar comparative reasoning was used to set the prior for the annual and colony-specific random effect ($\psi_{i,t}$) in breeding success. The prior for the dispersion of this variable was set to $\sigma_\psi \sim \Gamma(1, 5)$.

As regards the spatial scale of density dependence, determined by the half-saturation parameter $\delta_\varphi \sim Beta(8.7, 281.3)$, we used a prior that was predisposed to giving isolated colonies, so that any given colony tended to experience density dependence only due to its own members.

5.9 Between-colony recruitment: Natal dispersal ($\pi_{j\to j}$)

There is rich precedent in the metapopulation literature of formulating connectivity as a function of distance between nodes. In our seabird work, we have extended this to account for at-sea distance metrics and density-dependent selection of settling, by prospecting immatures. While the connectivity parameters are assumed constant, the value of connectivity between any two colonies will depend on the distance between them, other potential colonies available in the vicinity, and the level of density saturation of all proximate colonies. Hence, determining net flows in the network (and, by extension, whether a colony is a net donor or receiver of recruits) will depend not only on network structure, but also on the densities of all colonies in relation to their carrying capacities. An integrated population model may be asked to estimate all these quantities simultaneously, aiming at unbiased estimates of connectivity and migration fluxes, although informative priors on key parameters can help this estimation process considerably.

In developing a model for natal dispersal we need to account for potential strength of natal philopatry, and also the fact that prospecting by future recruits is a lengthy process taking an average of four years, in the case of kittiwakes, or even longer in other species that recruit at an older age. Natal philopatry is not merely the observation that the probability of recruiting at the natal colony is larger than the probability of settling in other colonies because, to some extent, distance dependence of the dispersal kernel accounts for lower recruitment probability at a distance. To be precise, natal philopatry is the *disproportionately large tendency* to recruit at the colony of birth, compared to other colonies, having accounted for the confounding effect of distance. To capture these possibilities in a single natal dispersal model we introduce the following:

$$\pi_{j\to i} = \frac{f(d_{ij})}{\sum_k f(d_{ik})} \tag{12}$$

where $\pi_{i\to j}$ is the probability that an individual born in the i^{th} colony joins the pool of recruits of the j^{th} colony, and d_{ij} is the at-sea distance between the two colonies. The kernel function f was defined as follows:

$$f(d_{ij}) = c^{\delta_{ij}} \exp(-\delta_\pi d_{ij}) \tag{13}$$

using the indicator function

$$\delta_{ij} = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{otherwise} \end{cases} \tag{14}$$

The constant $c \geq 0$ regulates the strength of natal site fidelity (so that $c = 1$, implies no philopatry). The parameter δ_π regulates the decay of recruitment probability with distance (so that $\delta_\pi \to 0$ generates global migrants with no distance constraints, a case of population perfect mixing). These two crucial parameters determine between-colony connectivity resulting from the pre-adult recruitment process. We eventually subjected these parameters to indirect inference as part of the broader metapopulation model, however, in the case of kittiwakes (and possibly, many other seabirds), we have evidence on transition distances from ringing data, which can be used to derive informative priors for the connectivity parameters.

5.10 Priors for between-colony recruitment parameters

The BTO Ringing Scheme is funded by a partnership of the British Trust for Ornithology, the Joint Nature Conservation Committee (on behalf of: Natural England, Natural Resources Wales, NatureScot and the Department of Agriculture, Environment & Rural Affairs, (Northern Ireland)), The National Parks and Wildlife Service (Ireland) and the ringers themselves. Following the exact protocol used by Coulson and DeMenergnies (1992), with the additional filter that only birds given just a metal BTO ring were included in the sample (i.e. colour-ringed birds were excluded since resighting probabilities of colour rings are likely to differ from recovery probabilities of metal rings but colour ringing is restricted to a small subsample of study colonies and to a limited time window that differs between studies and from general metal ringing). A total of 1,765 recoveries (including dead and resighted birds) remained for analysis after this filtering. Of these, 1,033 birds (59%) were recovered at breeding age during the breeding season at their colony of birth. However, 388 (22%) were recovered more than 100 km away from their colony of birth. A substantial number of these were recorded as being on a nest, at colonies such as Bulbjerg in Denmark, Nidingen in Sweden, Goulien in France, Great Saltee in Ireland, Boulogne in France, Cap Blanc Nez in France. 295 of the 1,765 recoveries (17%) were at distances of 400 to 1000 km from the site of birth. Ring recovery data were further filtered to include only birds ringed as chicks and recovered (dead or alive) when at least four years old and during the breeding season (defined as April to July inclusive). Repeated sightings of the same birds existed in the data set, over different years of observation. We examined if any of the observed birds were seen at different breeding colonies, but none were. The data set totalling 1135 recoveries comprised 613 recaptures at the natal site (54%). We have summarised the transitions data in Fig. 4a. This data set was analysed to quantify inter-colony connectivity through natal dispersal, and to derive informative priors for the parameters c and δ_π of the connectivity kernel.

However, quantifying connectivity is not as simple as fitting a curve to the frequency data in Fig. 4a because the observed transitions depend on:

1) The ringing effort, which varied across different colonies.
2) The availability of settling colonies at different distances, in relation to any colony of origin.
3) The observation and recovery effort, which was probably also heterogeneous across colonies.

The first challenge can be overcome by conditioning the observed transitions on the number of ringed birds recorded in the database (essentially, the number of ringing events in each colony provides direct information on ringing effort). Therefore, the entire analysis proceeds on a per-ring basis: As defined in eq. (12), we quantify the probability ($\pi_{i \to j}$) that a bird settles on the j^{th} colony, given that it was ringed in the i^{th} colony.

The second challenge is that the raw data do not account for the availability of colonies at different distances. In essence, it is not just a matter of how far the birds would wish to settle, it is also a question of whether there is a colony there. To visualise this we extracted the available target colonies for the exact mixture of ringing colonies contained in the BTO data (hence accounting for ringing effort). The resulting frequencies of available transitions by distance (Fig. 4b) present similarities with the available realised transitions (compare with Fig. 4a), but also a clear difference in that the data present strongly disproportionate return transitions (philopatry) compared to the relative frequency of zero distances in (Fig. 4b).

The third challenge is difficult to account for without a considerably more elaborate analysis framework (currently being developed under a contract with a different funder, but not expected to be on-line during the life of the Metakitti project). We will therefore make the unavoidable assumption that even though recovery effort may be heterogeneous across colonies, this does not introduce a consistent bias in the relationship between re-sighting probability and distance from any ringing colony. Although it is not currently possible to validate this assumption, and we cannot guarantee that sampling biases will not affect our connectivity estimates, it is important to note that the priors generated by this analysis of the BTO data were further refined through their participation in the integrated metapopulation model, so the final estimates of connectivity were corroborated by the broader data set of population time series.

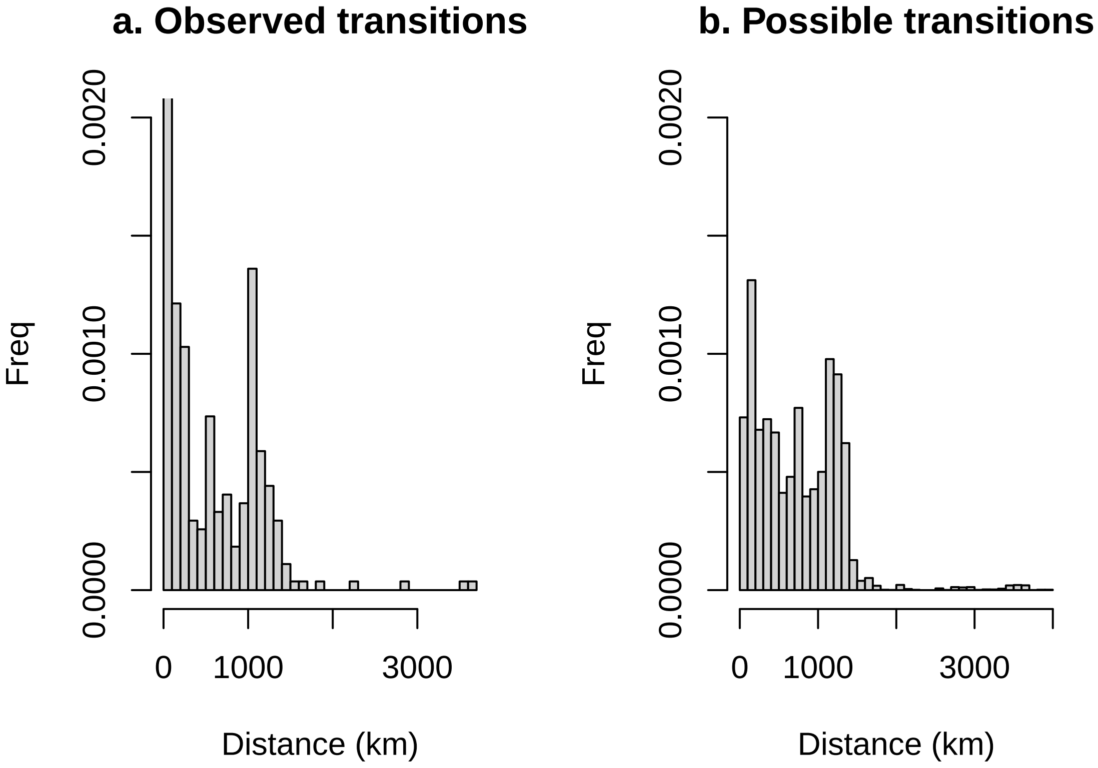


Figure 4: a) Relative frequency of transitions made from colony of origin to colonies at different distances as recorded in the BTO data and b) the availability of different distances in the network of colonies. Frequencies are truncated to transitions beyond 50 km to exclude returns to natal site, for visualisation only.

Our approach to estimating priors for the two key dispersal parameters c, δ_π must therefore take into account the structure of the entire network. A separate model was built to fit transition probabilities to observed transition data. We constructed this as a Bayesian model in JAGS because it affords flexibility in the construction of non-linear models and non-standard likelihoods.

Briefly (also see JAGS code in Appendix III), the model considers each ringing colony in sequence. It constructs a probability vector π_i of expected transitions, based on the zero-inflated, distance decay model (eqs (12) and (13)). The calculation of π_i is different for each colony of origin i because the distances to all other colonies are unique to its position in the network. The vector of observed transitions v_i is then modelled as a multinomial process based on π_i.

$$v_i \sim \text{Multinomial}(\pi_i, \sum_j v_{ij}) \tag{15}$$

This model converged well in both parameters. The inferred parameter values (including uncertainty) can be used to generate estimates of philopatry (Fig. 5a)) and the kernel of dispersal distances (Fig. 5b)), independently of any particular colony network. We found that both of these results were characterised by very high precision (as seen by the narrow range of y-axis values in Fig. 5a) and the narrow credible intervals, in grey, in Fig. 5b). Note that, for any given natal colony, these probabilities will be modulated by the availability of possible target colonies at different distance. This happens automatically in the application of these functions for purposes of model fitting and simulation. Hence, the bimodality in Fig. 4a is the result of bimodality on the availability of colonies (see Fig. 4b). Therefore, bimodality is not needed in modelling the probability of transition conditional on distance availability (Fig. 5b)). Of course, dispersal may also be affected by other drivers - such as conspecific attraction and breeding success in target colonies, in addition to distance. In future work, the contribution of these influences could readily be examined by using them as covariates in the metapopulation model.

We used a sample ($n = 5000$) from the joint posterior of this BTO data analysis to generate a parametric prior for the connectivity parameters of the metapopulation model. The rationale for the derivation is as follows: the most convenient joint distribution for sampling continuous parameters is the multivariate normal. We therefore convert the non-negative and shifted parameter values in the MCMC object to normalised variables via the transformation

$$x_1 = log(c-1) \quad , \quad x_2 = log(\delta_\pi) \tag{16}$$

This transformation is not strictly necessary if the data are normal enough but it is a precautionary measure. We then specify the prior in the normalised scale as:

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \sim MNorm\left(\begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix}, \begin{pmatrix} \sigma_1^2 & cov(x_1, x_2) \\ cov(x_1, x_2) & \sigma_2^2 \end{pmatrix} \right) \tag{17}$$

where the parameters $\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, cov(x1, x2)$ are calculated as simple summary statistics from the transformed MCMC sample. The implementation of this calculation for an MCMC data frame named `trs` is shown below and a comparison of the original MCMC sample with a new sample generated from the parametric approximation of eq. (17) can be seen in Fig. 6.

```
x1<-log(trs$c-1)
x2<-log(trs$deltaf)

mu1<-mean(x1)
mu2<-mean(x2)
v1<-var(x1)
```

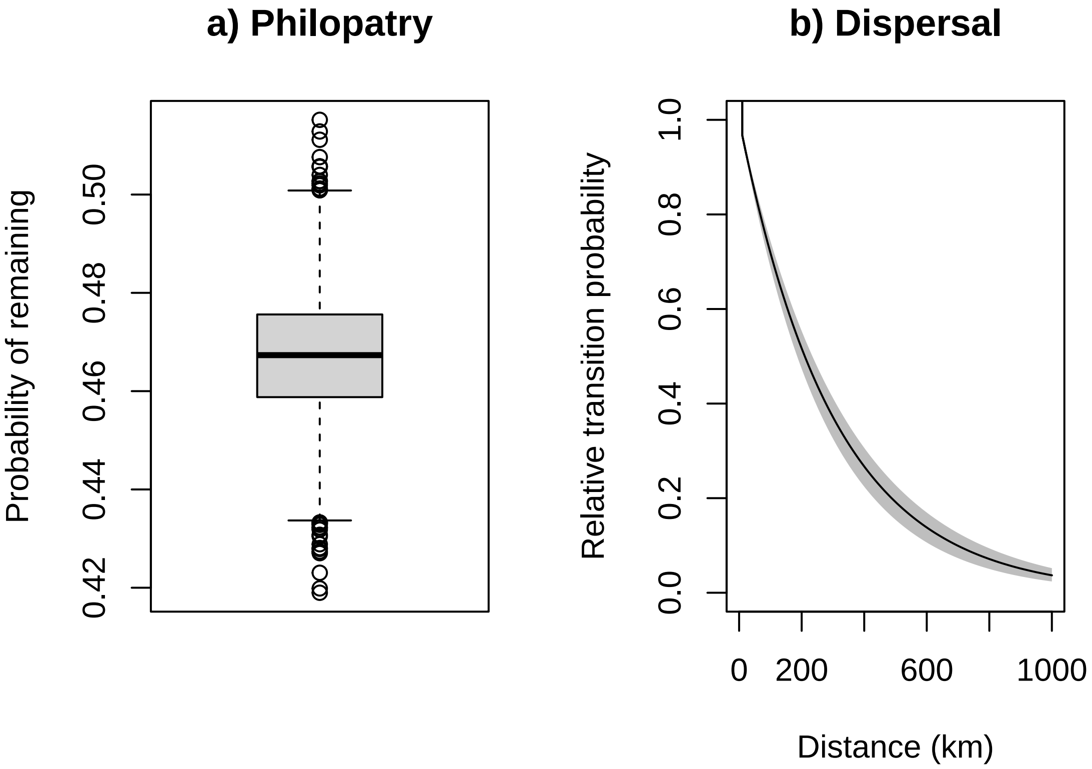


Figure 5: a) The level of philopatry estimated from ringing data, quantified as the probability that animals will remain in their natal colony. b) The connectivity kernel of natal dispersal as a function of distance from the colony of birth. The shaded area represents the 95% CI as generated from 5000 parameter samples from the joint posterior of the model. Note that these results are independent of the particular arrangement of the colony network in space. They are the underlying philopatry and dispersal kernels estimated from the data.

```
v2<-var(x2)
c12<-cov(x1,x2)

muCon<-c(mu1,mu2)
sigmaCon<-matrix(c(v1,c12,c12,v2), 2, 2)

newx<-mvrnorm(5000,muCon, sigmaCon)
new.c<-exp(newx[,1])+1
new.deltaf<-exp(newx[,2])
```

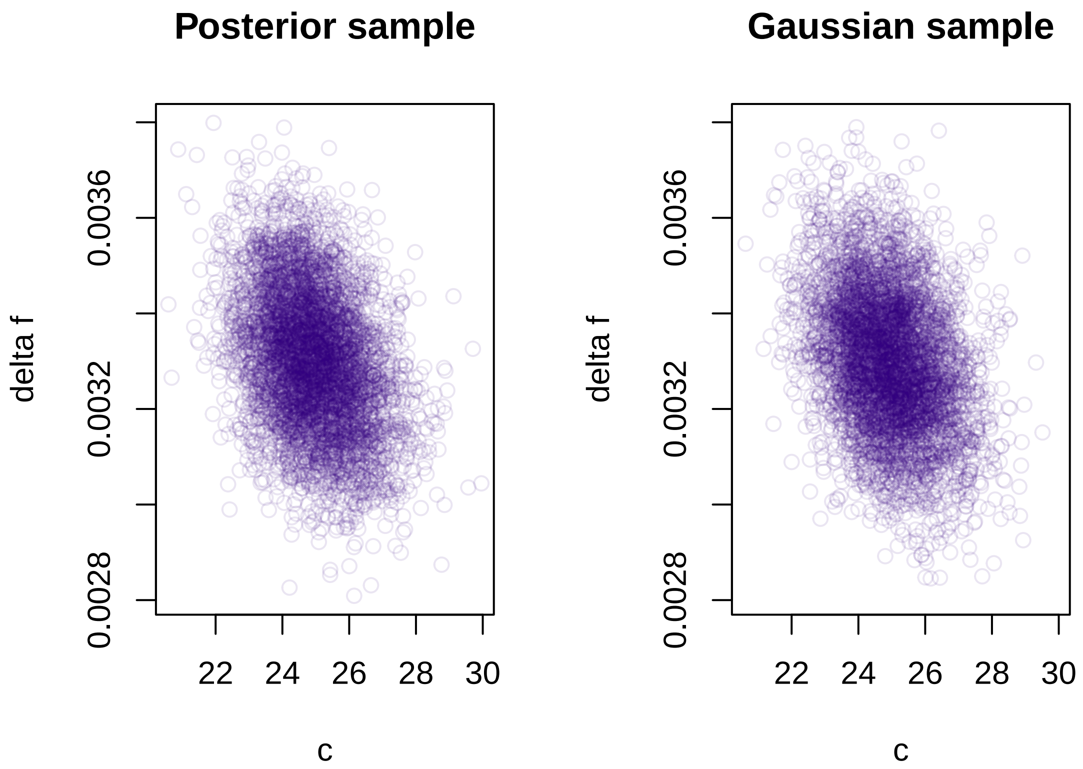


Figure 6: The joint posterior of connectivity parameters, as informed by the analysis of the BTO ringing data (a) shown together with its parametric approximation by a bivariate Gaussian function (b).

6 The observation model

The observation component of our state-space model acts as the interface between the process model and the data. It accounts for biases in observation, known and unknown imprecisions in the recorded data and missing observations in the recorded time series.

The observation model has the following three components, drawing information from population counts, survival data and breeding success data wherever and whenever available:

$$\begin{aligned} \hat{P}_{i,t} &\sim N(P_{i,t}, CV P_{i,t}) \\ \widehat{logit(s_{a,i,t})} &\sim N(s_{a,i,t}, CV s_{a,i,t}) \\ \hat{U}_{i,t} &\sim Poisson(b_{i,t}\hat{N}_{i,t}) \end{aligned} \tag{18}$$

The CV in the first of these expressions was set to 0.1, allowing for 10% unbiased observation error around the true population size. In theory, the CV could be estimated from the model, along with other parameters, but this entails considerable convergence difficulties (generally, observation and process parameters are not readily identifiable without strong priors, or calibrating data). In the above, we have followed the findings of our data survey which suggest that colony counts are accurate and likely unbiased. Of course, the 10% CV is arbitrary (albeit conservative) and future modelling could benefit from expert opinion or a focused calibrating survey.

The second expression in the observation model treats the recorded survival proportions as raw data. This was necessitated by the fact that no sample sizes were provided with the survival information. The observations of survival (logit transformed to a linear scale) were assumed to be unbiased around the modelled colony- and time-specific rate of survival $s_{a,i,t}$.

Finally, the third expression in the observation model looks at the number of nests examined in each available colony and year $\hat{N}_{i,t}$ and models the observed reproductive output $\hat{U}_{i,t}$ according to a Poisson process with colony- and time-specific per-capita rate ($b_{i,t}$) as imputed by the model.

7 Model validation

The basic version of the metapopulation model (without covariates) was fitted to simulated data based on arbitrary parameter values of comparable units, but numerically away from the prior means. The real network of colonies and their earliest counts were used. The availability and frequency of the simulated population data matched these of the real data set, for an equivalent run of years (1975-2023). We did not use any auxiliary data on breeding and survival, to examine the sufficiency of the population data for the purpose. This test was lenient in the sense that the model used for model fitting was exactly correct in comparison to the data-generating process. Simultaneously though, the test was strict in the sense that the priors were misleading and the data provided were a subset of the extent of the real data set. After fitting the model to data, using four parallel MCMC chains on an AMD Ryzen Threadripper 3960X 24-Core Processor, 3793 Mhz, 24 Core(s), 48 Logical Processor(s), convergence took three days of running time and $> 10^6$ iterations. These may be heavy computational loads, but they provide evidence that this is a tractable problem with available data, despite the large size of the metapopulation network and the functional complexity of the model (three types of density dependence, age & stage-structured model, spatially-explicit connectivity matrices).

8 A model with regional dynamics

The results of this section are based entirely on model 2, the model with regional dynamics. The JAGS model code for the model is in Appendix IV. The priors and posteriors for the key parameters are shown in Appendix V. Reconstructed population trajectories for all colonies are in Appendix VI.

Table 2: Reconstructed colony characteristics, presenting information on final population size (thousands AOS) in 2023, the estimated carrying capacity (thousands AOS) of each colony and each colony's current recruitment rate in the present.

