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Regulation and Risk: Developing models to assess the dynamism of seabird populations and their risk from anthropogenic mortality

By

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For Sadie and Christine for teaching me faith and tenacity; For Ena and Steve for teaching me love and commitment; For Mum and Dad for giving me the freedom to follow my own path and for Bruno, my best boy.

Declaration

This thesis, and the work contained in it, was conducted from September 2015 until November 2019 by myself, unless stated otherwise. No part of this thesis has been submitted for another degree.

Julie Anne Ogilvie Miller

Abstract

In the face of expanding industry, the assessments undertaken to preserve biodiversity from damaging impacts from anthropogenic development require robust approaches that capture population processes, associated uncertainties and predict outcome scenarios with increased precision. The offshore wind industry has the potential to negatively impact upon UK seabird populations via additional mortality, but arguably has many benefits towards globally reduced carbon output. Here, I examine current practice in impact assessment of seabirds and by use of state-space integrated modelling approaches provide methods of estimating demographic processes in models fitted to commonly available empirical data. By provision of these estimates I then simulate outcomes of additional anthropogenic mortality to real populations.

In this way, in chapter two I find intrinsic (density-dependence) and extrinsic (environmental stochasticity) regulation operates differently in sympatric species, affecting population persistence under thresholds of regulation and exacerbated by additional mortality. I find consideration of basic connectivity (a rescue-effect) confers some reduction in the magnitude of impacts observed.

By investigation of the regulation of a vulnerable, declining species, I show in chapter three evidence of age-specific regulation, potentially a result of a trade-off between experience and breeding costs. I highlight important covariates of regulation for productivity and the difficulty in identifying drivers in survival.

The exclusion of connectivity of seabird populations is an important omission in population assessment. In chapter four I identify a region of potential connectivity and in a hierarchical state-space model, fitted to incomplete time-series of two demographic indicators (productivity and adult nests), estimate transfer probability between 84 sub-populations of a species on the Shetland archipelago. In subsequent stochastic simulations, I apply mock additional mortality to the region under various treatments, finding different spatial patterns of decline and persistence, comparative to the traditional closed approach.

Together, these studies provide methods and evidence for increased ability to predict unknown outcomes across a range of potential scenarios with increased reality and representative uncertainty. The results capture the importance of consideration of the ecology of the species during parameterisation of models to represent important demographic regulation (the three sympatric species, differently responding to regulation). The results also make a case for further consideration of differential magnitude of effect of regulation to each vital rate and finally, in concordance with metapopulation theory the results highlight sub-population persistence dynamics vary comparative to closed population outlooks. These findings have immediate application to population modelling and provide a general method and framework for further investigations of both population dynamics and forecasting persistence.

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Chapter 1: General Introduction

As the offshore renewables industry seeks to expand, the methodology used to assess the impacts of offshore wind farms (OWF) to seabird populations requires continued reduction in uncertainty and refinement of realism in theoretical approaches. I introduce here the general background of assessment of OWF in the UK. Summarising seabird life history and demography, I introduce the potential ways OWF may impact on a population and, briefly describe a sample of modelling approaches used by industry. I portray some evidence for, or difficulties in understanding, empirically, the potential impacts of OWF to seabirds at population level. This introduction culminates in specific aims to address uncertainty in modelling impacts to populations and estimate demographic processes for which we have knowledge gaps. By applying modelling techniques to demographic data at both the population and metapopulation level, these objectives are systematically researched in chapters 2-4 of this thesis. These chapters are presented in the format of papers, consequently each has their own detailed introduction and discussion. As such, the purpose of this general introduction is to present the central background to this project, building on themes and detailing specific concepts and investigations in population biology and vulnerability to anthropogenic mortality throughout ensuing data chapters. Finally, I present in chapter 5 a general discussion synthesizing concepts and findings from this work under the umbrella of population biology, population assessment and vulnerability to extinction from anthropogenic threats. I end with comment on both the potential and limitations of this work towards informing industry and assessing conservation risk to UK seabird populations.

1.1 Offshore wind: Policy and Industry

The UK is a world leader in offshore renewable energy development and deployment. The EU renewables directive (European Commission 2009) looks to attain 20% of European energy needs from renewables by 2020. Renewable developments in UK waters are evaluated under the requirements of an Environmental Statement (ES), in which a proposed development is evaluated as to its likely effects to the environment in an Environmental Impact Assessment (EIA). This process, governed by the precautionary principle (SNIFFER 2006), seeks to assess the risk of proposed developments both alone and in combination with other developments, for example, to populations of seabirds in the UK, but additionally in terms of transboundary connectivity. The seabirds of the UK are subject to protective EU and domestic legislation ((Birds 2009/147/EC Birds Directive); Fauna and Flora 1992/43/EEC (EU Habitats Directive); Nature conservation (Scotland) Act 2004; Wildlife and Countryside Act 1981 (as amended)). Designated sites termed, 'Special Protection Areas' (SPA) include seabird populations as designated features at a network of 92 SPAs in the UK (JNCC 2008). Across the EU, similarly designated sites exist to form the 'Natura 2000' network of SPAs and Special Areas of Conservation (SAC). Cumulative documented risk from offshore wind farms (OWF) may advent restrictions on the industry. With limited amounts of empirical evidence for the effects of OWF to seabird populations, impacts such as mortality from collision risk are estimated in a theoretical framework.

Offshore wind farms may impact upon seabird populations during their construction, operational lifespan and decommissioning. Governed by legislation and in consultation with Statutory Nature Conservation Bodies (SNCBs) the EIA process moves in steps to assess the magnitude of effects to ornithological receptor species both at the proposed development and cumulatively, within the context of existing and consented developments. The assessment begins with a scoping approach to attempt to highlight sensitivities at the proposed development and across the wider area. From this, typically two years of bird activity surveys at the development are carried out. These surveys seek to characterise a baseline of avian activity at the proposed development site and from them density and abundance estimates of birds are acquired. These survey data then inform impact assessment by estimating additional mortality via collision risk modelling, usually in a version of the theoretical model developed by Band (2012). In reality, birds will display avoidance behaviour to structures. Precautionary avoidance rates, on a species by species basis are applied. The results of the collision risk modelling are assessed for the magnitude of the effect. A developer provides a Habitats Regulation Assessment (HRA) on the basis of a proposed development having assumed connectivity with a SPA and having a likely significant effect (LSE) to that population. The HRA usually presents the estimated risks in terms of population level impacts to the population described, within a modelling framework and is presented as information to inform the regulator. Two methods have been frequently used: Potential Biological Removal (PBR) (Wade 1998) and Population Viability Analysis (PVA) (Boyce 1992). PVA explores the risk to a colony, assessing different outcomes from varied parameter sets. PBR alternatively presents a threshold figure of removal of individuals from a population, above which deleterious effects to the population are assumed. If the integrity of a SPA feature (e.g. seabird population) has an impact