Colony	Size	95% CI	K	95% CI	% Recr.	95% CI
Ailsa Craig SPA	0.5	(0.4-0.6)	17.1	(7-34.7)	0.4	(0-1.1)
Buchan Ness to Colli	3.7	(1.3-7)	9.7	(6.3-13.7)	1.9	(0.7-3.9)
Calf of Eday SPA	0.2	(0-1.1)	0.9	(0.4-12.7)	0.0	(0-4.1)
Canna and Sanday SPA	1.4	(1.2-1.7)	6.7	(0.4-30.9)	0.6	(0-1.2)
Cape Wrath SPA	1.5	(0.5-3.6)	6.3	(4.7-13)	1.4	(0.5-2.8)
Copinsay SPA	1.6	(0.4-3.4)	0.8	(0.4-2)	0.0	(0-4.7)
East Caithness Cliff	7.8	(2.7-14.2)	19.0	(6.2-48.9)	3.5	(0-7.4)
Fair Isle SPA	0.5	(0.4-0.6)	11.6	(6.2-21.3)	4.5	(1.4-9.4)
Flannan Isles SPA	0.8	(0.7-1)	2.4	(0.4-3)	0.9	(0-1.8)
Forth Islands SPA	7.4	(6-9)	17.1	(11.2-34.5)	3.0	(0-5.9)
Foula SPA	0.4	(0.3-0.5)	10.4	(4.6-32.3)	1.0	(0.2-2.6)
Fowlsheugh SPA	10.6	(3-17.5)	15.0	(6.6-37)	0.0	(0-7.4)
Handa SPA	1.4	(0.5-3.2)	2.8	(1.3-25.3)	1.4	(0-3.4)
Hermaness, Saxa Vord	13.0	(8.6-19.1)	18.4	(3.5-43.9)	4.7	(0-10.8)
Hoy SPA	1.1	(0.3-2.6)	0.5	(0.4-28.9)	0.0	(0-2.9)
Marwick Head SPA	2.9	(0.8-5.8)	6.6	(2.5-16.2)	1.5	(0-4.4)
Mingulay and Bernera	2.4	(2-3)	6.0	(3.7-12.9)	0.8	(0.2-2.4)
North Caithness Clif	31.6	(0.4-45.1)	24.9	(10.6-42.1)	0.0	(0-0)
North Colonsay and W	1.8	(0.4-4.8)	3.7	(2.1-28.8)	0.6	(0-1.6)
North Rona and Sula	0.7	(0.6-0.9)	2.6	(0.4-15.9)	1.1	(0-2)
Noss SPA	0.1	(0.1-0.1)	25.5	(12.6-43.1)	0.0	(0-0.1)
Rousay SPA	1.1	(0.3-3)	0.6	(0.4-1.3)	0.0	(0-3.4)
Rum SPA	0.8	(0.6-0.9)	11.5	(7.8-15.5)	1.0	(0.3-2.9)
Shiant Isles SPA	0.9	(0.3-2)	1.0	(0.4-1.9)	0.8	(0-2.4)
St Abb's Head to Fas	17.3	(12.4-22.1)	8.1	(6.8-10)	0.0	(0-0)
St Kilda SPA	0.8	(0.3-1.5)	24.9	(13.9-36)	0.9	(0.3-1.8)
Sumburgh Head SPA	29.7	(20.1-41.2)	13.4	(9.9-41.5)	0.0	(0-2.9)
Troup, Pennan and Li	3.1	(1.2-5.6)	24.1	(5-38.2)	5.6	(2.1-10.7)
West Westray SPA	3.7	(0.9-8.4)	29.9	(17-51.3)	4.0	(1.3-8.6)
Farne Islands SPA	4.3	(3.5-5.2)	14.6	(6.3-26.6)	3.3	(1.1-6.1)
Flamborough and File	24.6	(20.7-29.6)	23.1	(18.9-28.2)	0.0	(0-0)
Skomer, Skokholm and	1.4	(1.2-1.7)	3.8	(1.8-24.5)	0.8	(0.2-1.7)
Rathlin Island SPA	12.8	(10.9-15.6)	22.4	(10.9-41.7)	0.7	(0-2.5)
Tyne	2.3	(1.9-2.7)	2.1	(0.8-32.3)	0.1	(0-4.1)
Angus	2.0	(0.5-4.6)	6.7	(2.9-34.1)	1.7	(0-3.3)

Table 2: Reconstructed colony characteristics, presenting information on final population size (thousands AOS) in 2023, the estimated carrying capacity (thousands AOS) of each colony and each colony's current recruitment rate in the present. *(continued)*

Colony	Size	95% CI	K	95% CI	% Recr.	95% CI
Argyll & Bute	1.3	(0.3-2.8)	2.6	(0.7-10)	0.5	(0-1.5)
Banff & Buchan	1.1	(0.3-2.7)	0.5	(0.4-3.4)	0.0	(0-3.9)
Berwickshire	1.7	(0.1-4.5)	1.3	(0.4-3.3)	0.0	(0-3.3)
Caithness	0.0	(0-0)	1.0	(0.4-28.2)	0.0	(0-0)
Aberdeen	1.8	(0.6-4.1)	0.8	(0.4-3.5)	0.0	(0-5.9)
Dunfermline	0.0	(0-0.1)	9.7	(0.6-36.6)	0.0	(0-0.1)
East Lothian & NE Fi	0.0	(0-10.7)	14.0	(9.2-24.7)	0.0	(0-0)
Gordon	1.0	(0.4-2.2)	0.5	(0.4-0.8)	0.0	(0-3.7)
Kincardine & Deeside	2.2	(0.6-5.2)	3.2	(0.5-19.5)	1.6	(0-4.4)
Kirkcaldy	2.6	(0.6-12.1)	0.9	(0.4-19)	0.0	(0-2.3)
Kyle & Carrick	0.1	(0-1.5)	7.1	(1.4-27)	0.0	(0-0.6)
Lochaber	0.1	(0-0.9)	7.1	(0.6-33.3)	0.1	(0-0.8)
Moray	1.9	(0.4-4.8)	8.3	(0.4-24.5)	1.6	(0-3.5)
Orkney	1.8	(0.5-4)	7.1	(1.2-19.6)	1.6	(0-3.3)
Ross & Cromarty	0.6	(0.1-1.6)	0.7	(0.4-1.5)	0.8	(0-1.9)
Shetland	4.0	(0.9-8.5)	28.2	(3.6-61.2)	2.0	(0-5.2)
Skye & Lochalsh	1.0	(0.3-2.1)	2.0	(0.8-21.7)	0.8	(0-1.6)
Stewartry	0.2	(0-1)	11.7	(0.4-60.2)	0.1	(0-0.6)
Sutherland	1.5	(0.4-3.4)	0.8	(0.4-9.7)	0.0	(0-5.3)
Western Isles	1.0	(0.2-2.4)	11.5	(2.8-26.5)	0.9	(0.3-1.8)
Wigtown	0.6	(0.1-1.4)	1.2	(0.4-19.3)	0.3	(0-0.9)
Cleveland	4.4	(1-9)	10.6	(6.5-31.2)	2.7	(0-7.4)
Cornwall	0.8	(0.1-2)	3.8	(1.4-11.7)	0.5	(0-1.2)
Cumbria	0.7	(0.1-2)	0.9	(0.4-16.8)	0.3	(0-1.2)
Devon	0.7	(0.1-1.6)	3.6	(0.4-45.8)	0.5	(0-1.3)
Dorset	0.0	(0-0)	10.4	(0.8-34.8)	0.0	(0-0)
East Sussex	0.4	(0-1.2)	4.8	(0.4-26.6)	0.2	(0-1)
Humberside	1.0	(0-3)	9.5	(1-43.4)	1.0	(0-2.4)
Isles of Scilly	0.0	(0-0)	1.8	(0.4-58)	0.0	(0-0)
Kent	0.0	(0-0)	14.0	(1.6-50.6)	0.0	(0-0)
Lancashire	0.3	(0-0.9)	1.9	(0.4-19.5)	0.2	(0-0.6)
N Yorkshire	4.0	(1-9.3)	6.4	(1.1-36.8)	4.2	(0-9.2)
Northumberland	7.6	(2.6-16.6)	19.9	(7.5-29.4)	2.4	(0-5)
Suffolk	0.5	(0-1.4)	3.9	(0.4-28.6)	0.4	(0-1.1)
Tyne & Wear	3.5	(1.2-7.5)	4.2	(1.6-32.5)	2.3	(0-6.4)
Dyfed	0.8	(0.1-1.8)	2.8	(0.4-18.4)	0.5	(0-1.1)
Gwynedd	1.6	(0.3-6)	4.8	(2.4-20.3)	1.2	(0-2.7)

Table 2: Reconstructed colony characteristics, presenting information on final population size (thousands AOS) in 2023, the estimated carrying capacity (thousands AOS) of each colony and each colony's current recruitment rate in the present. *(continued)*

Colony	Size	95% CI	K	95% CI	% Recr.	95% CI
West Glamorgan	0.1	(0-0.4)	9.5	(0.6-25.9)	0.0	(0-0.5)
Antrim	1.7	(0.4-4.2)	7.0	(1.9-59.1)	0.5	(0.1-1.6)
Down	0.7	(0.1-2.1)	6.0	(0.5-25.3)	0.3	(0-0.9)
Londonderry	0.6	(0-1.4)	7.0	(0.5-32.7)	0.3	(0-0.8)
Clare	3.5	(1.1-7.1)	10.4	(3.9-19.3)	0.6	(0-2.9)
Cork	1.2	(0.3-2.9)	6.6	(1.9-22.8)	0.9	(0.2-2.3)
Donegal	2.2	(0.5-6.1)	15.2	(5.3-47.3)	0.5	(0.1-1.8)
Dublin	3.2	(0.7-9.4)	8.0	(2.8-30.5)	0.7	(0-3.5)
Galway	0.2	(0-0.8)	3.2	(0.6-26)	0.1	(0-0.5)
Kerry	1.9	(0.4-4.4)	3.5	(1.4-32.2)	1.1	(0-3)
Mayo	2.1	(0.5-5.5)	14.1	(3.8-31.9)	0.5	(0-1.7)
Sligo	0.7	(0.1-4.2)	3.1	(0.4-16.4)	0.3	(0-1)
Waterford	0.9	(0.2-2.1)	7.9	(1.5-26.8)	0.6	(0-1.3)
Wexford	1.0	(0.3-2.4)	6.8	(1.9-19.1)	0.7	(0-1.5)
Wicklow	1.2	(0.2-3.1)	4.5	(1.3-24.7)	0.4	(0-1.2)
Isle of Mann	0.1	(0-2.1)	7.7	(0.4-20.1)	0.0	(0-0.7)
Channel Islands	0.7	(0.1-1.6)	1.4	(0.6-4.6)	0.5	(0-1.2)

Inspecting the final population outcomes by colony (Table 2) indicates variable degrees of uncertainty for population size. The approximate CV implied by the credible intervals of population size vary from a minimum of 0.11 to a maximum of ∞. Clearly, the count data collectively are more informative for some colonies than for others. In contrast, the estimates for carrying capacity are consistently uncertain. The approximate CV implied by the credible intervals of population size vary from a minimum of 0.12 to a maximum of 36.38. The final columns in (Table 2) apportion total recruitment, occurring across the metapopulation, to different individual colonies. Hence, a median % Recr, value of, say, 2% implies that of the total number of new breeding recruits across the entire colony network, 2% established in a particular colony.

Comparison of the scales for the two processes generating connectivity between colonies is shown in Fig. 7. The first, shown in green, is the competition between colonies for resources. It is evident that the half-distance of this form of competition is small (equivalent to 32km). This means that an individuals from a colony at that distance exerts half the competitive influence that it would exert to conspecifics from the same colony. In contrast, the second mechanism of connectivity, due to exchange of recruits between colonies is much further-reaching (half-distance equivalent to 214km). This means that a single individual that has decided to disperse from its native colony, has half the probability of moving to a colony at that distance, compared to the probability of settling at colony next to its native location.

To examine the relative status, through time, of SPA and non-SPA colonies, we aggregated population sizes and uncertainty therein, into these two categories (Fig. 8). Despite the higher-quality

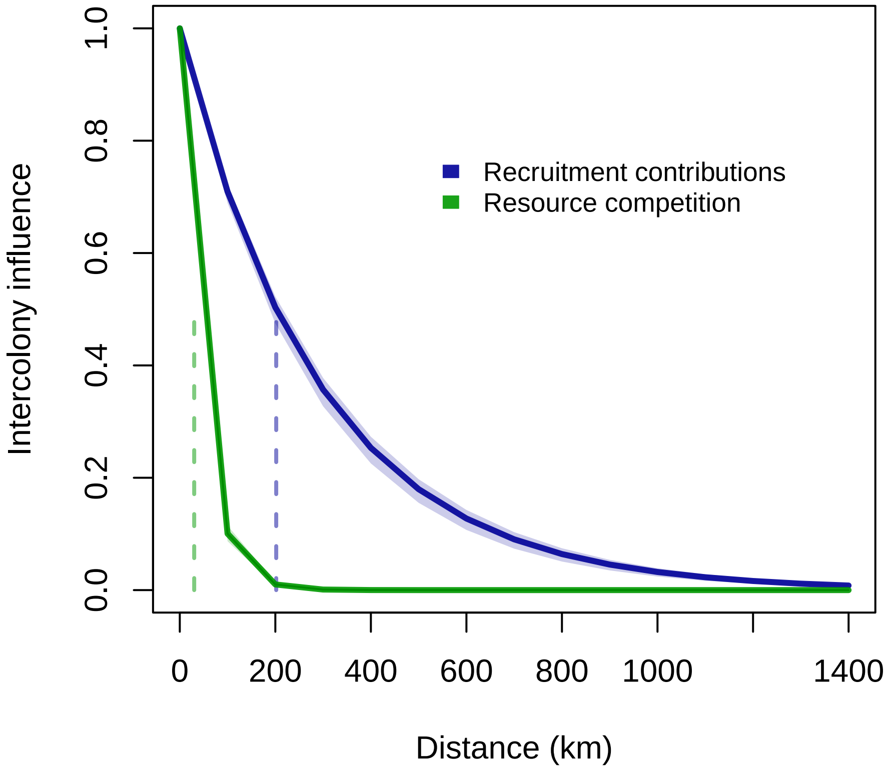


Figure 7: A comparison of the spatial scales of connectivity between colonies. The decay of intensity of competition for resources, as a function of the distance between colonies, is shown in green and the connectivity of colonies in terms of contributions of recruits is shown in blue. Both scales on the y axis are relevant to a maximum, representing the strength of intracolony competition and the probability of return to the colony, excluding the effect of philopatry. The effective radii of each mechanism are defined as the half saturation points of each median curve. The shaded areas correspond to the 95 percentile parameter values.

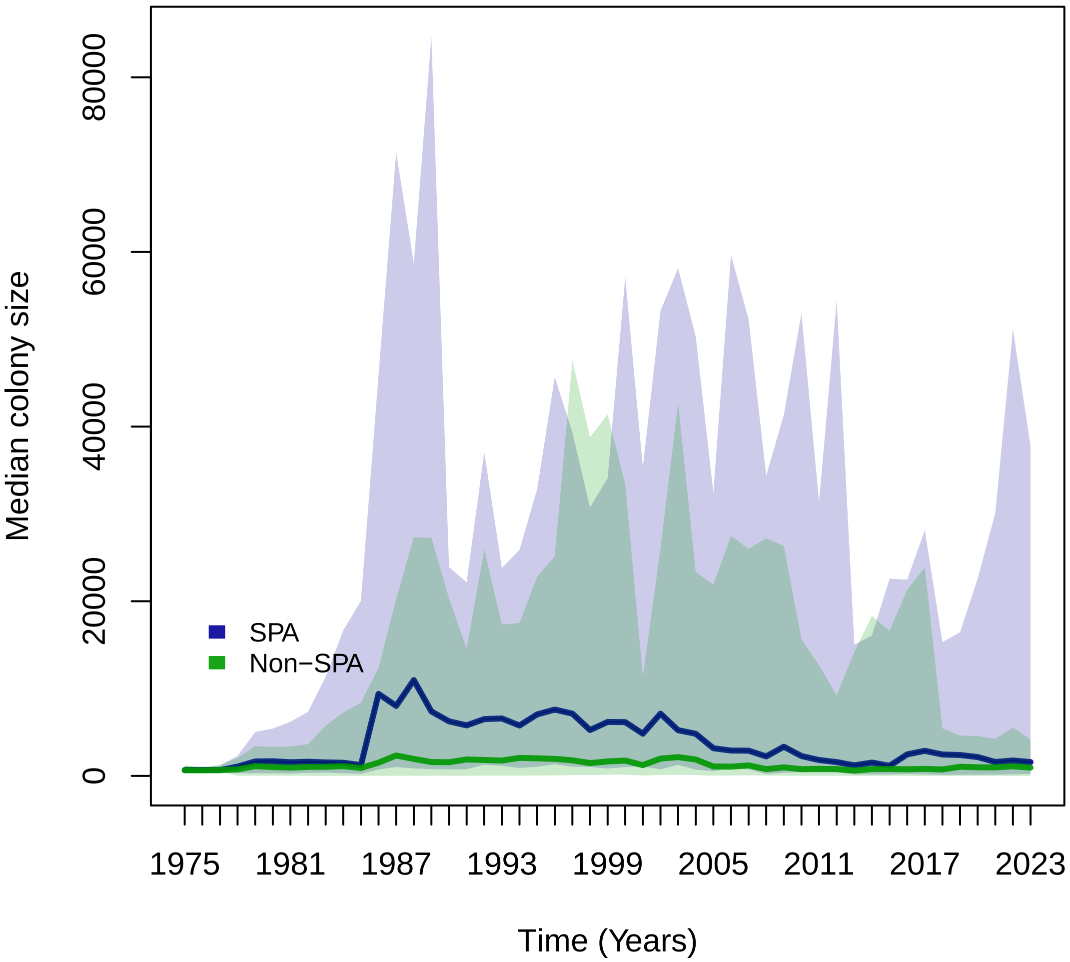


Figure 8: Median population trajectories for populations at Special Protected Areas and the remaining population components. The 95% credible intervals represent variability between median predictions across all colonies (so they are the Bayesian equivalent of confidence intervals, rather than prediction intervals).

data available for the SPA colonies, we found comparable degree of uncertainty in the resulting trajectories (compare the blue and green credible intervals in Fig. 8). At the same time, the median trajectory of SPA populations presents a drastic decline during the millennium years, following an apparent increase during the 1970s.

Trajectories for the whole metapopulation (Fig. 9a), but also, its demographic components of survival (Fig. 9b) and breeding success (Fig. 9c), show very gradual declining trends. During the initial phase of the fitted trajectories, around 1985, estimated population numbers depend on initial conditions that are unobserved, requiring the model to estimate them. This often creates artefacts that are sensitive to the priors used for initial conditions. Figs 9a&c show sharp initial increases in the time series with tight credible intervals. This is most likely the result of the priors for initial populations and breeding success having low means and standard deviations. We did not undertake a systematic sensitivity on initial conditions here because we were mostly interested in the later parts of the trajectory, but a more precautionary approach to these priors may have some merit in future iterations of model fitting.

We also generated plots of population size, adult survival and breeding success for each of the six regions in the model (Fig. 10). These indicated predominantly declining trends for all regions (except, most recently, regions 2 and 4). 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). These results also make it clear that the artefacts present at the early stages of population and breeding success appear to have originated mainly from regions 2 and 4 (i.e. the east and northeast of the map).

A final output from this fitted model (Fig. 11) provides an overview of the change in subpopulation sizes, but also the estimated levels of connectivity in the network. For the synoptic comparison across time we have used estimated median population sizes in 1985 and 2023 respectively. The vast majority of colonies in this map have declined in size, but to a variable degree, and there is no apparent spatial pattern in this effect. To illustrate connectivity, we have plotted connections due to exchange of recruits in orange bars. To avoid overwhelming the map with linkages we plotted the top 3% of the ranked strength of pairwise connections. This threshold was chosen purely for visual convenience but it highlights six subdivisions of the broader network (Orkney-Shetland,East of Scotland, West of Scotland, Western Ireland, Irish Sea, south of England and Cornwall).

9 A next-generation PVA tool for seabird metapopulations

The distinction between model fitting/selection and simulation/forecasting is pertinent here. Model fitting requires running the model hundreds of thousands of times in order to either optimise the parameter values (in a frequentist approach), or obtain an approximation of their joint posterior distribution (in a Bayesian approach, such as ours). This is a computationally expensive task, but once completed successfully, it results in a fully parameterised model that can express what it has learnt about the real system under new, future scenarios. Simulating from a model like this is comparatively cheap, even if stochastic outcomes are considered. Therefore, using the fully fitted model in its simulation mode offers superior PVA capability over any currently existing approach - such as the JNCC/Natural England PVA tool - for five distinct reasons:

1) The parameterisation of the PVA is not piece-wise (i.e., achieved by collating independently estimated parameter values, often without uncertainty, as is customarily the case), but inte-

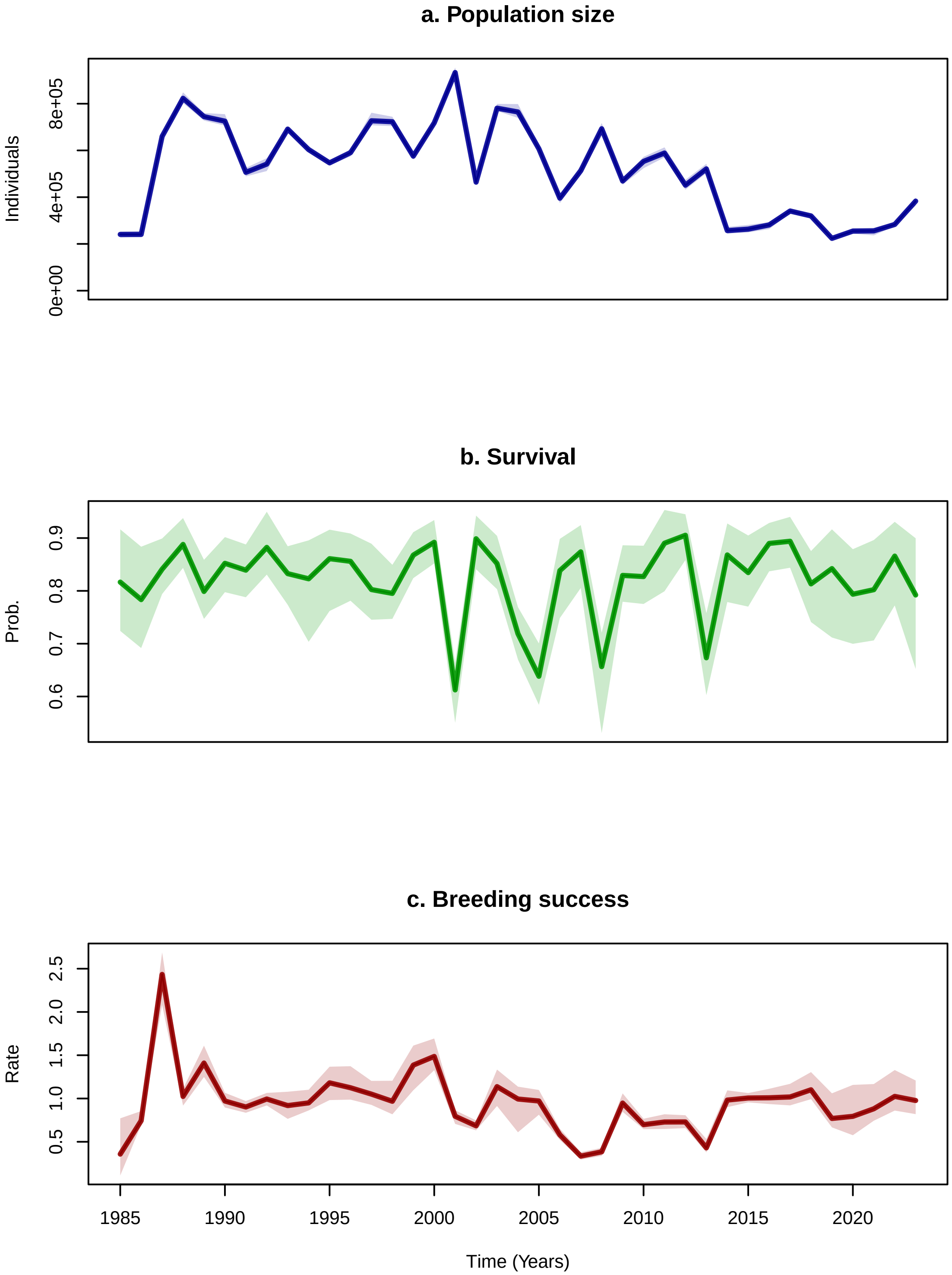


Figure 9: Reconstructed metapopulation size (a), aggregate adult survival (b) and aggregate breeding success (c).

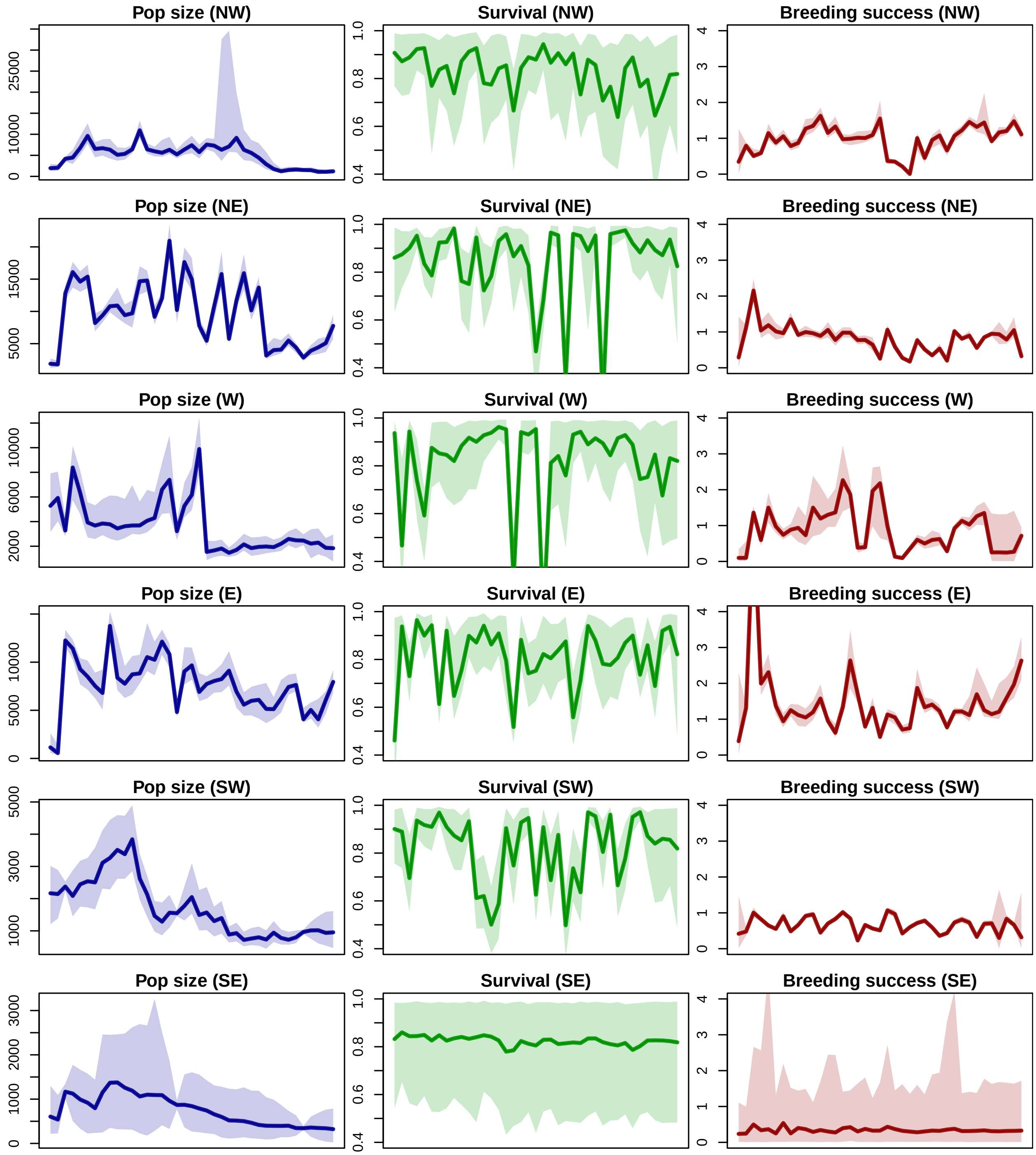


Figure 10: Regional dynamics model. Each region (annotated by compass point shorthand) was allowed independent random effects for breeding and fecundity rates. Average colony size (column 1), regional adult survival (column 2) and regional breeding success (column 3).

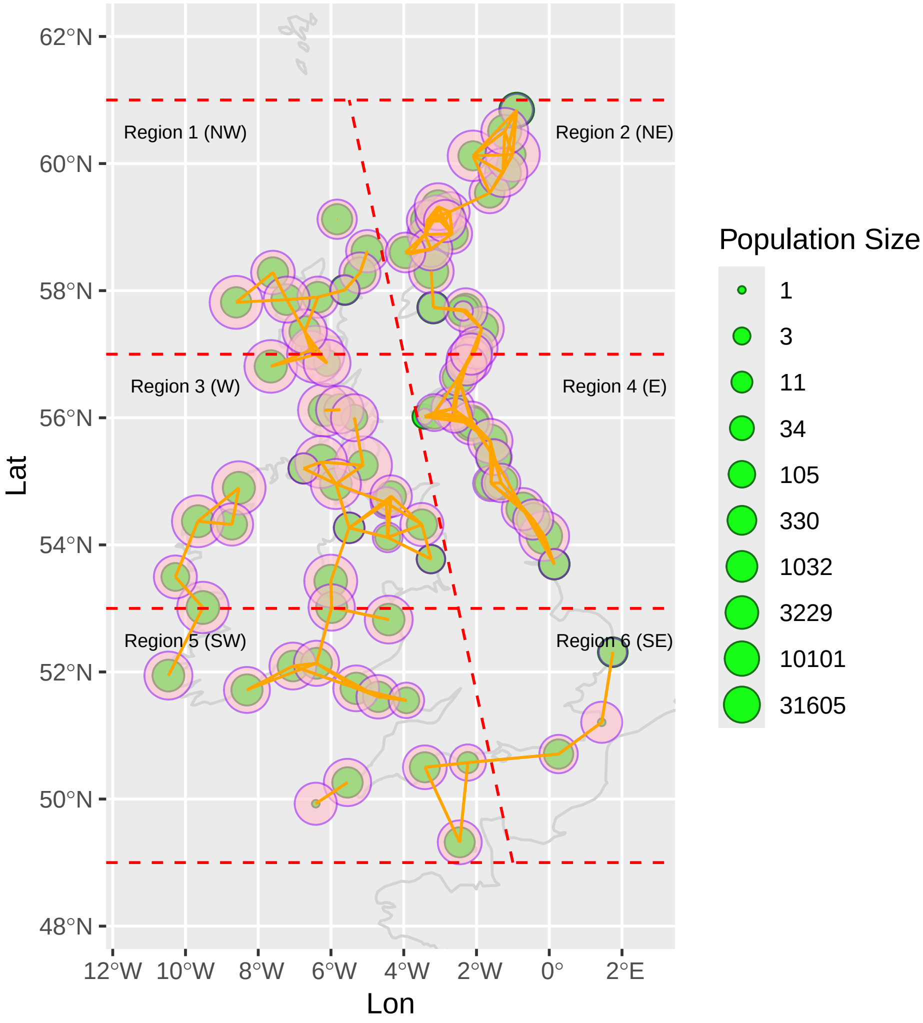


Figure 11: Spatial representations of the metapopulation. Pink and green circles are sized according to the estimated sizes of the populations in 1985 and 2023 respectively. The orange bars indicate potential levels of recruitment in the top 3% of pairwise connectivity.

grated, based on the entirety of available knowledge and data across the UK metapopulation and abroad.

2) Connectivity (as estimated at model fitting) is fully embedded in the projected dynamics, and can be switched on/off to examine the underlying source/sink properties of particular sub-populations.
3) Covariates of demographic trends may be embedded in the fitted model, and - assuming that covariate forecasts exist - be used to make covariate-driven predictions.
4) 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.
5) 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 has formed a point of discussion and detailed consideration under a parallel ORJIP project named ASSESS which has demonstrated that careless inclusion of uncertainty can either lead to suffocation of marine development due to over-precaution, or environmentally risky decision making due to overoptimism. Our PVA models here, strike an optimal balance between precautionary and optimistic projections, navigating the ever-narrowing straights between economic development and environmental protection.

These key differences also make it difficult to embed our results as evidence into the JNCC/Natural England PVA tool, unless the tool is updated in the above five directions. In this section we demonstrate the use of a whole-metapopulation PVA. Updates of this simulation model with future data will require periodic refitting of the model to augmented data sets. The code for the PVA tool is seen in Appendix VI.

To generate predictions from the fitted model while fully propagating the uncertainty in the joint parameter posterior, the simulation model is run multiple times (5000 in the demonstrations shown below), each time with a different parameterisation, drawn from the joint posterior of the fitted JAGS model. The model-fitting code from earlier sections dumps 5000 thinned MCMC trials into a data-file (~200Mb) that is uploaded and available for simulation use. Therefore, there is no need for a user of the PVA to re-fit the model, all that is required is this sample/data-file of joint-posterior parameterisations.

Having fitted the metapopulation model to all the available data (Section 7), we used the simulation model to project the metapopulatiuon forward for 50 years. In (Fig. 12) we plotted two representations of these results. In part (a) we looked at the aggregate breeding and floater populations across all colonies, with associated 96% credible intervals. In part (b) we plotted the projected trajectories of all the sub-populations (coloured by SPA and non-SPA classification), on the log-scale and without credible intervals - to help facilitate visual inspection of so many polygons. 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. 12). This is a direct result of the recent increasing trends observed in regions 2 and 4 (Fig. 10). However, subject to model assumptions, the estimated parameters for demography and environmental stochasticity, the population is expected to decline after that. This projection would not be correct, 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).

To explore spatial patterns in the expected extinctions, we looked at a possible definition of extinction, namely the mean number of years it would take for breeding colonies to drop below 10 AOS (other definitions of extinction are of course possible) and plotted these numbers on a map (Fig. 13).

10 Other models explored

In addition to the regional dynamics model we obtained two more types of results based on **The Regional summaries model** and **The regional trends model**.

10.1 Regional summaries model

This model allowed the demographic patterns of each colony to vary independently across time, but assumed the same baseline parameters for the probabilities of survival and the rate of breeding. For the output of this model we plotted the average trajectories from the colonies belonging to each of the six geographic regions (Fig. 14). This model allowed each colony an independent survival/breeding set of trajectories with their own annual random effects, which meant that for the same year, colonies in each region were allowed to move in opposite directions. Hence, the averages of these trajectories are predictably characterised by limited apparent fluctuations. However, they are also indicative of no discernible upward or downward trends in the demographic rates. There were also no differences between the overall levels of survival or fecundity between regions detected by this model. In terms of population trends, region 4 is the only one that has shown any evidence of recent recovery.

10.2 Regional trends model

This was a variation on the regional dynamics model. For each demographic rate in each of the six regions, a time series was modelled comprising a region-specific baseline value, a linear temporal trend and annual random effect values. The difference between the regional dynamics and regional trends models was the addition of the linear temporal trend in the latter. For this model, in addition to the region/year random effects, each region was equipped with a temporal trend and a unique baseline for survival and fecundity. Trends were permitted for all the demographic processes and were linear in the scale of each process's predictor. The slopes of these trends did not differ from zero, as evaluated from the credible intervals of the slope coefficients. Therefore despite offering the model this capability, it was not used. Instead, the model used the region-specific annual random effects to create fluctuating demographic rates very similar to the regional dynamics model.

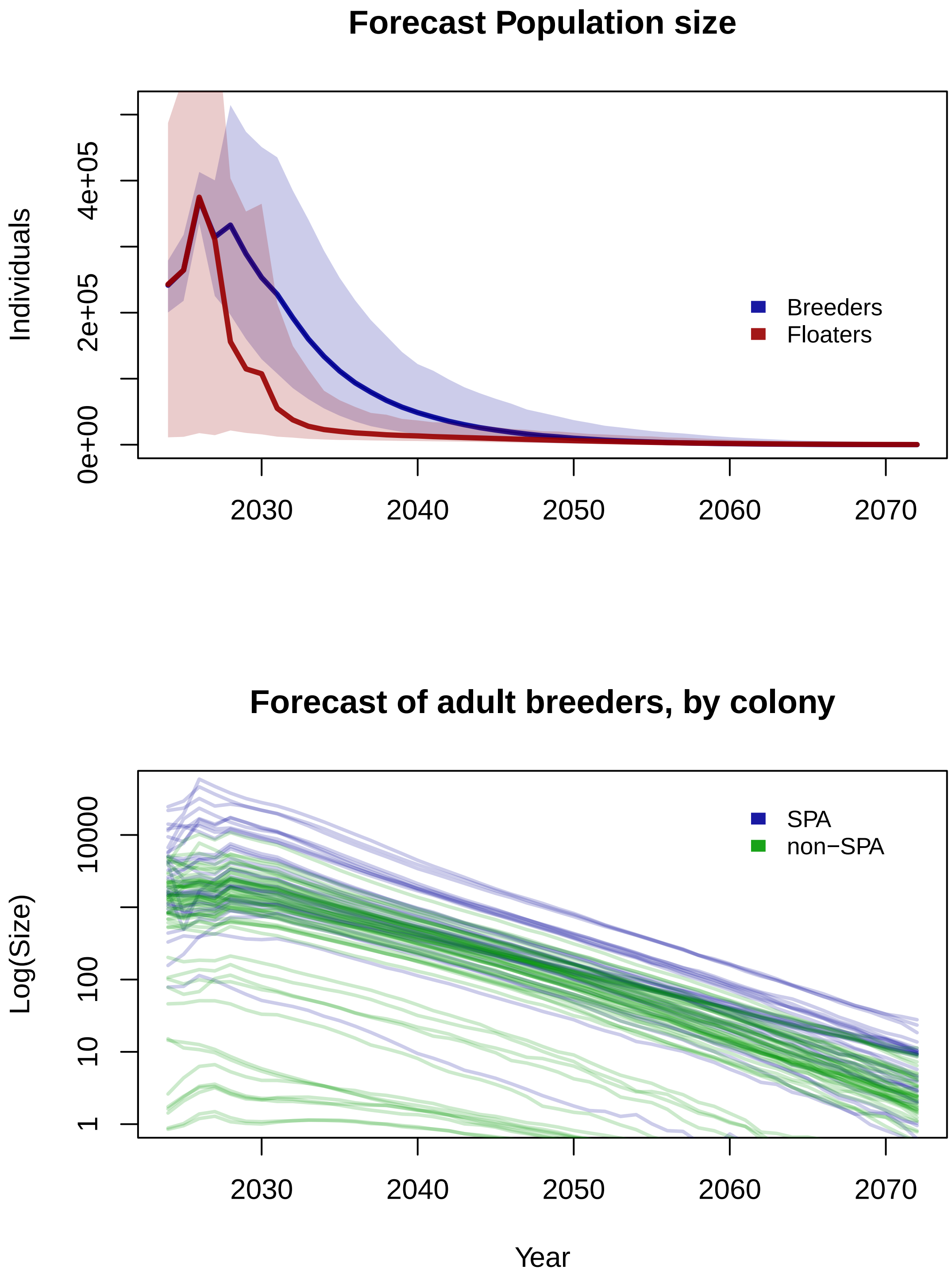


Figure 12: a) Aggregate population sizes for the main adult components of breeders and floaters. Shaded regions indicate 95% credible intervals. b) Individual mean trajectories of breeders in different colonies coloured by SPA (blue) and non-SPA (green).

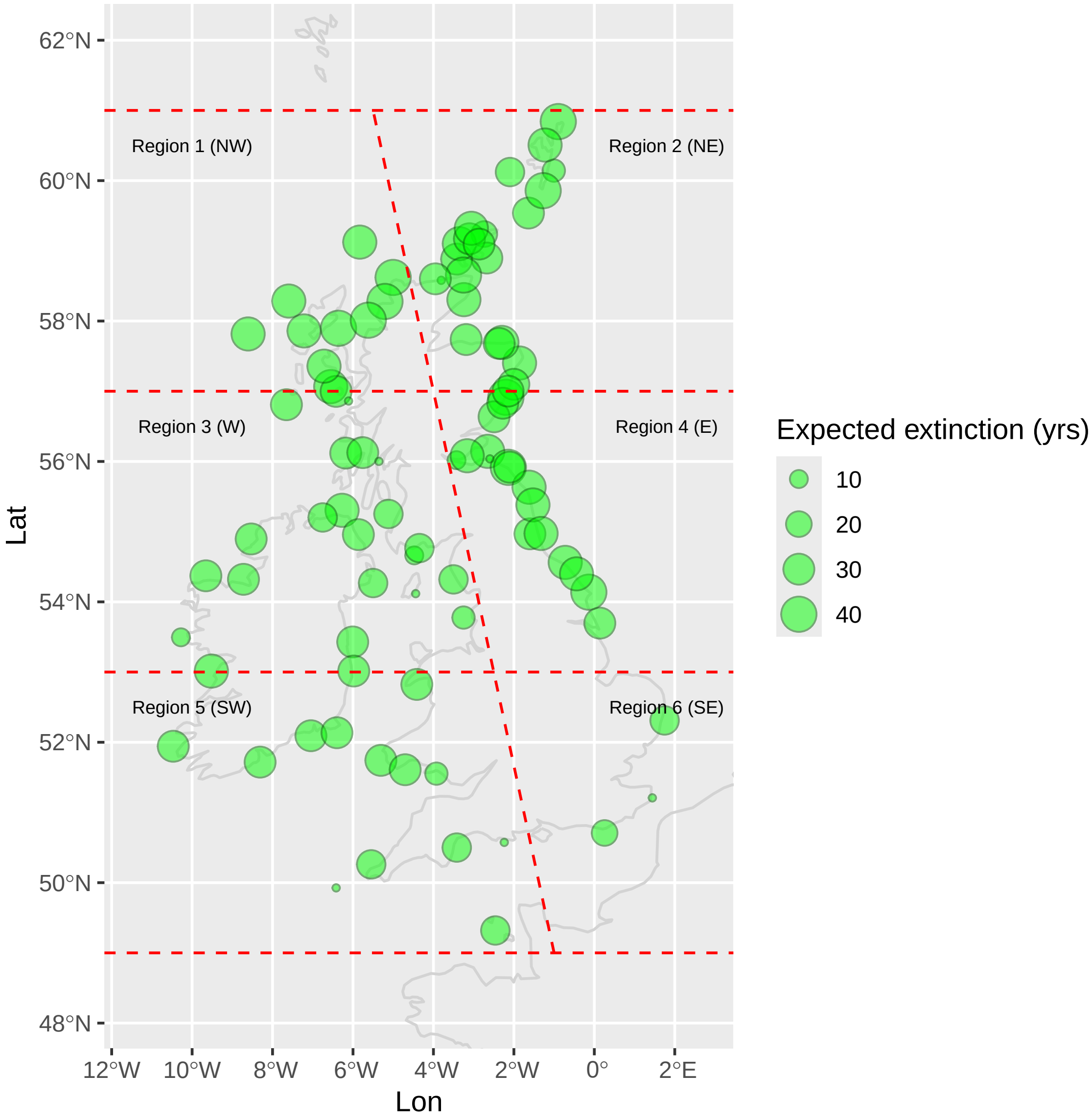


Figure 13: Mean extinction times as calculated by the PVA projection. Point sizes are continuous rather than discretised so that information is not lost. The legend presents four sizes for scale.

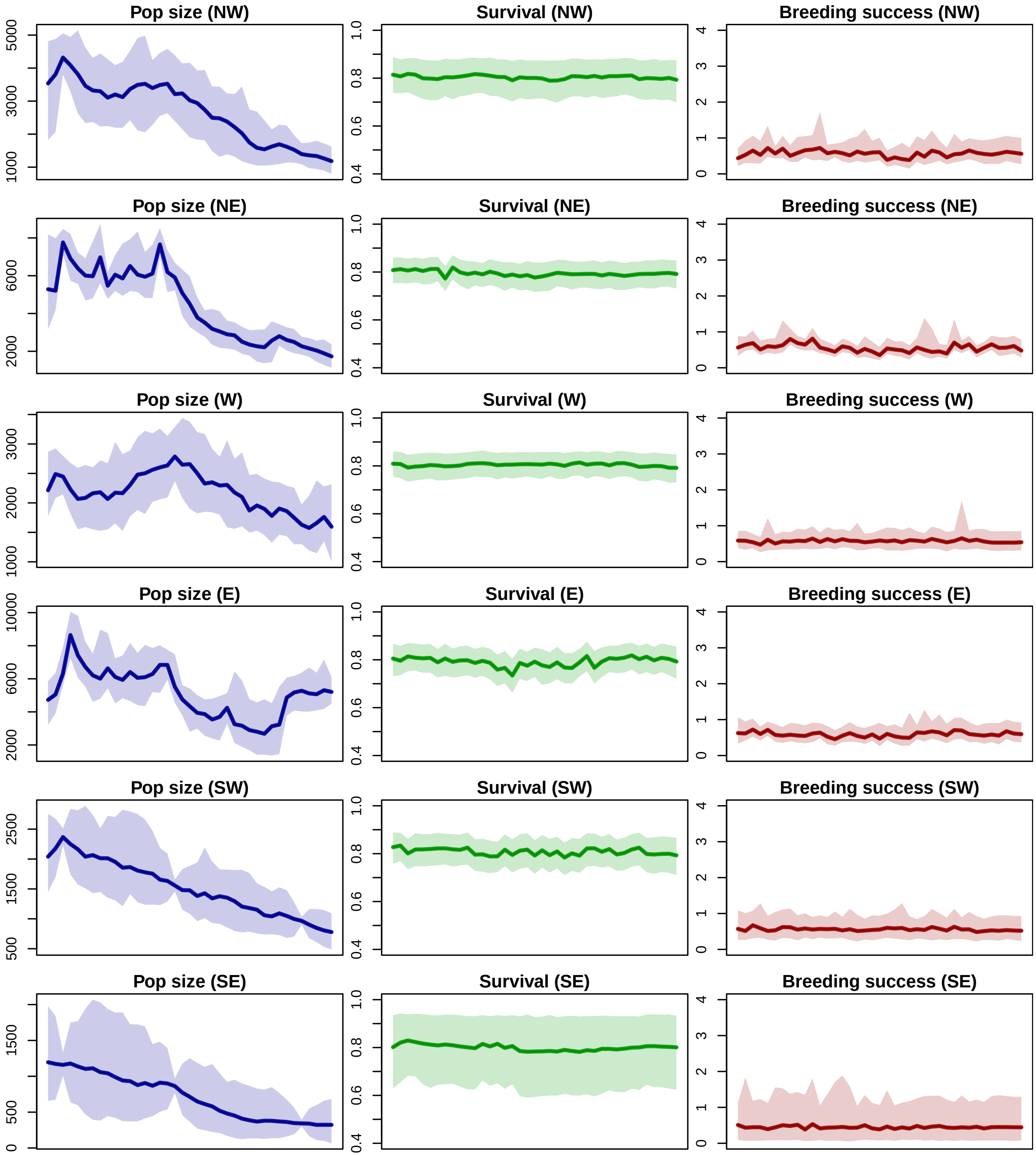


Figure 14: Regional summaries model. Each colony was allowed independent random effects for breeding and fecundity rates. We have aggregated those as averages for each of the six regions examined in this project. Average colony size (column 1), regional adult survival (column 2) and regional breeding success (column 3).

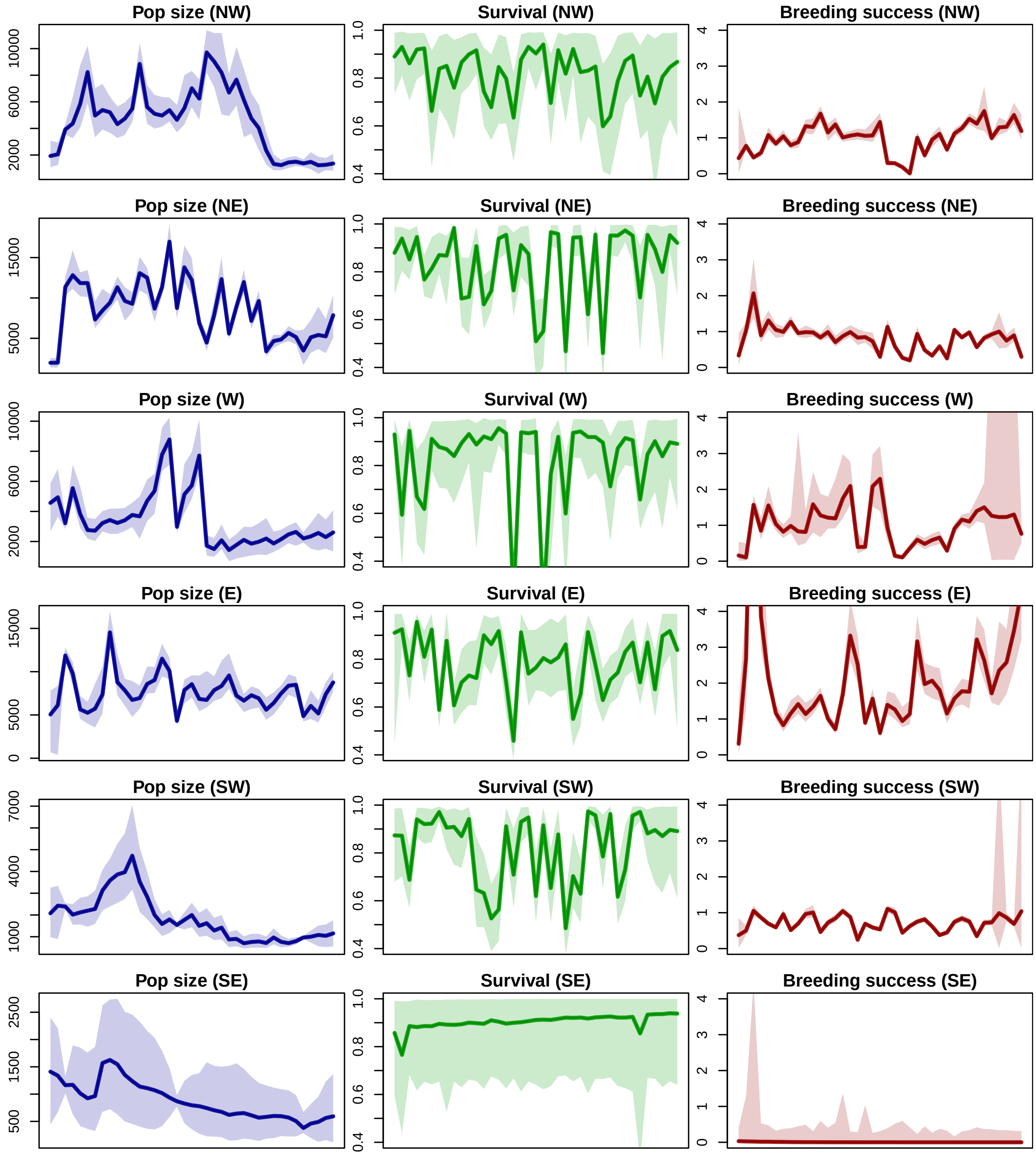


Figure 15: Regional trends model. Each region was allowed independent random effects for breeding and fecundity rates and there was also a region-specific temporal trend in the demographic rates. Average colony size (column 1), regional adult survival (column 2) and regional breeding success (column 3).

11 Conectivity-related modelling

We investigated the effects of connectivity on the underlying sub-population dynamics of the kittiwake network. Given a list of sub-population sizes (either from survey data, or modelling predictions), our fully fitted model (Model 2, regional dynamics model) was directed at quantifying the consequences of connectivity. Distance-based connectivity estimates are only part of this question because even under osmotic connectivity, the net flow of individuals will depend on the relative size of each population (Donor/receiver status). Having fitted the metapopulation model, it is possible to simulate from it and forecast population sizes of any given colony, subject to the estimated subsidies that it is receiving. The level of subsidies will of course also depend on how neighbouring colonies are growing, so even if we are interested in a focal colony, any forecasts and counterfactuals are best based on forward simulation of the entire network. We examined two aspects of this problem. The instantaneous status of each colony as a donor or receiver of recruits and the ability of a colony to survive in isolation (source), or based on subsidies from other colonies (sink).

11.1 Donor/receiver status

Even if a colony is below its carrying capacity and declining, some of its sub-adults are likely to emigrate and settle elsewhere. The traffic between colonies will depend on their overall connectivity and size, relative to other colonies within its reach. For any given yearly snapshot, it is straightforward (i.e., even without simulation) to determine which colonies are net donors and which are net receivers of recruits. We want to quantify the net number of animals (ΔP_i) donated or received by the i^{th} colony, as the difference between departing and incoming individuals (E_i and I_i, respectively). The characterisation of the entire metapopulation in terms of net *donors* (i.e., net receivers will have a negative value) is this difference in vector form:

$$\Delta \mathbf{P} = \mathbf{E} - \mathbf{I} \tag{19}$$

The level of donations in any given year t will depend on the connectivity between colonies and the number of their offspring that reach maturity. For computational expediency (mainly arising from MCMC memory storage), we did not monitor these numbers during inference, but rather used the breeding population in year $t-3$ as a proxy.

Our calculation uses the following quantities:

- π is the matrix of conditional probabilities of transition from the colony of origin to any other available colony (as estimated by eq. (12)),
- $\mathbf{P}_{t-3}$ is a proxy of available recruits in each colony,
- $\text{diag}(\pi)$ is the proportion of animals returning to their home colony

The vector of animals coming to colonies is $\mathbf{P}_{t-3} \times \pi$, but this includes returning individuals, so $\mathbf{I} = \mathbf{P_{t-3}} \times \pi - \text{diag}(\pi)\mathbf{P_{t-3}}$. Also, the number of animals leaving the colonies is $\mathbf{E} = (\mathbf{1} - \text{diag}(\pi))\mathbf{P_{t-3}}$, which simplifies eq.(19) to

$$\Delta \mathbf{P} = \mathbf{P_{t-3}} - \mathbf{P_{t-3}} \times \pi \tag{20}$$

By drawing repeat MCMC trials for the parameters (c, δ_π) (see section 5.9), we can generate robust estimates of this quantity for different colonies. First, in Fig. 16 we look at a histogram of the net donations across the metapopulation (+ve for donors, -ve for receivers) in 2023, the most recent year in the data set. As a second visualisation, we place these estimates in space, to examine which regions, colonies are likely to act as net donors for others (Fig. 16). Notably, not all colonies are SPAs.

11.2 Source/sink status

A particular counterfactual that is of interest for policy and development is whether the projected impacts on open and closed populations differ. 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. Here, we determine which colonies cannot be self-sustaining by switching off connectivity, and simulating the metapopulation forward. This enables us to establish which colonies decline and which persist. We can extend these characterisations to any subset of colonies that are currently denoted as SPAs, particularly those presenting a high consent risk for offshore wind development. Particular compensation measures for these SPA colonies may be targeted at their source/donor colonies as a method of indirect mitigation. Again, our fitted model can be specified to reverse-engineer these mitigation effects, to maximise the effect of compensation measures.

The finding from the previous sections that all the major colonies are in decline 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 (Fig. 17). This was done by use of the fully parameterised simulation model, turning the connectivity feature off. We found only small differences compared to the connected projections (Fig. 12), only in the sense that some of the smaller colonies are likely to go extinct even sooner than current projections.

11.3 Source/sink dynamics

In principle, the above calculations, and graphical panels of vulnerability and source sink status can be animated into the future, with the aid of projected scenarios for climate and anthropogenic disturbance. However, the project thus far has revealed and documented in detail the decline of the kittiwake metapopulation as a whole and the forecasts for the population's extirpation in the future. This prevented us from fully investigating some of the project's original aspirations, regarding source and sink populations. We instead diverted attention to a set of more topical questions looking at the demographic causes and prospects of metapopulation extirpation, and possibilities for mitigation.

12 Compensatory measures

In this section we explore the potential for global and regional mitigation/compensation. Global intervention would involve mechanisms of improvement likely to benefit all colonies, such as fishing moratoria for prey species such as sandeels (Wanless, Harris, and Greenstreet 1998; Tasker and

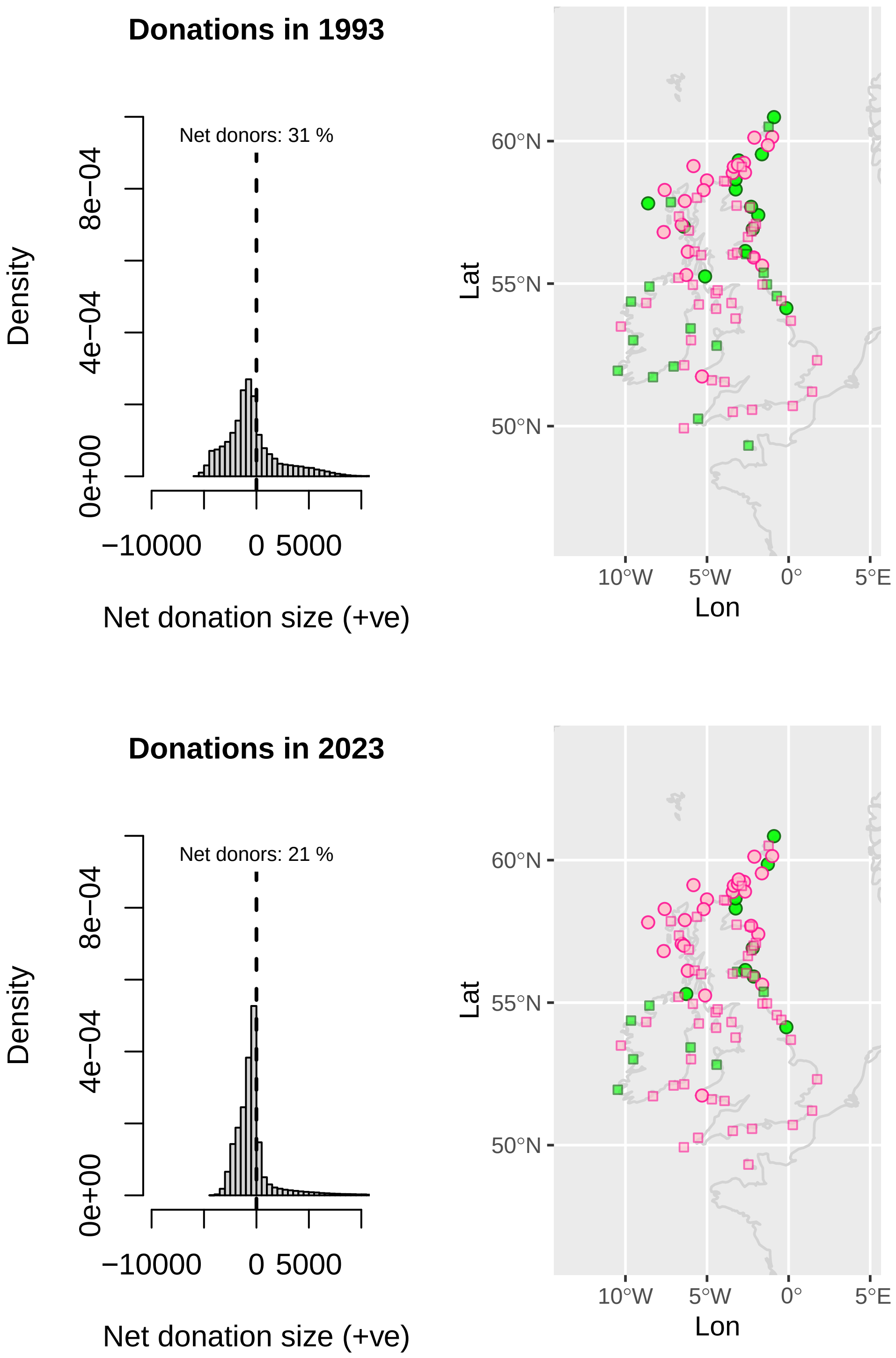


Figure 16: Aggregate histogram of the net numbers of animals donated (positive values), or received (negative values) by different colonies in the metapopulation. The proportion of net donors represents the number of colonies on the right-hand side of the dashed line. Replication is used with different MCMC trials to capture parameter uncertainty.Estimates of the donor (green) or receiver (pink) status of different colonies in the model. Circles indicate SPAs and smaller squares indicate non.SPAs.

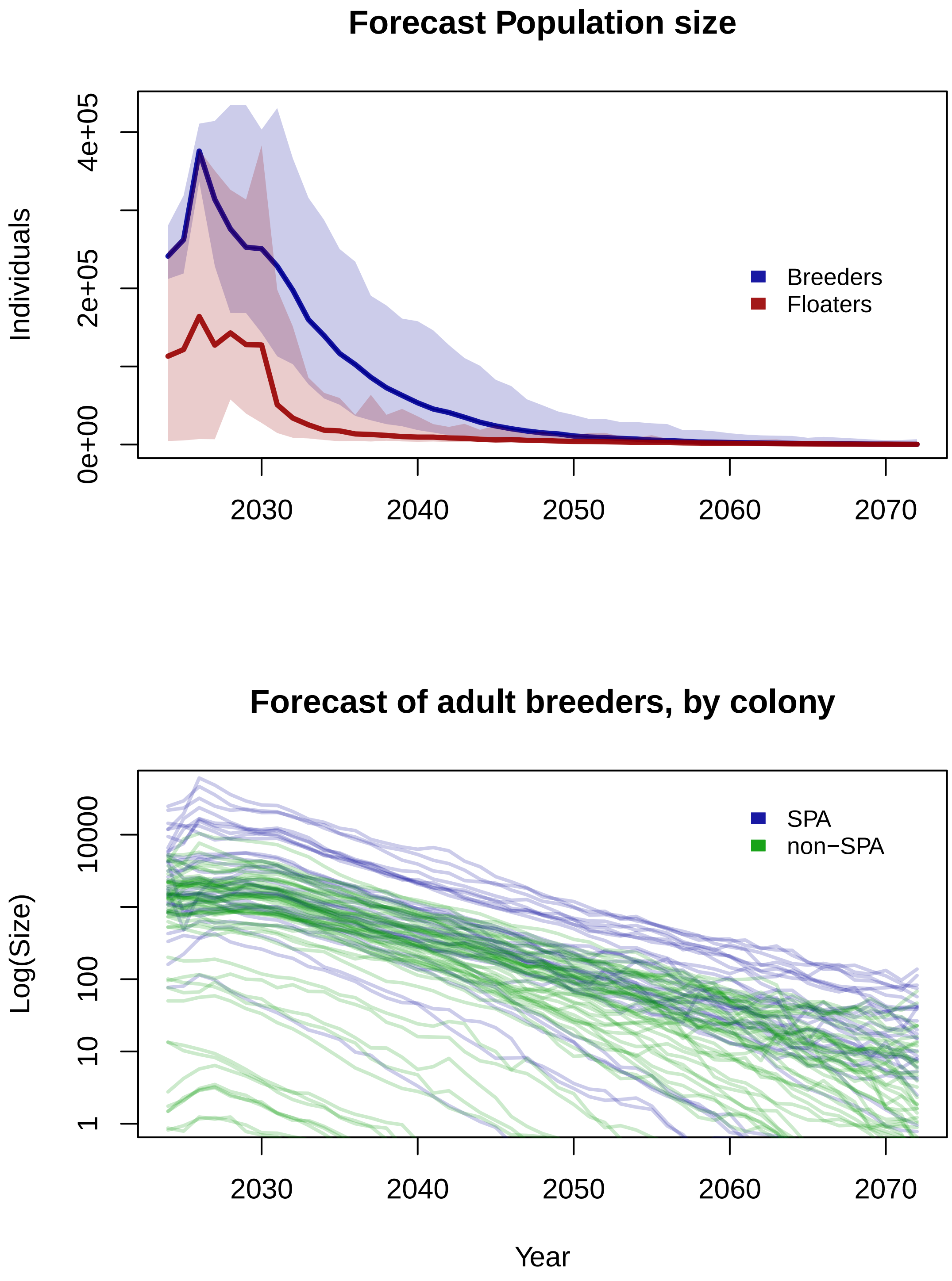


Figure 17: a) Aggregate population sizes for the main adult components of breeders and floaters. b) Individual mean trajectories of breeders in different colonies coloured by SPA (blue) and non-SPA (green).

Sydeman 2023). Any such improvements may occur at the same time as other environmental drivers are causing global deterioration in one or more vital rates. In the first subsection, 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 actions such as the construction of artificial nesting structures (ANS) (Browner, Randall, and Carolan 2021; D. O. Wind 2024). In the second subsection, we have investigated an illustrative example of ANS to exemplify how such an impact could be quantified via our metapopulation PVA.

12.1 Investigation of demographic sensitivity

We systematically explored combinations of increments and decrements in current values of adult/pre-breeder/floater survivals and breeding success (S_a,a, S_r, S_f and b, respectively). We explored multipliers applied to the vital rates. A multiplier of 1, left the current baseline value unaffected, values <1 represented a deterioration and values >1 an improvement. We explored following values $S_r \in \{0.70, 0.85, 1.00, 1.15, 1.30\}$, $S_f \in \{0.70, 0.85, 1.00, 1.15, 1.30\}$, $S_a \in \{0.7, 0.73, ..., 1, ..., 1.27, 1.3\}$, $b \in \{0.5, 0.55, ..., 1, ..., 1.45, 1.5\}$. We ran the PVA 20 times for each four-parameter value combination and calculated the average proportional change in total population size over a 50y time horizon. For each of the 20 replicates, this was defined as

$$\Delta P = \frac{P_{2075} - P_{2025}}{P_{2025}} \tag{21}$$

We plotted these mean values in a factorial design plot (Fig. 18). These 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 sub-adult 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 (Spencer et al. 2022) and Scottish Seabird Conservation Action Plan (Government 2025), and the Welsh strategy when it becomes available. It would also be useful in informing future compensation measures.

12.2 A PVA experiment using artificial nesting structures

For this experiment, we positioned five hypothetical ANSs around the UK at coordinates (Lat,Lon)={(57,08),(54,1.5),(51,-6),(56.5,-1),(59.5,-4)} (Fig. 19). We assigned each ANS an initial population of 4600 breeding pairs (the average colony size estimated by the model for 2023) and allowed each a carrying capacity of 10000 breeding pairs. We have considered a very optimistic scenario for the ANSs. As part of that, we did not start them at zero size, but at approx. half their carrying capacity to ensure they would not go extinct. More precautionary scenarios should be investigated when such analyses are expanded to real ANS construction proposals. We further assumed that, at the ANSs only, the breeding success of kittiwakes was twice as great as the baseline estimated for other colonies (this is at the upper end of values estimated by O. D. O. Wind (2023)) and the adult survival was either 50% larger than the estimated baseline, or close to 0.99 (whichever value was smallest). Other values are possible, pending the availability of published

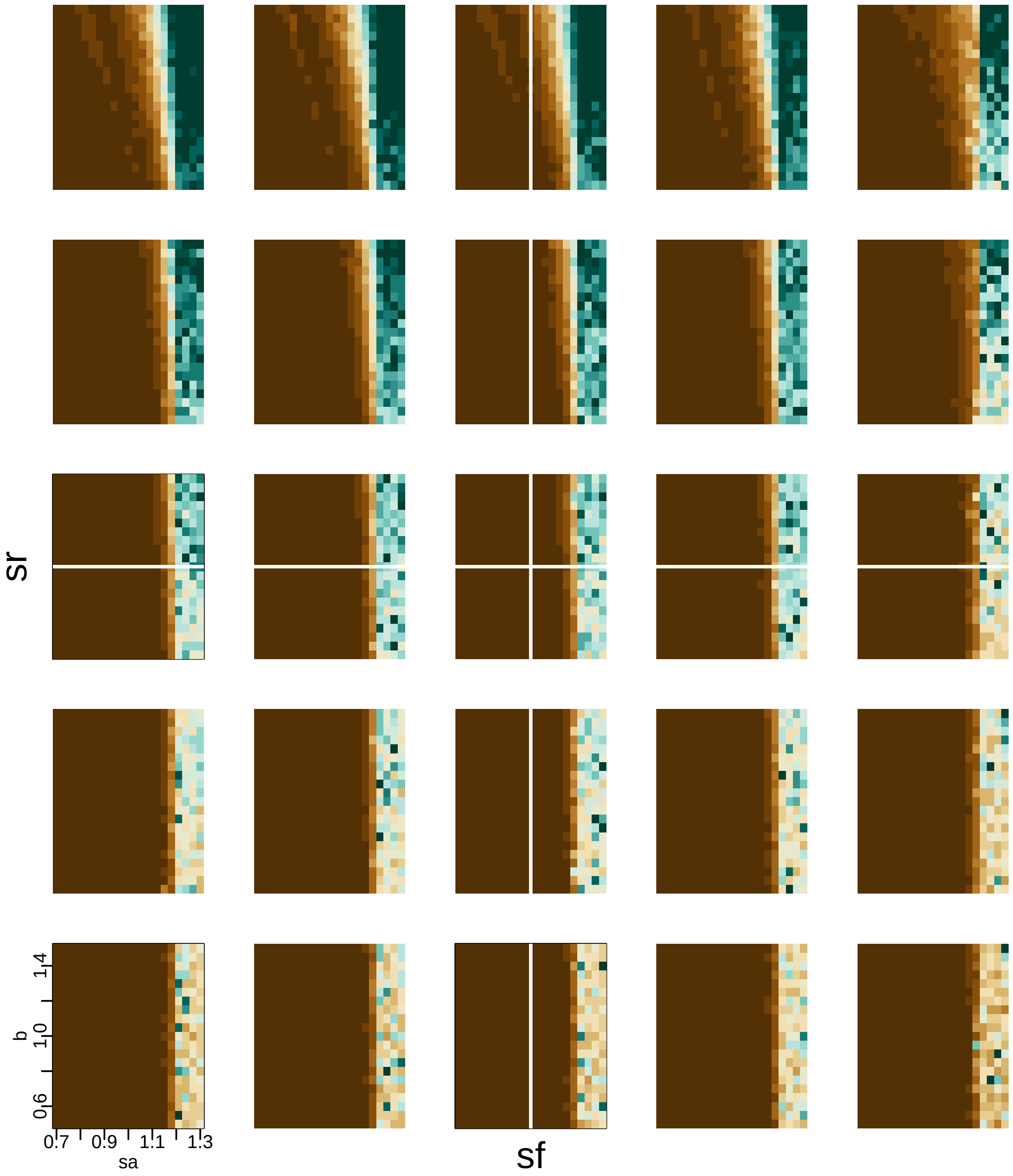


Figure 18: Proportional gains (in blue shades) and losses (in brown shades) in the total population size, as a result of incremental additions/reductions in the model's four baseline rates adult survival (sa), breeding success (b), pre-breeder survival (sr) and floater survival (sf). Note that the values cited on the axes are multipliers of the current situation. Values above 1 represent increases, and values below 1 decreases. All survival values were capped at 1. The status quo is represented by the scenario at the centre of the middle plate shown in this compound figure (white cross-hairs). Any combinations in the first quadrant of the composite plot and individual plates represent improvements in vital rates.

data. The ANSs were connected to the network according to distance, and were therefore 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 (Fig. 20). Comparing with (Fig. 12), we see that the ANSs do, nevertheless, manage to slow down the decline of individual colonies, but those differences are hardly noticeable at the level of the metapopulation.

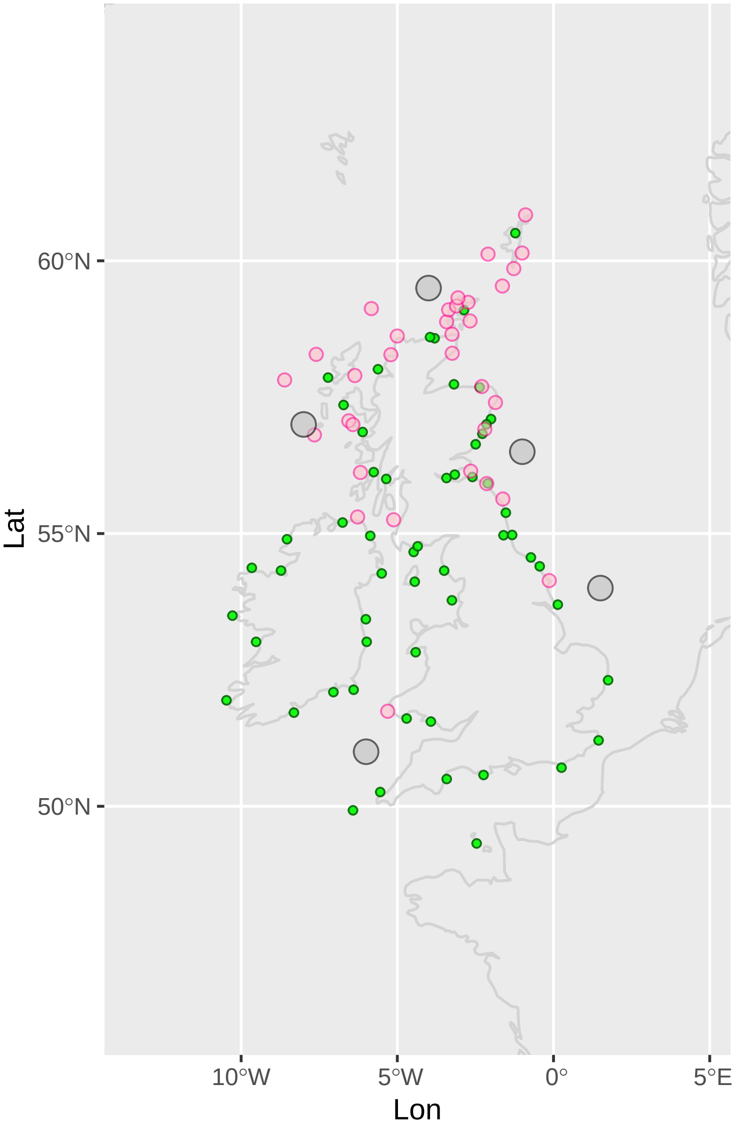


Figure 19: The network of SPAs (large pink circles) and approximate management areas (small green circles) corresponding to named administrative regions. Five grey circles represent the locations of five hypothetical artificial nesting structures (ANSs).

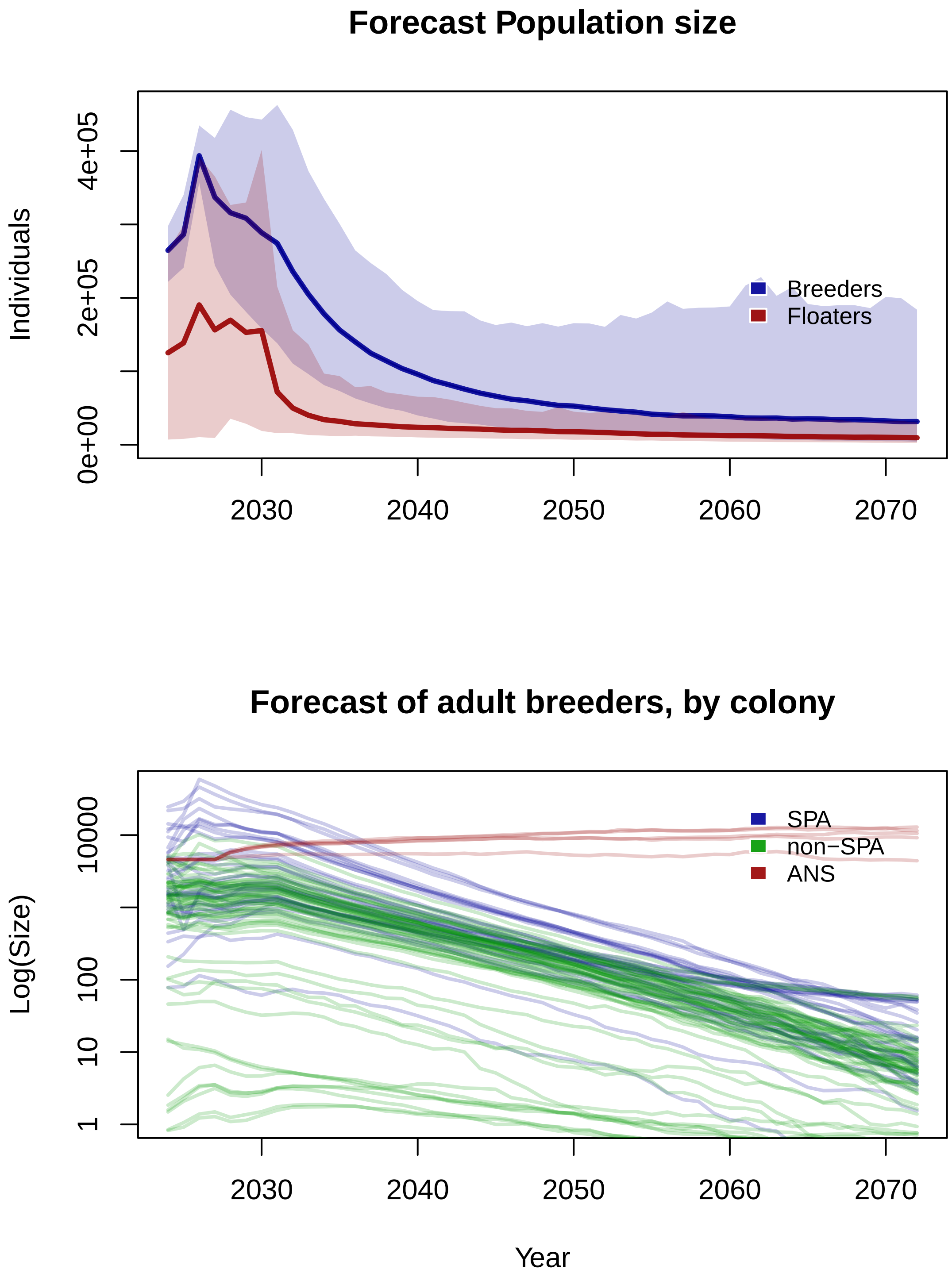


Figure 20: a) Overall forecast population size for a PVA with ANSs and b) predictions by colony, including the five artificial colonies added in this illustrative example.

13 Considerations regarding covariates

The spatiotemporal patterns of heterogeneity in breeding success and survival revealed in Figs 10 and 15, do not have the appearance of random fluctuations. They show clear evidence of autocorrelation in time and some evidence of a spatial longitudinal gradient in the mean values and amplitude of fluctuations in breeding success. These patterns invite explanation in terms of environmental covariates such as climate change, prey availability, human disturbance, land predators, weather events etc. We can distinguish between anthropogenic and natural covariates, acknowledging that we may not be able to intervene and manage the natural ones (Fig. 21, columns). For seabirds in particular, we can distinguish between colony-located (local geomorphology, nesting site availability, coastal human disturbance etc.) and marine covariates (OWF, SST, prey proxies, bathymetry, shipping, primary production, etc)(Table 21, rows).

	1. Anthropogenic	**2. Natural**
a. Colony-based	Noise pollution Light pollution Walkers & dogs Vehicle traffic	Coastal steepness Wind exposure Competing spp colonies Land predators
b. Marine-related	OWF Shipping Fish farms Benthic infrastructure	Bathymetry SST Primary production Prey distribution

Figure 21: A classification of 16 candidate covariates into four distinct classes that can be used to evaluate processing and priority.

The advantage of having covariates in the model is that features such as spatiotemporal autocorrelation (i.e. gradual fluctuations in the environment, and spatial gradients) are automatically captured by the covariate data. Additionally, any 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 placement of covariates into the linear predictors for breeding, survival and recruitment is anticipated in the mathematical description of the model above). From a practical perspective there is a question mark on whether such investigations can and should be pursued, and it was decided that this analysis could not form part of this project. Nevertheless, it is important to summarise here discussions held with the steering group and collaborators, as well as some of the challenges of pursuing covariate investigations, as relevant avenues for future work.

13.1 Demographic covariates

A review of the literature on variables influencing demographic rates can be found in (Catharine Horswill and Robinson 2015).

Prey availability Kittiwake breeding success and adult survival can be influenced by sandeel total stock biomass (Oro and Furness 2002; Frederiksen et al. 2004; M. J. Carroll et al. 2017). Direct prey availability data are patchy in both space and time. Fisheries datasets are not readily available at a resolution and scale that is ecologically/biologically relevant to breeding kittiwakes.

Proxies of fish prey availability such as sea surface temperature (SST) and oceanographic fronts may be useful, however studies looking at the relationship between indices of kittiwake breeding performance and SST have shown contrasting results (Oro 2014) and it is still unclear whether hydrographic features (e.g., fronts) are good predictors of fish prey availability to sea-surface feeding seabirds.

Equally, there are no reliable future forecasts of trends in sandeel abundance, although prediction based on relationships between SST and Sandeel biomass may be possible (M. J. Carroll et al. 2017). Work under ECOWIND-funded PELAgIO (Beth Scott unpub.) is developing fish prey availability maps for the North Sea, so these may be of use.

It may be more reliable to explore primary productivity (mean/max), in the vicinity of colonies during the breeding season. Depending on the spatial resolution required, there are various options for examining productivity, including modelled datasets (e.g. POLCOMS-ERSEM 2006-2100 @ ~11 km resolution - Marine biogeochemistry data for the Northwest European Shelf and Mediterranean Sea from 2006 up to 2100 derived from climate projections) which could be summarised to provide covariates that would also allow forecasting.

Additionally, prey abundance (even if good data or proxies were available) does not necessarily act in isolation. For most purposes, it interacts with conspecific density as the primary currency of scramble competition. Therefore, putting prey abundance directly as a covariate into e.g., kittiwake breeding success, may not return much of a signal. The suggestion that we should additionally examine inter-specific scramble competition adds an even subtler level of mechanistic complexity. Prey abundance also interacts with heterospecific density. For instance Wanless, Harris, and Greenstreet (1998) showed that in 1997 40,000 breeding pairs of gannets were consuming 67% of fish caught by seabirds in the Forth and Tay, by 2021 Gannet population had doubled to 81,000 breeding pairs and all other species - Kittiwake, Guillemot and Puffin - had declined. It seems possible that the rapidly increasing Gannet population is having a negative impact on seabird species that rely on the same prey in the F&T and more widely. This hypothesis will be inadvertently tested through the sharp decline of gannets as a result of the High Pathogenicity Avian Influenza mortality event in 2022 (Lane et al. 2024). On the other hand, despite some dietary overlaps between gannets and kittiwakes, competition for food may be ameliorated by fluctuations on alternative prey such as mackerel, which forms a prey for gannet and has increased in recent years (Clark et al. 2024).

Climate covariates Evidence and literature currently being reviewed by NatureScot is indicating a high sensitivity of kittiwakes in particular to climate variables (M. Carroll et al. 2015). Whether these are operating directly through thermal tolerances, or indirectly through affecting the abundance and spatial availability of prey, is not clear. However, it would be important to construct, or extract biologically-considered climate covariates for investigation.

Land predators Of relevance to kittiwakes are mostly raptors, large gulls, corvids, skuas, potentially foxes and even American mink (see citations in Catharine Horswill and Robinson (2015)), although impacts of terrestrial mammal predators on kittiwakes are likely to be small. Some control/deterring measures are available for some of the predators (e.g. mink, foxes). Colony-based land predator data are not readily available.

Site availability and carrying capacity at colonies This information is not routinely recorded, and indeed may be difficult to estimate with certainty. Most sites just focus on recording total numbers of breeding birds in linear coastal sections, rather than having information on potential available nest sites. There are examples where the area of suitable habitat is used as a proxy of maximum population sizes (Tinker et al. 2022; J. Matthiopoulos et al. 2025). Local knowledge may be available though, and it might be worth contacting local reserve managers or researchers working on particular colonies. For some of the sites where old photographs of sections of colonies have been taken, and where numbers have been declining, an exercise could be done to look at where gaps may be – but this would require quite a lot of data processing. Numbers of available sites may also be affected by climate change and by changes in predator communities. For example, south-facing cliffs may become unsuitable due to increased overheating of adults and eggs/chicks in nests, and potential nest sites may be lost on lower parts of cliffs due to increased wave height and storminess while potential nests sites may also be lost if predators can access some ledges or parts of the colony.

Offshore wind farms The location and extent of wind farms is known both in time and in space. It is additionally possible, using novel methodology (Niven et al. 2025), to estimate the exact overlap between the foraging range of colonies and the operational or in-construction wind farm footprints. Such an investigation is currently being undertaken by our group, for gannets, so it could readily be extended to kittiwakes. A coarser investigation involving a fixed overhead of mortality on colonies close to OWF was discussed with the steering group during project development, but was discouraged.

Other covariates There is currently no evidence that fish farms, benthic infrastructures or shipping are influential for kittiwake demographic rates. Also, terrestrial human disturbance (e.g. walkers and dogs) may not have strong effects on kittiwake breeding success, given the inaccessible nature of most nesting sites.

13.2 Connectivity covariates

At-sea competition Ultimately, it may be useful to consider whether interspecific seabird competition/pressure could be estimated for different colonies/regions and used as a covariate. This would require an estimate of colony locations and sizes for other species to be incorporated as covariates in the term of the model that describes colony interference due to scramble competition at sea. Although this was never envisaged as part of this project, it is nevertheless a feasible investigation, especially if no temporal variations are considered for the other species.

Inter-colony connectivity Distance to neighbouring colonies and the donor colony size both came into the calculation of the recruits donated by one colony to others. However, we also know that good breeding performance can attract kittiwakes to a target colony (Boulinier et al. 1996, 2008); there may also be some influence of age/breeding experience (Ponchon, Garnier, et al. 2015).

13.3 Challenges in the use of covariates

There are several challenges in finding and using environmental covariates. Unlike other (structural) improvements to any model, the search for covariates is practically endless. There is always one more variable, variable transformation, or variable combination that could be considered. The key objectives of the Metakitti project (quantifying connectivity and density dependence for a next-gen PVA analysis) were achieved without any covariates, but it is clear that causality and mitigation can be better handled if we know what the likely drivers of change are. As a result of the work conducted here, we now have a framework into which to incorporate covariates. Doing this requires us to deal with missing data, for parts of the time series. Some level of data-missingness can be addressed via imputation methods (essentially asking the model to reconstruct some of the missing covariate values, at the same time as it is using the others for fitting). However, it is computationally costly to bring sparse or non-existent covariate data to bear on a demographic process. Additionally, most covariates (e.g., prey density or far-future windfarms) are of limited use for forecasting, since their future values are unknown. Therefore, covariates with existing predicted states (e.g. climate scenarios, or near-future windfarm plans) are more useful.

14 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. The most important investigation at present, is the quantification of the likely effect of external covariates on the system across time, and in local, regional, global scales (see previous section). Beyond this, there are several other possible extensions that we discuss below.

14.1 Extensive validation

While the model validation protocol demonstrates 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. In particular:

- Predictive Performance Testing: Posterior predictive checks or forecast validation, which are essential for evaluating the model's ability to replicate observed population trajectories.
- Cross-Validation on Real Data: These techniques would provide a more realistic assessment of the model's generalisability across space and time, and help quantify uncertainty in forecasts at unobserved sites.
- Functionality Testing: Model functionality testing is the process of verifying that a model behaves as intended across a range of conditions and input scenarios. It is essential for ensuring that outputs respond logically and consistently to changes in individual parameters. By systematically varying key inputs and observing their effects, functionality testing helps identify structural flaws, unintended interactions, and hidden errors in the model logic. This process enhances transparency, builds user confidence, and demonstrates that the model can produce credible and interpretable results under realistic and diverse conditions.
- Sensitivity analysis: Model sensitivity analysis is the process of systematically examining how changes in input data and assumed structures affect a model's outputs. It identifies which variables have the greatest influence on model behaviour and highlights where uncertainty in inputs could lead to significant variation in results.

14.2 Modelling residual autocorrelation

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 autocorrelation in the demographic trends. These have not been modelled explicitly, but they could. For instance, instead of assuming independent annual residuals within a colony, or region, we could implement a random walk model. There may be other, more appropriate formulations if the demographic time series are not stationary (e.g., if there are regime shifts in the environment). Similarly, spatial autocorrelation may be captured by a distance-based variance covariance structure in residuals. In this way, proximate colonies will be assumed to be experiencing more similar conditions than distant ones. Such an approach would sit somewhere in-between our regional and colony-independent models, and it would inform us directly about the appropriate scale of similarity in environments for different colonies.

14.3 Improvements on the connectivity model

The prior for our natal dispersal connectivity was based on an expedient analysis of ringing data. As described in that section, the analysis methodology is being extended to use information from birds that were ringed but never recaptured. This will certainly increase the effective sample size of the data in the analysis and therefore enhance its precision. Additional gains in accuracy and precision can be made by integrating other types of data, such as genetics or telemetry. These inferential methods for joint analysis of such diverse data do not however exist, at present. Finally, as discussed in the preceding section, the metapopulation model may also be able to incorporate covariates, such as the breeding success of target colonies (Ponchon, Garnier, et al. 2015). This is a particularly elegant extension, because, during fitting, the metapopulation model estimates breeding success for all colonies in the network already, so it would be recycling these estimates as covariates of natal dispersal.

Our model did not include a provision for breeding dispersal, since evidence suggests that most breeding adults return to exactly the same nest site year after year (Coulson 2011) but a few will move to another nearby nest site, usually as a consequence of breeding failure suggesting that a move may be to seek a higher quality nest site (Danchin and Monnat 1992). Based on data in Danchin and Monnat (1992), Catharine Horswill and Robinson (2015) estimated that between 1% (in an increasing population) and 6% (in a decreasing population) of adult kittiwakes may show breeding dispersal each year. There are several examples of kittiwakes abandoning particular colonies that were subject to extreme breeding failure, or predation impact, or exclusion from nest sites by human actions such as putting up exclusion netting, and moving to a nearby safer nesting area (Coulson 2011; Ponchon, Chambert, et al. 2015). However, where kittiwakes achieve moderate to high breeding success such movements are rare (Porter and Coulson 1987).

14.4 Modelling the floater class

This is a key component of the population that is postulated to have both beneficial and detrimental impacts on the breeders (López-Sepulcre and Kokko 2005). Regardless of the adaptive aspects of having a pool of surplus individuals, their impact for population assessments could be quite high (Ainley et al. 2024). 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 the floater class follows an approximate, and colony specific formulation that makes the following key assumptions:

1) Immatures from the previous year that failed to recruit enter the floater class, and have the same survival rate and chance of future recruitment as sabbatical birds. Both of these are modelled implicitly in the floater class.

2) Although they may not have recruited into the breeding population, floaters in our model remain associated with their colony of attempted recruitment, and become gradually absorbed into the breeders of that colony, or die.

Both of the above assumptions may be incorrect. In particular, the implicit breeding site-fidelity implied by assumption (2) above, could be relaxed so that non-recruited individuals are capable of either joining a whole-metapopulation pool, or revising their choice of attempted breeding colony annually. The first of those versions seemed unrealistic since we have here found evidence of distance dependent dispersal in breeders. The second version, a possibly more realistic approach was computationally expensive (the dispersal redistribution steps in this model are very time consuming), but could be revisited in the future.

14.5 Improvements to naive priors

There may be expert knowledge that can be elicited to inform priors for some of the more difficult parameters of our model. In particular, in this realisation of the model, there was no information on the critical threshold of colony size at which the local population achieves critical mass (the Allee effect threshold, represented by our parameter P_A). Equally, it was difficult to identify priors for the colony-specific carrying capacities $P_{C,i}$. Although these density dependent parameters are unlikely to have been very influential for our results (since none of the colonies are likely to have been close to carrying capacity), it should in principle be possible to acquire local expert knowledge on the number of nests that could be accommodated by a colony region, as is done with similar models in other species (Jeglinski et al. 2023). Population sizes preceding our time horizon for the data used here for model fitting would be useful, but it is important to remember that they can only act as a minimum for carrying capacity. Even some of the more informed parameters of the model, such as the baseline demographic rates could benefit from further information. For instance, our prior for baseline immature survival is based on the key reference from Coulson and White (1959) which did not use conventional mark-recapture analytical methods, had small sample sizes and a short study duration. More recent methodological work (Emmanuelle Cam, Cooch, and Monnat 2005; Link, Cooch, and Cam 2002) could improve on these parameter priors.

14.6 Artificial Nesting Structures

Evidence gathered to date suggests that the numbers present on Offshore breeding structures could be significant (Christensen-Dalsgaard, Langset, and Anker-Nilssen 2020), 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, but it is important to acquire data on the location and carrying capacity of these locations, but more importantly, data on the survival and breeding success of pairs breeding there. However, even when parameterised very beneficially, the benefits of such structures for total population carrying capacity are likely to be negligible, since space at colonies is not the limiting factor. However, if they can offer distinct advantages for survival or fecundity, then they would operate as refuges. In this report we have shown that their utility for re-seeding other colonies may also be limited.

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.

14.7 Overwinter dynamics

The question of where any seabird species spends the winter is emerging across the board for many of these protected species. Our team in the University of Glasgow is leading work funded by the Crown Estate to investigate these questions via telemetry tagging in northern gannets (*Morus bassanus*). Once such data are available, the following steps will need to be undertaken:

1) Analyse telemetry data to identify the locations and extents of overwintering hotspots.
2) Run a Species Distribution Modelling (SDM) analysis on those location to determine their key environmental characteristics.
3) Use telemetry data again to represent proportion of animals from different broad breeding regions spending time at each overwintering hotspot.
4) Allow the influence of each overwintering hotspot, weighted by the proportion of birds of each breeding region that use it, to enter as a covariate in the breeding or survival performance of each colony.
5) If there was any additional data (e.g., annual weather, or primary production data) at the hotspots, then these (instead of the hotspot IDs) could enter the analysis in a weighted way (see step 3 above).

This is a technically demanding and data-hungry undertaking. In the past, we have successfully addressed the connections between breeding and overwintering areas for a species of pinniped (Russell et al. 2013), which may serve as a useful methodological model for similar future aspirations in seabirds.

14.8 User-friendly implementation

Code developed for all the tasks in this report is made available in the appendices. However, greater gains in usability can be made by packaging this functionality into an R package. The package would contain 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.

15 Summary

1. We developed a novel modelling framework that incorporates some of the often neglected features of seabird natural history: A full representation of the colony network, connectivity through natal dispersal and adult competition for food at sea, Allee effects, the input of floaters (both sabbatical birds and new recruits) and density dependence, both at the colonies and at sea. This wave of additional features was overdue given their ubiquity in seabird populations.

2. We fitted this model using efficient Bayesian methods to the full, integrated data set on breeding colony counts, for both SPA and non-SPA sites. The data used also included information on breeding success and survival, where available, as well as ring resighting data from the BTO, in the form of connectivity priors.

3. Spatially, the model considered a total of 89 breeding colonies (33 SPA colonies and 56 non-SPA locations). Space was also divided into six compass-point regions to allow for clustering/similarity in the temporal effects on breeding and survival.

4. 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 of these numbers were confirmed by the metapopulation model-fitting.

5. 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.

6. 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 than the rest.

7. 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.

8. The model fitted above was implemented as a fully parameterised, stochastic simulation (a next generation PVA), including all the novel biological features and the full posterior parameterisation (expressing parameter uncertainty).

9. 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. This is a significant finding because the model estimates the Allee threshold size of a kittiwake colony (i.e the size at which a colony becomes self-sustaining) to be in the region of 500 breeding pairs.

10. 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).

11. 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.

12. 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.

13. 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.

14. 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.

16 Appendix I: Mathematical notation.

Indexes

- t: Time, in years.
- i, j: Colony serial numbers.

State variables

- $\mathbf{P}_t = \{P_{i,t}, i = 1, ..., I\}$: Vector of breeding populations of the i^{th} colony (in units of breeding pairs).
- $\mathbf{F}_t = \{F_{i,t}, i = 1, ..., I\}$: Vector of floater populations of the i^{th} colony (females only, to account for breeding pair counting unit).
- $\mathbf{R}_t = \{R_{i,t}, i = 1, ..., I\}$: Vector of pre-breeders that can joint the floater population of the i^{th} colony (females only, to account for breeding pair counting unit).
- $s()$: Survivors from any given class (a binomial variate).
- $q()$: Number of recruits into the breeding population (binomial variate).
- $b()$: Number of births in a colony (Poisson variate).
- $\Psi_{i,t}$: The number of pre-breeders entering the pool of floaters associated with the i^{th} colony.

Other variables and covariates

- d_{ij}: The at-sea distance between colonies i and j.
- $X_{m,i,t}$: Value of the m^{th} environmental covariate prevailing at a time and colony.
- $\varepsilon_{i,t}$: Random effect on survival.
- $\psi_{i,t}$: Random effect on breeding success.

Functions

- $s_{\star,i,t}$: Annual, per-capita survival (time- and colony-specific) of adults, floaters, pre-breeders $\star = \{a, f, r\}$.
- $S_{\star,i,t}$: Linear predictor for survival function of adults, floaters, pre-breeders $\star = \{a, f, r\}$.
- $b_{i,t}$: Per capita breeding success of animals in colony i, at time t.
- $q_{i,t}$: Net recruitment of floaters into breeding population.
- $\pi_{i \to j}$: The probability that an individual born in the i^{th} colony joins the pool of recruits of the j^{th} colony.
- $\varphi_{i \to j}$: The strength of density dependence effect of the i^{th} on the breeding success of individuals in the j^{th} colony.

- $f(d)$: The kernel that determines how relocation of pre-breeders varies with distance between two colonies.

- δ_{ij}: Indicator function for on- and off-diagonal elements of square pairwise colony matrix.

Parameters

- ρ_0: Coefficient of baseline probability of recruitment at zero density.
- ρ_A: The strength of the Allee effect (depensatory density dependence)
- $\rho_{C,i}$: Crowding coefficient (compensatory density dependence).
- $\sigma_{\star,0}$: Baseline survival in linear predictor scale (intercept) fof each of three classes.
- $\sigma_{\star,m}$: Coefficient of the m^{th} covariate of survival.
- σ: Standard deviation parameter for random effect on survival.
- P_A: Allee effect threshold population.
- $P_{C,i}$: Local carrying capacity of a colony.
- β_0: Baseline breeding success (linear predictor).
- β_D: Density dependence at sea (competition between colonies).
- $\beta_{m,i}$: Coefficient of m^{th} covariate at a colony.
- β: The standard deviation of the random effect on breeding.
- δ_φ: Distance decay parameter for the effect of competition between colonies.
- δ_π: Distance decay parameter for the exchange of recruits between colonies.

17 Appendix II: A model for compensatory and depensatory density dependence.

Depensatory density dependence is represented by an unstable equilibrium (P_A) that can be considered as the extinction population threshold- the population size below which a colony does not survive without external subsidies. Compensatory density dependence is represented by a stable equilibrium (P_C) - the population's carrying capacity. This is the local carrying capacity, that relates to availability of breeding habitat, not foraging habitat (which is considered in the breeding density dependence part of the model). Note that the stability properties of these two equilibria are assumed, not guaranteed. For instance, judiciously selecting the population's vital rates to favour extinction, would make the P_C equilibrium unstable. We will revisit these requirements later in this appendix, to constrain the parameters ρ.

We wish to derive a formulate linking the depensatory and compensatory equilibria of the system to the regression parameters $\rho_0, \rho_A, \rho_{C,i}$ in the linear predictor of the recruitment probability (see also eq. (7)):

$$\begin{aligned} Q_{i,t} &= \rho_0 + \rho_A P_{i,t} - \rho_{C,i} P_{i,t}^2 \\ q_{i,t} &= logit^{-1}(Q_{i,t}) \end{aligned} \tag{22}$$

The required relationships must refer to a population receiving no subsidies and experiencing no resource limitations at sea. We are interested in the steady states of the population, so we will exclude stochasticity and variability in the demographic rates from the considerations below. We therefore begin by considering an isolated population undergoing deterministic dynamics. In this case, eqs (1) simplify to:

$$\begin{aligned} P_{t+1} &= s_a P_t + s_a q_{i,t} F_t \\ F_{t+1} &= s_f (1 - q_{i,t}) F_t + b s_r P_{t-3} \end{aligned} \tag{23}$$

Denoting by (P, F) the equilibria of the system and q_E the probability of recruitment at equilibrium, we obtain the system of equations

$$\begin{aligned} P &= s_a P + s_a q F_t \\ F &= s_f (1 - q) F + b s_r P \end{aligned} \tag{24}$$

We can solve this to find the characteristic recruitment rate at equilibrium in terms of constant demographic rates:

$$q_E = \frac{(1 - s_a)(1 - s_f)}{b s_a s_r - s_f + s_a s_f} \tag{25}$$

Using eqs (22) we set

$$Q_E = \ln\left(\frac{q_E}{1 - q_E}\right) = \rho_0 + \rho_A P_t - \rho_C P_t^2 \tag{26}$$

We introduce the following two temporary variables

$$\beta = -\frac{\rho_A}{\rho_C} \quad , \quad \gamma = -\frac{\rho_0 - Q_E}{\rho_C} \tag{27}$$

which simplifies eq. (26) to the following quadratic in P:

$$P^2 + \beta P + \gamma = 0 \tag{28}$$

Now, since both P_A and P_C are required to be system equilibria, they must both satisfy the equations:

$$\begin{aligned} P_A^2 + \beta P_A + \gamma = 0 \\ P_C^2 + \beta P_C + \gamma = 0 \end{aligned} \tag{29}$$

Which has the solution

$$\beta = -(P_A + P_C) \quad , \quad \gamma = P_A P_C \tag{30}$$

Substituting back eqs (27) gives expressions for two out of the ρ parameters in terms of the third:

$$\begin{aligned} \rho_A &= (Q_E - \rho_0)\frac{(P_A + P_C)}{P_A P_C} \\ \rho_C &= (Q_E - \rho_0)\frac{1}{P_A P_C} \end{aligned} \tag{31}$$

In order for the system to have the stability properties assumed at the start of this Appendix (and throughout the report), we require that $\rho_A, \rho_C > 0$, and hence (from eqs (31), (25) and (26)) that:

$$\rho_0 < \text{logit}\left(\frac{(1 - s_a)(1 - s_f)}{b s_a s_r - s_f + s_a s_f}\right) \tag{32}$$

18 Appendix III: JAGS listing for connectivity analysis using the BTO transitions data

```
###### Model statement ######
NatDisp<-  "model{

  # Connectivity vector
  for(i in 1:origins)
  {
    for(j in 1:noCols)
    {
    p[i,j]<-(c^home[i,j])*exp(-(deltaf*BTOd[i,j]))

    }
    ### Likelihood ###
    # Multinomial likelihood under vector p
    BTOt[i,1:noCols]~dmulti(p[i,1:noCols],nTrans[i])
  }

 ### Priors ###
  # Connectivity
  deltaf~dgamma(1,100) # Decay parameter (non-negative)

  # zero Inflation
  cDum~dgamma(10,10)
  c<-1+cDum        #Parameter c, cannot be less than 1

  #data# noCols, home, origins, nTrans, BTOd, BTOt
  #monitor# c, deltaf
  #inits# cDum, deltaf
}"


######################################################## Model Running ###


nTrans<-rowSums(BTOtrans)# Total number of transitions
ids<-nTrans>0 # Looks for rows that have ringed birds at origin
nTrans<-nTrans[ids]
BTOt<-BTOtrans[ids,] # Selects transition counts rows
BTOd<-btoDM[ids,] # Selects transition distances rows
origins<-length(nTrans) # Number of colonies with ringing effort
inds<-(1:origins)[ids] # records the indexes of rows with rings
home<-1*(BTOd<1)# Occurrences of near-zero distance from origin
noCols<-ncol(BTOt)
```

```r
# Initialisation of parameters for four chains
cDum<-list(chain1=.6,chain2=.10, chain3=.5, chain4=.20)
deltaf<-list(chain1=.001,chain2=.002, chain3=.0005, chain4=.006)

resultsDisp <- run.jags(NatDisp, n.chains=4, adapt=5000, burnin=5000,
                    sample=10000, thin=1, method="parallel")

su<-summary(resultsDisp)
```

19 Appendix IV: JAGS Code for metapopulation model

```
###### Model statement ######
kitti<-  "model{

# State variable initialization
for(i in 1:n)
{
  for(t in 1:4)
  {
    Pd[i,t]~dgamma(1,0.001)
    PopS[i,t]<-round(Pd[i,t])
    Fd[i,t]~dgamma(1,0.001)
    F[i,t]<-round(Fd[i,t])
  }

  for(t in 1:3)
  {
    sr[i,t]~dbeta(1,1)
    births[i,t]~dpois(1.1*PopS[i,t])
  }

}



# Connectivity effects
for(i in 1:n)
{
  for(j in 1:n)
 {
    de[i,j]<-exp(-delf*DM[i,j]) # Depletion interference matrix.
    piU[i,j]<-cc^delij[i,j]*exp(-delp*DM[i,j]) # dg from pre-analysis above
    pi[i,j]<-piU[i,j]/sum(piU[i,1:n])
 }
}

############ PROCESS MODEL ###################
for(t in 4:(Tmax-1))
{
  # At-sea density dependence (effective population size of competitors)
  comp[1:n,t]<-PopS[1:n,t]%*%de
  newF[1:n,t]<-Rmat[1:n,t]%*%pi

  for(re in 1:6)
  {
    psi[re,t]~dnorm(0,1/siPsi^2)
```

```
    eps[re,t]~dnorm(0,1/siEps^2)
  }

  for(i in 1:n)
  {
    #################### Breeding #######################

    b[i,t]<-exp(b0L[region[i]]-bD*comp[i,t]+psi[region[i],t])
    births[i,t]~dpois(b[i,t]*PopS[i,t])

    ################### Recruitment ######################
    logit(q[i,t])<-rho0+rhoA[i]*PopS[i,t]-rhoC[i]*PopS[i,t]^2
    recruits[i,t]<-q[i,t]*F[i,t]

    ##################### Survival #######################


    # Breeder survival
    logit(sa[i,t])<-sa0L[region[i]]+eps[region[i],t]
    survA[i,t]<-sa[i,t]*PopS[i,t] # Survivor resident adults

    # Sub-adult survival
    logit(sr[i,t])<-sr0L[region[i]]+eps[region[i],t]
    survRec[i,t]<-sr[i,t]*recruits[i,t] # Survivor new recruits

    # Floater survival
    logit(sf[i,t])<-sf0L[region[i]]+eps[region[i],t]
    floats[i,t]<-max(0,F[i,t]-recruits[i,t])
    survF[i,t]<-sf[i,t]*floats[i,t] # Survivor floaters

    ###################### Maturity ######################
    srcum[i,t]<-sr[i,t-3]*sr[i,t-2]*sr[i,t-1]
    Rmat[i,t]<-srcum[i,t]*births[i,t-3]

    ################## Update Equations ###################
    Pod[i,t]~dgamma(theta,theta)
    PopS[i,t+1]~dpois(Pod[i,t]*(survA[i,t]+survRec[i,t])) # Breeders
    Fod[i,t]~dgamma(theta,theta)
    F[i,t+1]~dpois(Fod[i,t]*(survF[i,t]+round(newF[i,t]))) # Floaters

    ################## Observation model for pop size##################
    colPop[i,t]~dnorm(PopS[i,t], 1/(0.00000001+PopS[i,t]*0.1)^2)

  }

  breedingSuc[t]<-sum(b[1:n,t])/n
  survival[t]<-sum(sa[1:n,t])/n
```

```
    ############# Tracking pops and demo, by region ############
  for(i in 1:6)
  {
    regBreed[i,t]<-sum(b[regM[i,1:regL[i]],t])/regL[i]
    regSurvA[i,t]<-sum(sa[regM[i,1:regL[i]],t])/regL[i]
    regPop[i,t]<-sum(PopS[regM[i,1:regL[i]],t])/regL[i]
  }


  ########## Observation model for survival data ###########

  for(i in 1:ns)
  {

    adSurvs[t,i]~dnorm(sa[nsns[i],t],1/(0.00000001+sa[nsns[i],t]*0.1)^2)
  }

 ########## Observation model for fecundity data ###########
  for(i in 1:nb)
  {
    fledge[i,t]~dpois(b[i,t]*count[i,t])
  }

}

for(i in 1:n)
{
  recies[i]<-recruits[i,Tmax-1]
  propRecs[i]<-recies[i]/sum(recies[1:n])
}





###### PRIORS #########

# Demographic parameters, by region
templ<-50

for (i in 1:6)
{
  # Baseline fecundity (female chicks)
  b0dum[i]~dbeta(templ,templ)
  b0[i]<-0.3+b0dum[i]*0.06
  b0L[i]<-log(b0[i]) # Baseline fecundity (in linear predictor)
```

```
  # Baseline adult survival
  sa0dum[i]~dbeta(templ,templ)
  sa0[i]<-0.8+0.04*sa0dum[i]
  sa0L[i]<-log(sa0[i]/(1-sa0[i]))

  # Baseline adult non-breeder survival
  sf0dum[i]~dbeta(templ,templ)
  sf0[i]<-0.74+0.04*sf0dum[i]
  sf0L[i]<-log(sf0[i]/(1-sf0[i]))

  # Baseline juv survival
  sr0dum[i]~dbeta(templ,templ)
  sr0[i]<-0.65+0.04*sr0dum[i]
  sr0L[i]<-log(sr0[i]/(1-sr0[i]))

}

# Random effects
siPsi~dbeta(1,5) # Standard deviation for breeding
siEps~dbeta(1,5) # Standard deviation for survival

# Density-dependence in fecundity
bD~dbeta(1,50000) # Crowding

# Recruitment parameters
for(i in 1:n)
{
  Pcd[i]~dgamma(1,0.0001)
  Pc[i]<-Pa+Pcd[i]  # Carrying capacities for each population
}

Pa~dgamma(10,0.1)  # Allee effect threshold population size (same for all)
qE<-min(0.999999999999,max(0.00000000001,(1-sa0)*(1-sf0)/(b0*sa0*sr0-sf0+sa0*sf0)))
QE<-log(qE/(1-qE))
rho0D~dgamma(10,10)
rho0<- QE-rho0D #Baseline recruitment rate on linear predictor
for(i in 1:n)
{
  rhoA[i]<- (QE-rho0)*(Pa+Pc[i])/(Pa*Pc[i])# Allee effect
  rhoC[i]<- (QE-rho0)*1/(Pa*Pc[i])# Local crowding effect
}


# Prospecting matrix parameters
mu[1]<-3.174
mu[2]<--5.714
vi[1,1]<-0.00257
```

```
vi[2,2]<-0.00179
vi[1,2]<- -0.0007473
vi[2,1]<- -0.0007473
x[1:2]~dmnorm.vcov(mu[1:2],vi[1:2,1:2])
cc<-exp(x[1])+1
delp<-exp(x[2])

delf~dbeta(8.7,281.3) # Distance-decay parameter for colony intereferences

# Overdispersion Parameters
thetaDum~dbeta(1,10)
theta<-10+1000*(1-thetaDum)

#data# n, Tmax, DM, delij, adSurvs, ns, colPop, nsns, nb, fledge, count, region, regM, regL
#monitor# b0, sa0,sf0,sr0,bD,rho0, cc,delp,delf,Pa,Pc,PopS,propRecs
#monitor# breedingSuc,survival, siPsi, siEps, theta, regBreed, regSurvA, regPop

}"
```

20 Appendix V: Prior-posterior plots from model without covariates

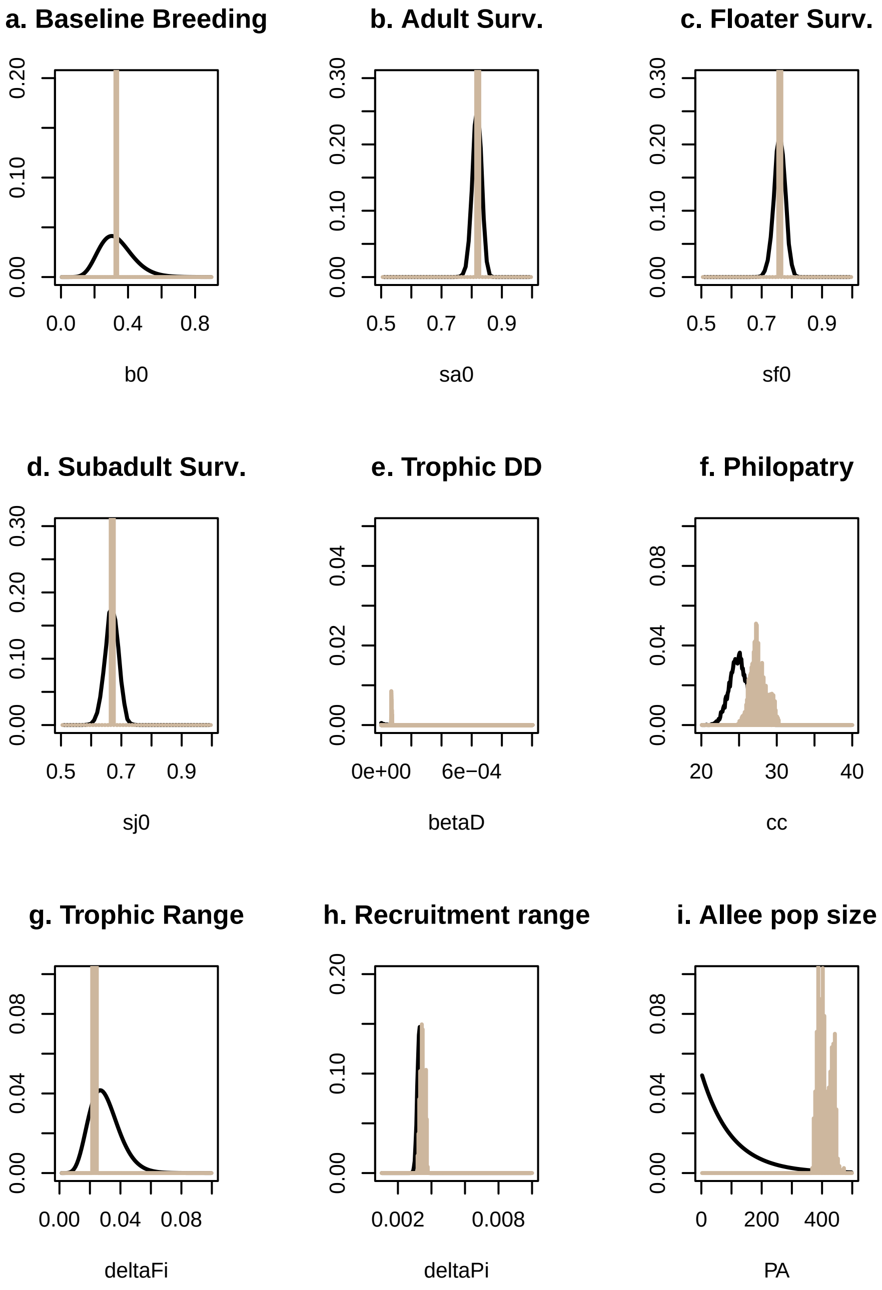
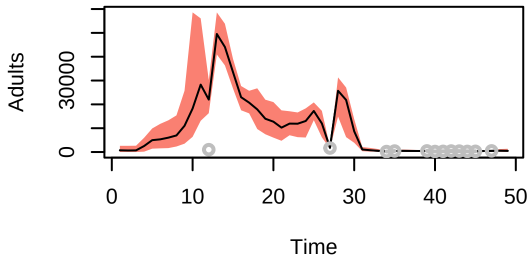


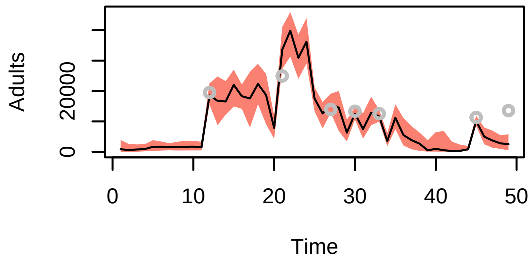
Figure 22: Prior (black curves) and posterior (brown histograms) distributions for the nine key model parameters.

21 Appendix VI: Reconstructed population trajectories, by colony

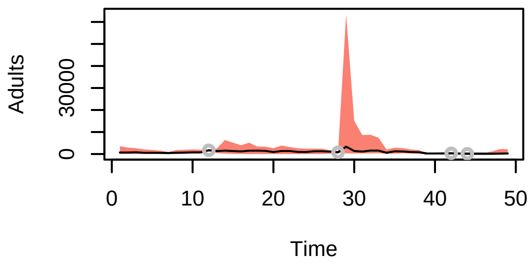
Ailsa Craig SPA



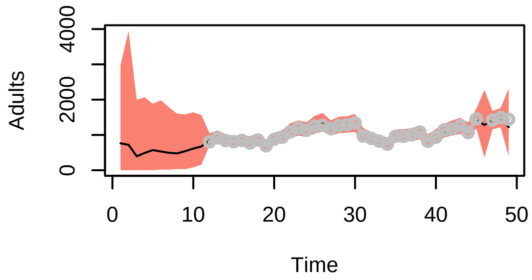
Buchan Ness to Collieston Coast SPA



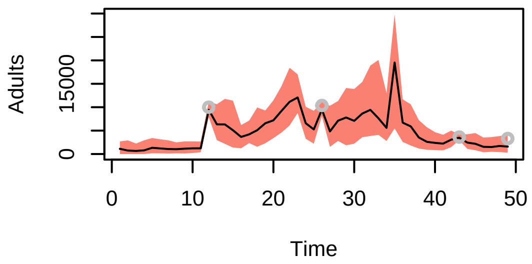
Calf of Eday SPA



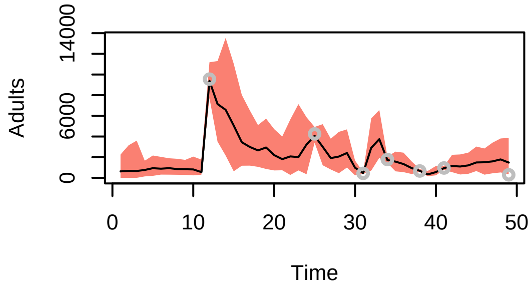
Canna and Sanday SPA



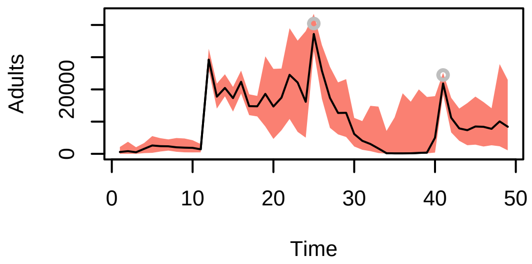
Cape Wrath SPA



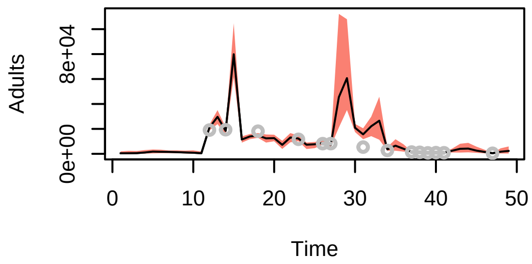
Copinsay SPA



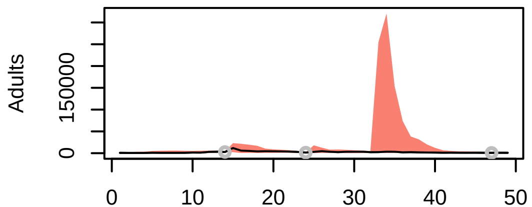
East Caithness Cliffs SPA



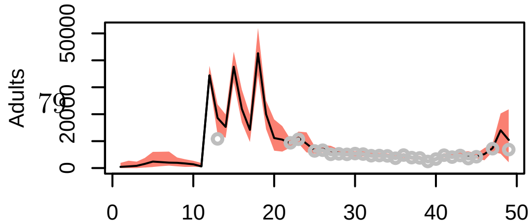
Fair Isle SPA

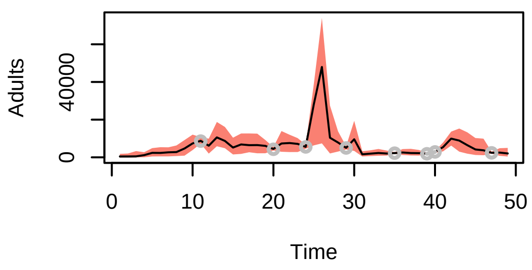


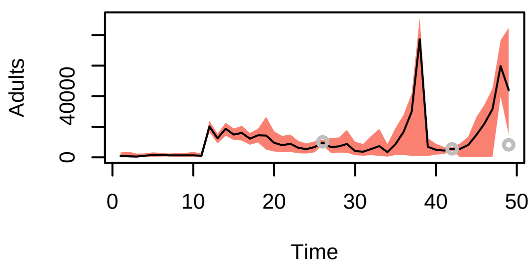
Flannan Isles SPA

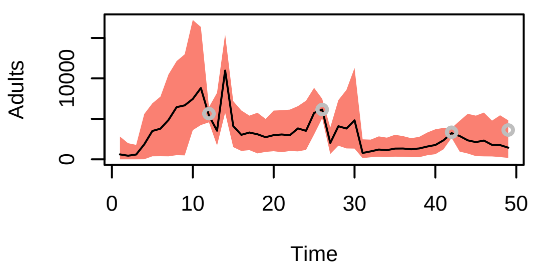


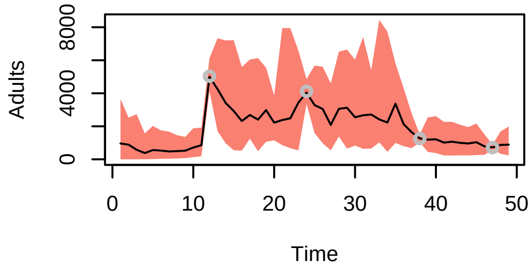
Forth Islands SPA

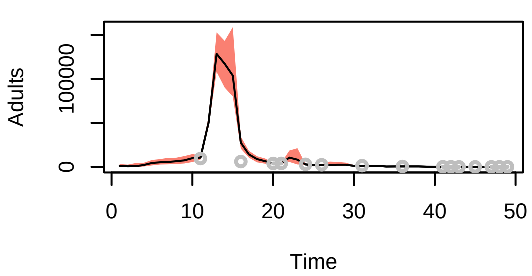


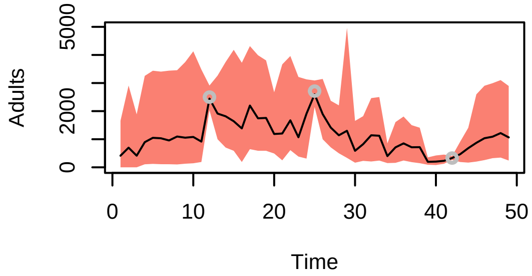

Mingulay and Berneray SPA


North Caithness Cliffs SPA


North Colonsay and Western Cliffs SPA


North Rona and Sula Sgeir SPA


Noss SPA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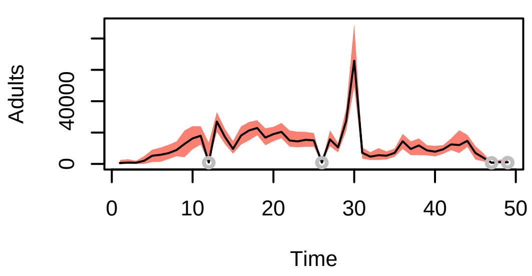
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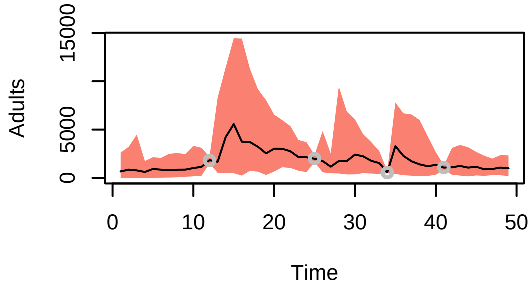
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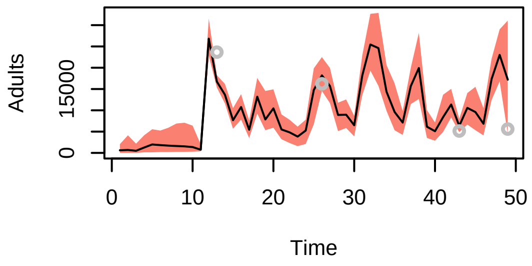
St Abb's Head to Fast Castle SPA



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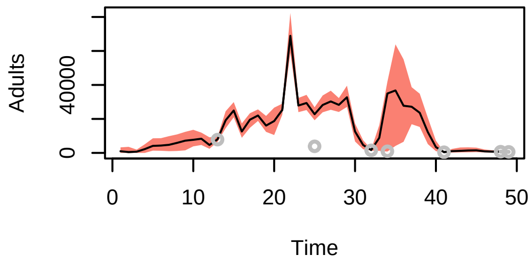
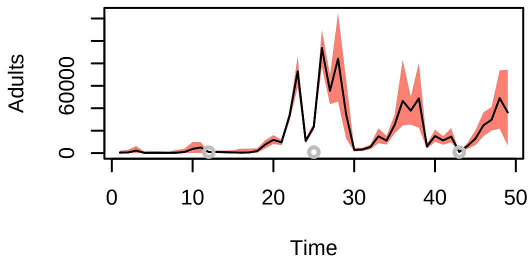
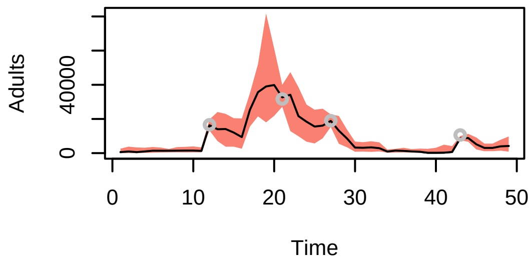


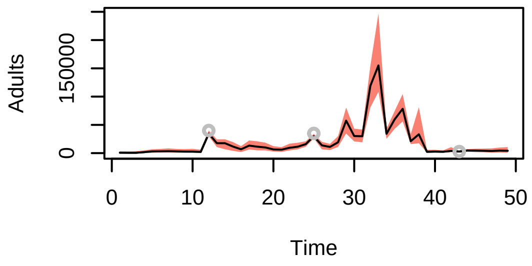
Sumburgh Head SPA



Troup, Pennan and Lion's Heads SPA



West Westray SPA



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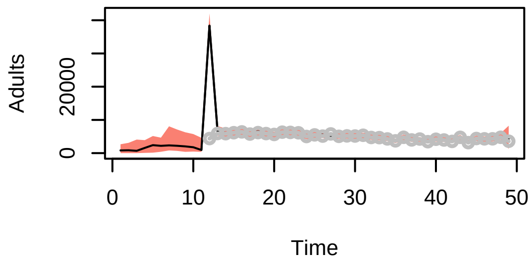
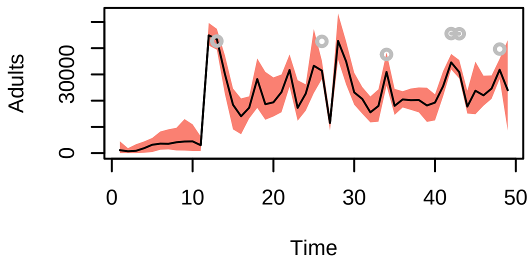


Flamborough and Filey Coast SPA



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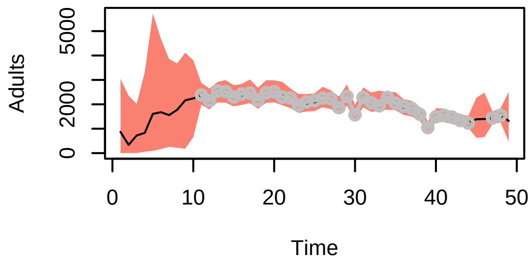

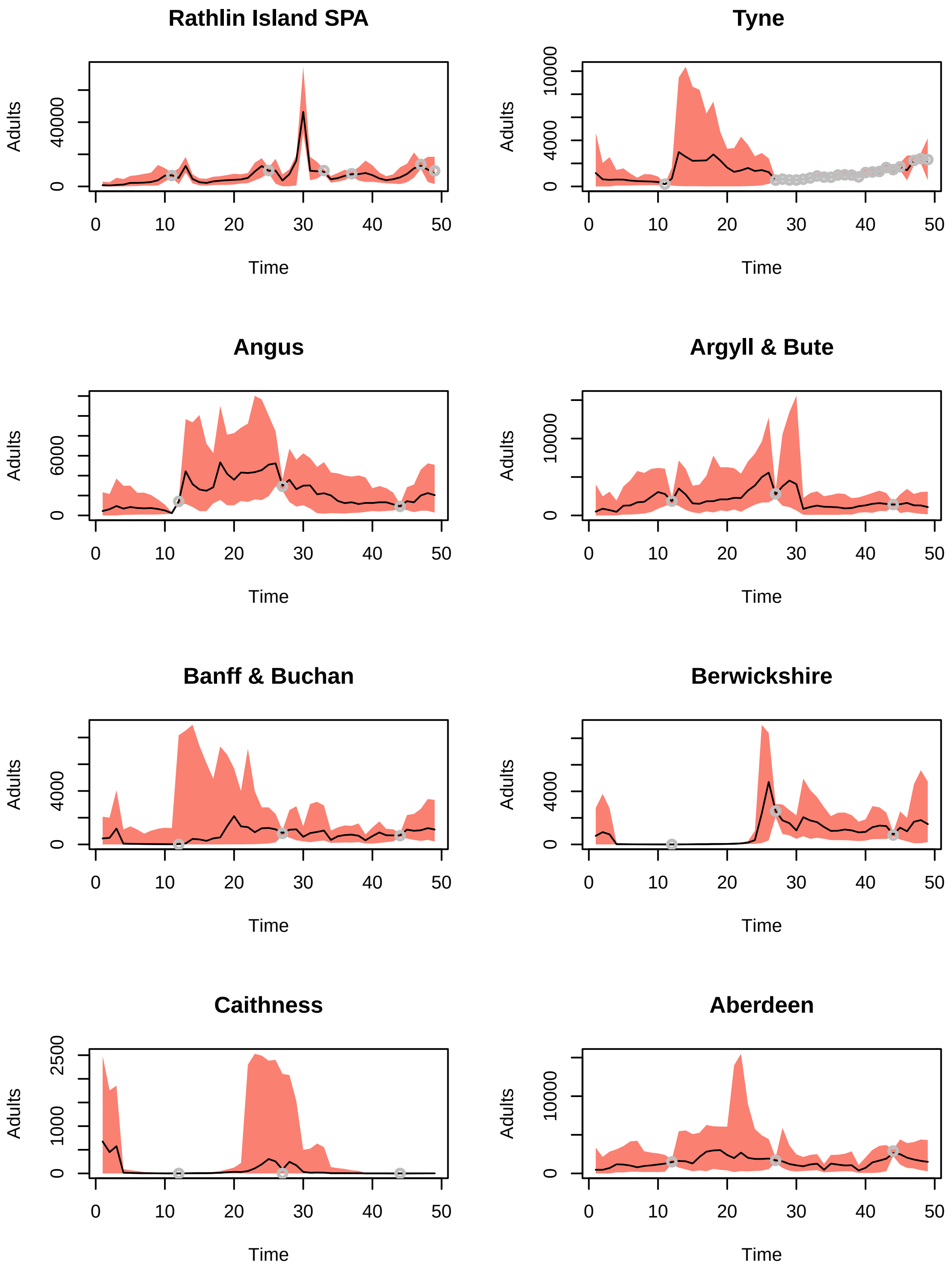
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Time
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Tyne
Adults
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Time
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10
20
30
40
50
Angus
Adults
0
6000
Time
0
10
20
30
40
50
Argyll & Bute
Adults
0
10000
Time
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20
30
40
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Banff & Buchan
Adults
0
4000
Time
0
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20
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40
50
Berwickshire
Adults
0
4000
Time
0
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20
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Caithness
Adults
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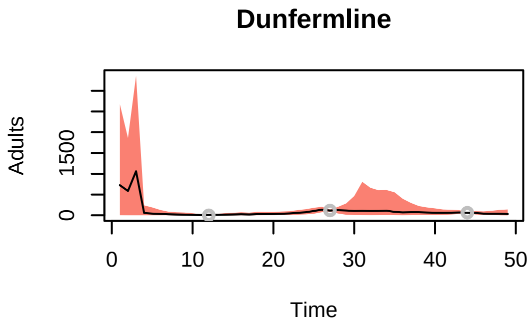
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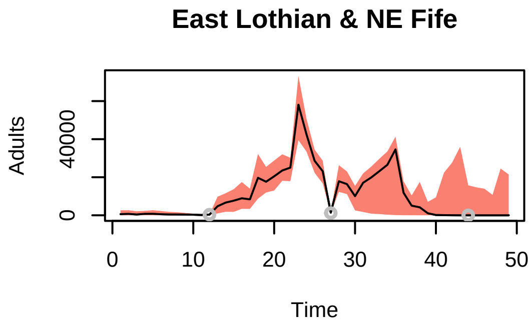
East Lothian & NE Fife
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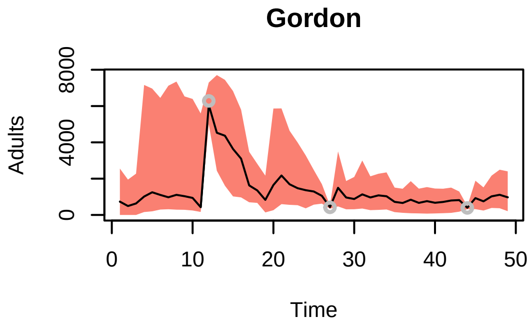
Time


Gordon
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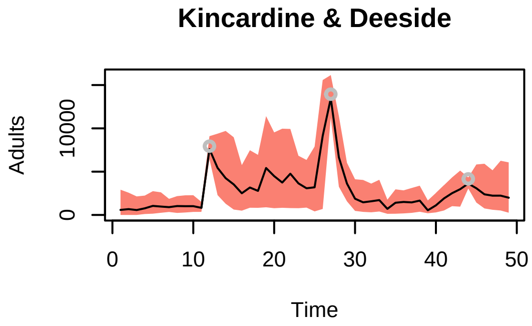
Time


Kincardine & Deeside
Adults
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10000
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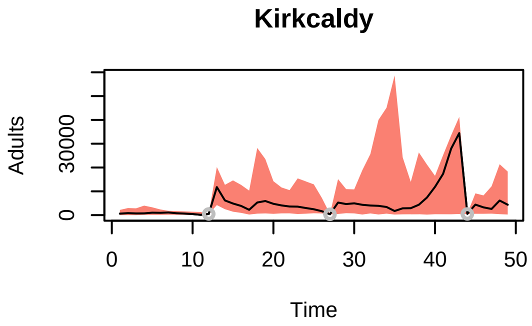
Time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Adults
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30000
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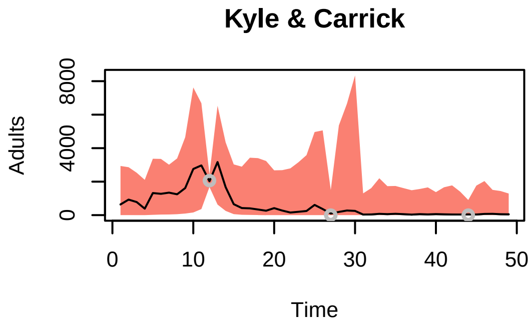
Time


Kyle & Carrick
Adults
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4000
8000
0
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20
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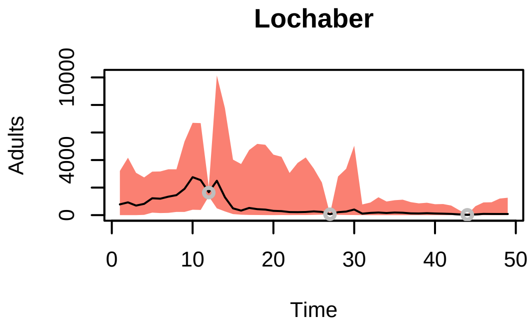
40
50
Time


Lochaber
Adults
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10000
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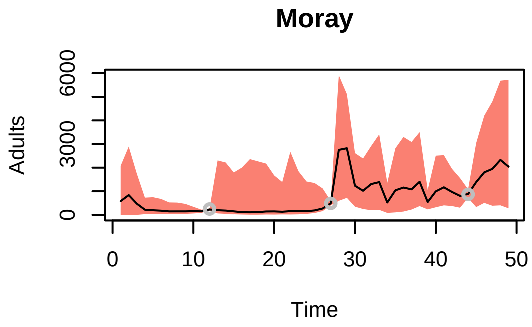
Time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Adults
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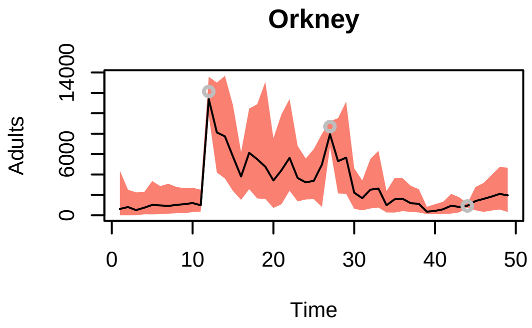
50
Time


Orkney
Adults
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14000
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30
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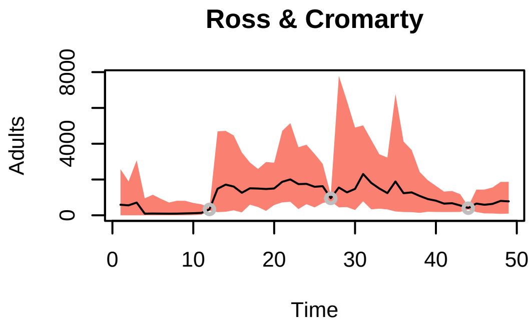
50
Time


Ross & Cromarty
Adults
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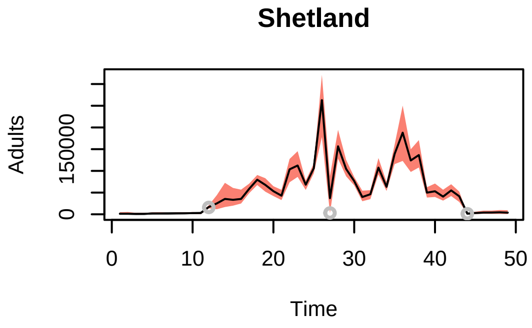
Time


Shetland
Adults
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150000
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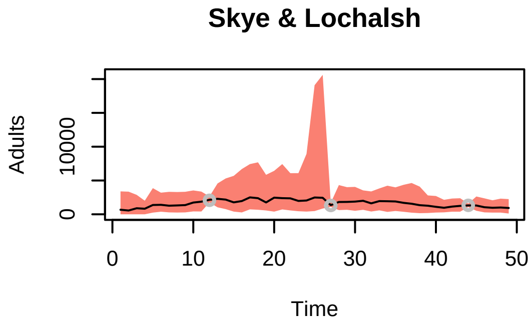
Time


Skye & Lochalsh
Adults
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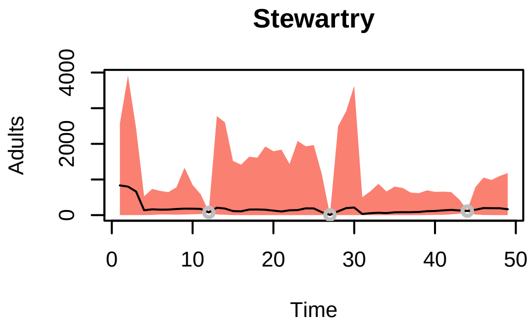
20
30
40
50
Time


Stewartry
Adults
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4000
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20
30
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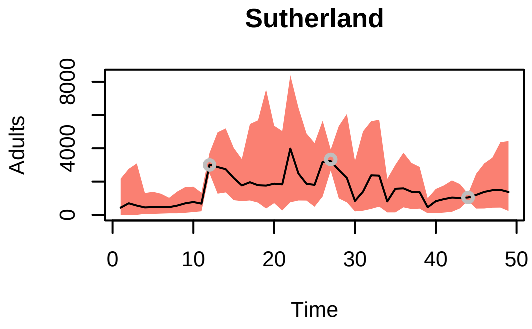
50
Time


Sutherland
Adults
0
4000
8000
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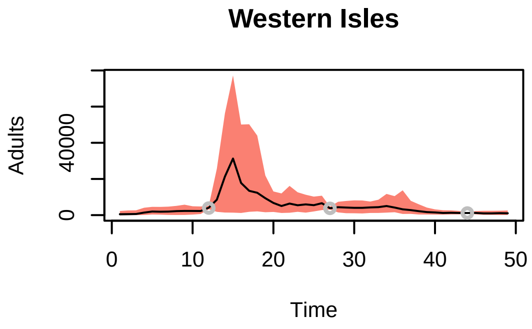
20
30
40
50
Time


Western Isles
Adults
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40000
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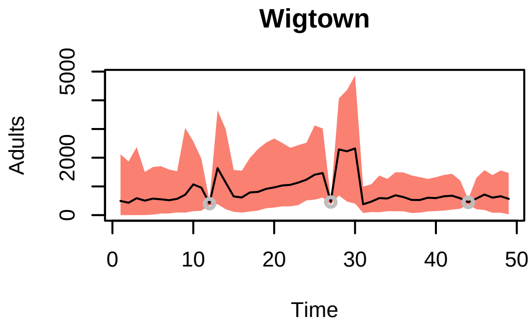
20
30
40
50
Time


Wigtown
Adults
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5000
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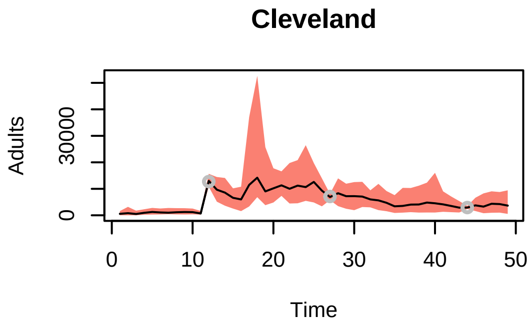
20
30
40
50
Time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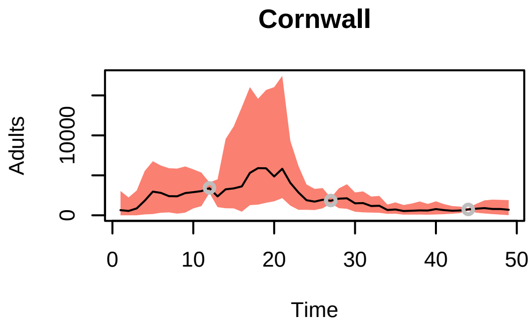
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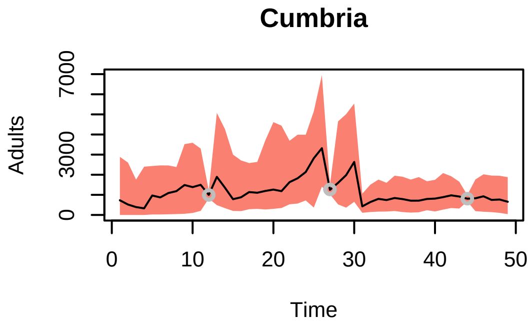
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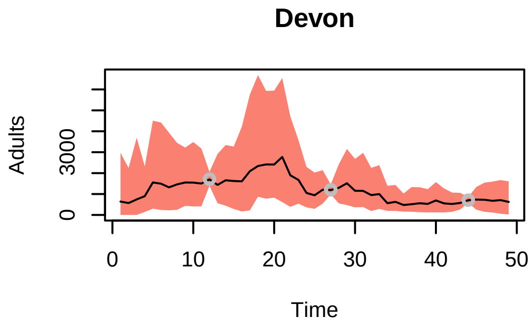
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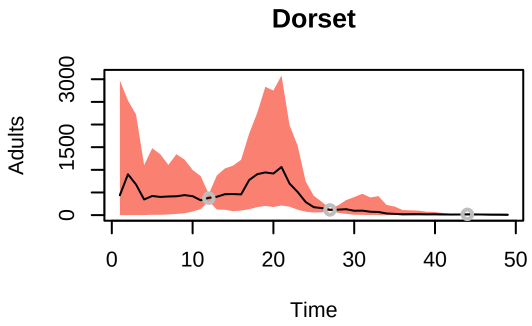
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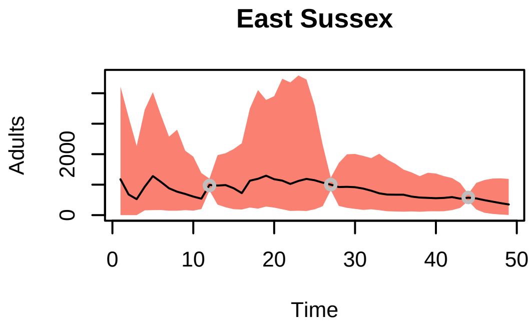
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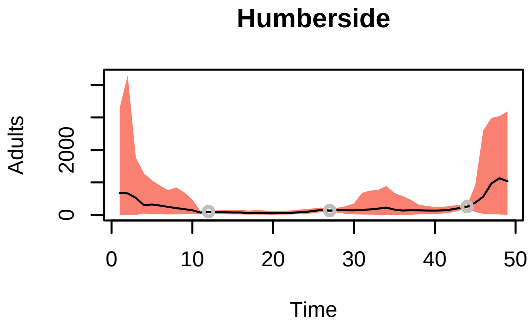
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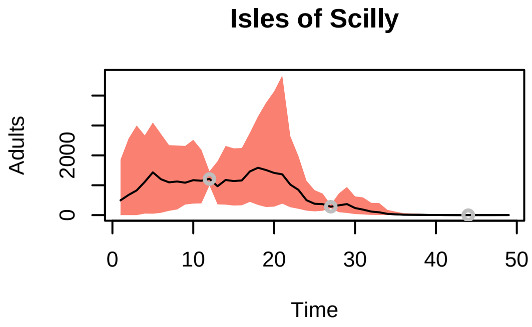
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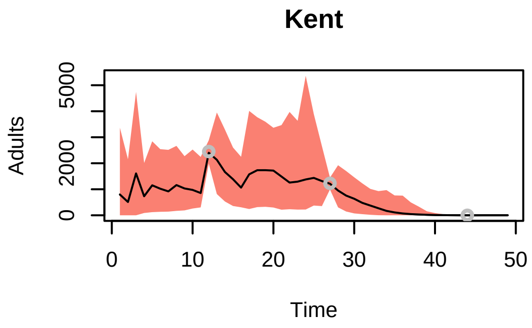
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Adults
0
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5000
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10
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30
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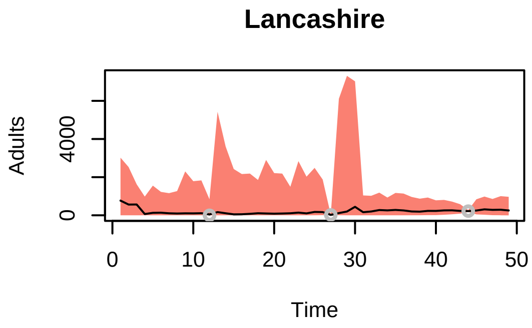
50
Time


Lancashire
Adults
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4000
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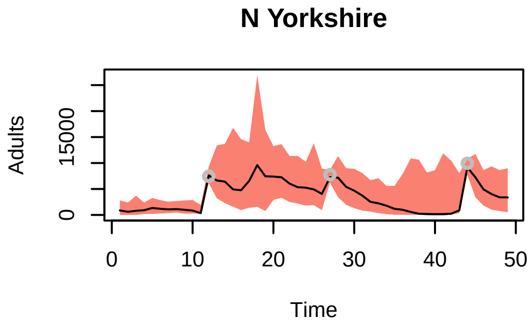
Time


N Yorkshire
Adults
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15000
0
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30
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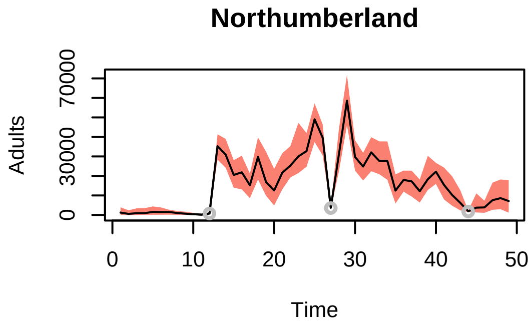
50
Time


Northumberland
Adults
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70000
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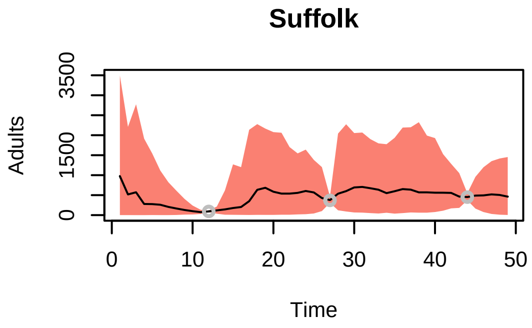
50
Time


Suffolk
Adults
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3500
0
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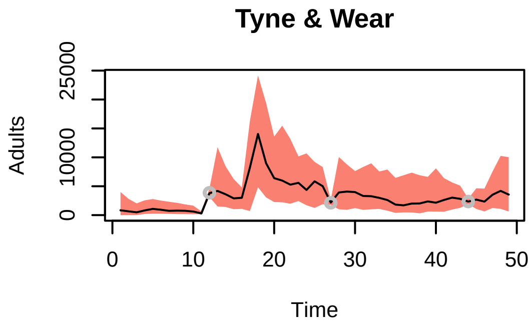
20
30
40
50
Time


Tyne & Wear
Adults
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25000
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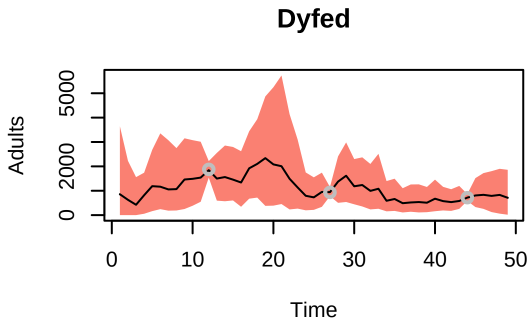
50
Time


Dyfed
Adults
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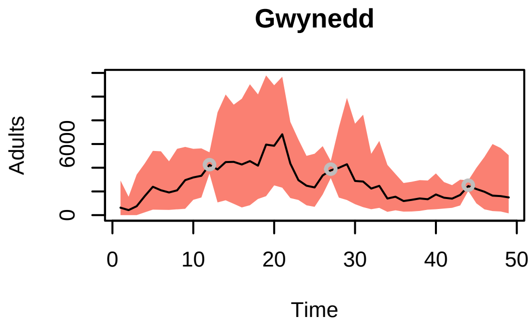
5000
0
10
20
30
40
50
Time


Gwynedd
Adults
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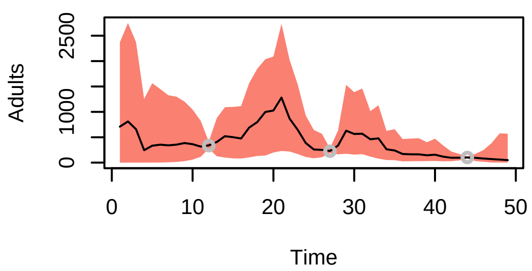
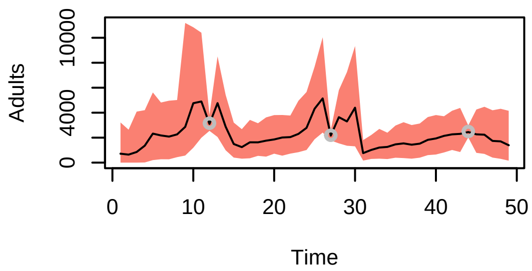
6000
0
10
20
30
40
50
Time



West Glamorgan



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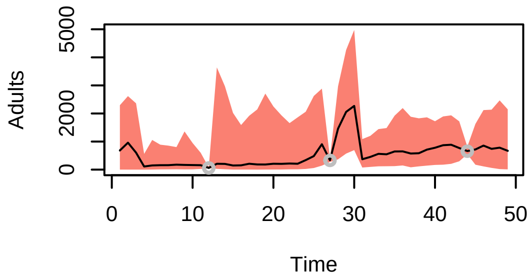

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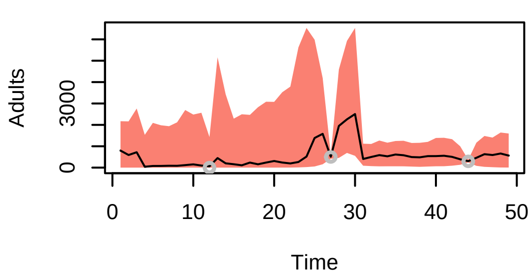

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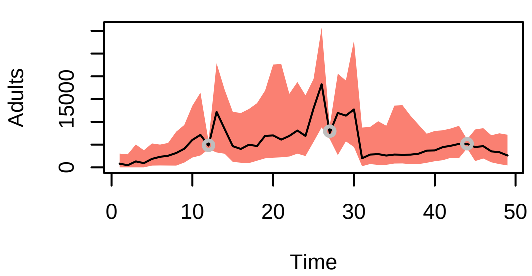

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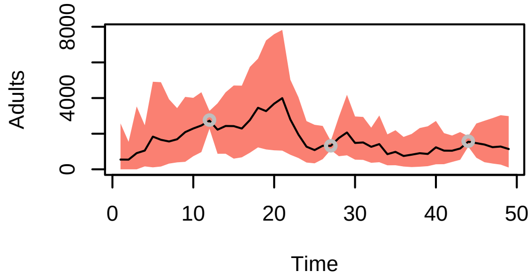
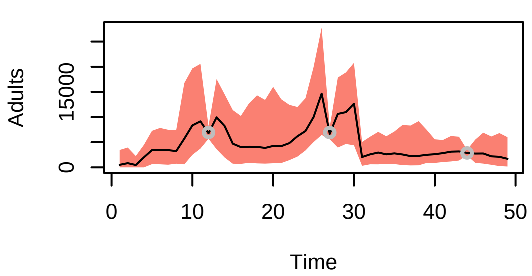
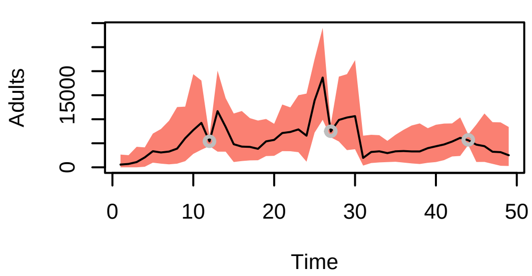


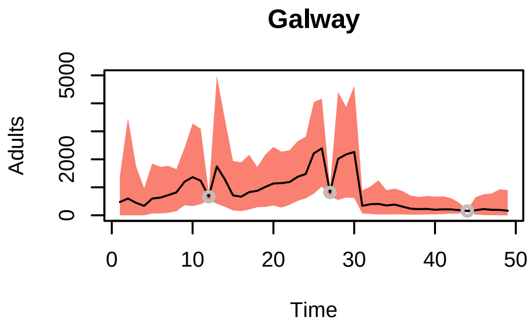
Cork



Donegal



Dublin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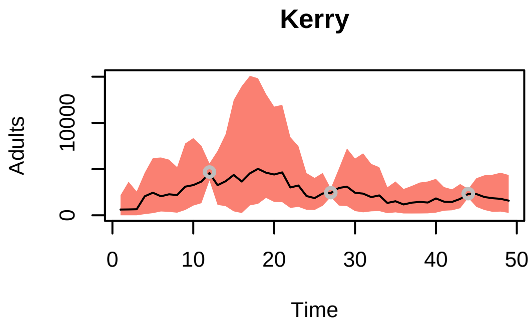
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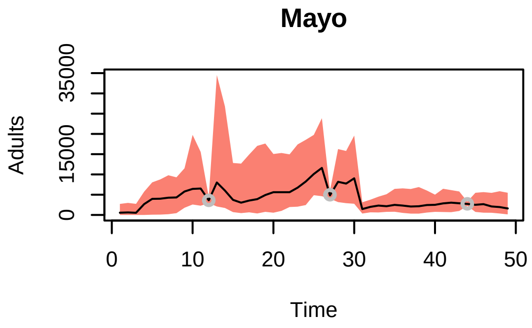
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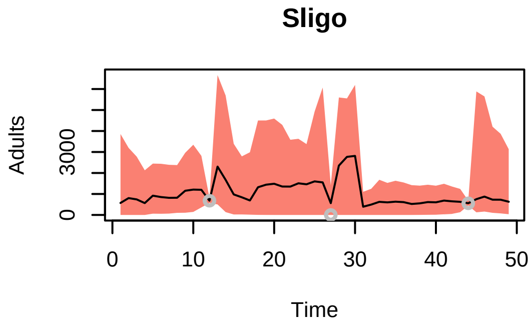
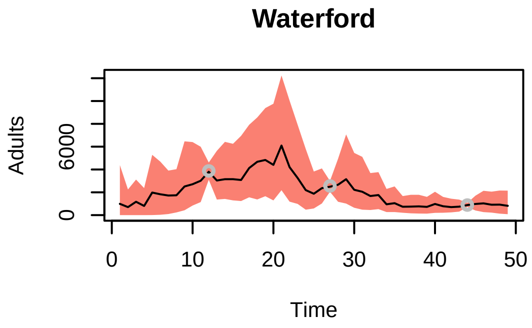
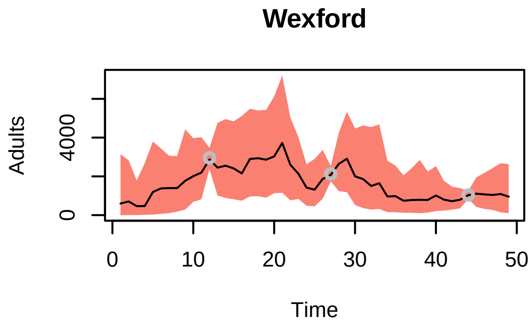
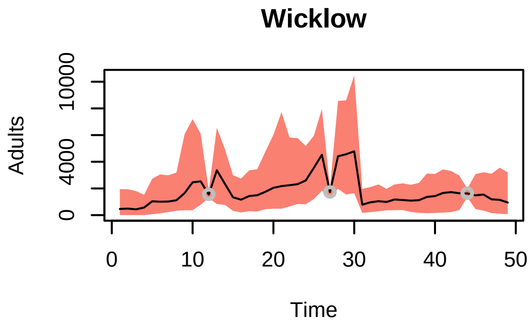
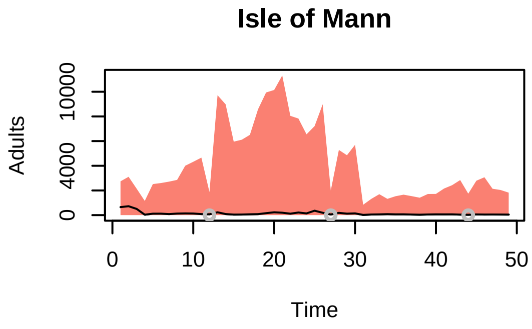
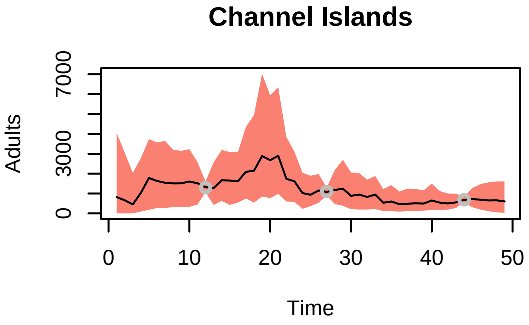

Sligo


Waterford


Wexford


Wicklow


Isle of Mann


Channel Islands
Adults
0
3000
7000
0
10
20
30
40
50
Time

22 Appendix VI: R code for simulation

This is a translation of the JAGS code into R, aimed at using the JAGS coda parameters for running simulations from the fitted model.

```
### Arguments

# Input states
# PopSI:  Initial population sizes for dtm years. A (n-by-dtm) matrix,
#         where dtm is the number of years to maturity.
# FlI: Initial number of floaters for dtm years. A (n-by-dtm) matrix,
#      where dtm is the number of years to maturity.
# srI: Survival of subadults in first dtm years. A (n-by-dtm) matrix,
#      where dtm is the number of years to maturity. Defaults to 0.8 if not given.
# births: Births by colony in first dtm years. A (n-by-dtm) matrix,
#      where dtm is the number of years to maturity. Defaults to 10 if not given.

# Input data
# DM: The nxn matrix of distances between colonies

# Parameters
# Tmax: The number of years for which simulation will be run
# delf: The depletion interference parameter
# delp: The connectivity parameter
# cc: The philopatry parameter
# siPsi: Stdev for breeding random effect
# siEps: Stdev for survival random effect
# rho0: Recruitment intercept
# Pa: Estimated Allee effect parameter
# Pc: Estimated carrying
# b0L: Breeding success intercept (a vector,length the number of colonies)
# bD: Density dependence in fecundity
# sa0L: Adult survival intercept (a vector,length the number of colonies)
# sr0L: Sub-adult survival intercept (a vector,length the number of colonies)
# sf0L: Floater survival intercept (a vector,length the number of colonies)
# theta: Parameter for overdispersion


 ###### Model statement ######
  kittiSim<-function(PopSI, FlI=1000, srI=0.8, birthsI=1000,
                     DM, region, nreg=6,
                     Tmax, delf, delp, cc, siPsi, siEps, rho0, Pa, Pc, b0,
                     bD, sa0, sr0, sf0, theta)
  {
  n<-nrow(PopSI)  # Number of colonies
  dtm<-ncol(PopSI) # Years to maturity
  sa0L<-as.numeric(log(sa0/(1-sa0)))
  sf0L<-as.numeric(log(sf0/(1-sf0)))
```

```
sr0L<-as.numeric(log(sr0/(1-sr0)))

b0L<-as.numeric(log(b0))

# Initialization
PopS<-Fl<-births<-sr<-matrix(0, nrow=n, ncol=Tmax)
PopS[1:n,1:dtm]<-PopSI
Fl[1:n,1:dtm]<-FlI
sr[1:n,1:dtm]<-srI
births[1:n,1:dtm]<-birthsI

# Connectivity effects
de<-exp(-delf*DM) # Depletion interference matrix.
delij<-diag(n)
piU<-cc^delij*exp(-delp*DM) # dg from pre-analysis above
pi<-piU/rowSums(piU)
qE<-pmin(0.999999999999,pmax(0.00000000001,(1-sa0)*(1-sf0)/(b0*sa0*sr0-sf0+sa0*sf0)))
QE<-log(qE/(1-qE))
# Density dependence parameters
rhoA<- (QE-rho0)*(Pa+Pc)/(Pa*Pc)# Allee effect
rhoC<- (QE-rho0)*1/(Pa*Pc)# Local crowding effect

############ PROCESS MODEL ###################
for(t in dtm:(Tmax-1))
{
  # At-sea density dependence (effective population size of competitors)
  comp<-PopS[,t]%*%de


  #################### Breeding ########################
  psi<-rnorm(nreg,0,siPsi)
  b<-exp(b0L-bD*comp+psi[region])
  births[,t]<-rpois(n,b*PopS[,t])

  ################### Recruitment ######################
  Lq<-pmin(100, rho0+rhoA*PopS[,t]-rhoC*PopS[,t]^2)
  q<-exp(Lq)/(1+exp(Lq))
  recruits<-q*Fl[,t]

  ##################### Survival #######################
  eps<-rnorm(nreg,0,siEps)

  # Breeder survival
  Ls<-sa0L+eps[region]
  sa<-exp(Ls)/(1+exp(Ls))
  survA<-round(sa*PopS[,t]) # Survivor resident adults
```

```
    # Sub-adult survival
    Ls<-sr0L+eps[region]
    sr[,t]<-exp(Ls)/(1+exp(Ls))
    survRec<-sr[,t]*recruits # Survivor new recruits

    # Floater survival
    Ls<-sf0L+eps[region]
    sf<-exp(Ls)/(1+exp(Ls))
    floats<-pmax(0,Fl[,t]-recruits)
    survF<-round(sf*floats) # Survivor floaters

    ############### Maturity & Dispersal ################
    srcum<-apply(sr[,(t-dtm+1):(t-1)], 1, prod)
    Rmat<-round(srcum*births[,t-dtm+1])
    newF<-Rmat%*%pi

    ################## Update Equations ###################
    Pod<-rgamma(n,theta,theta)
    PopS[,t+1]<-rpois(n, Pod*(survA+survRec)) # Breeders
    Fod<-rgamma(n,theta,theta)
    Fl[,t+1]<-rpois(n,Fod*(survF+newF)) # Floaters

  }

return(list(PopS,Fl))
}
```

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+44 (0) 20 7170 7000

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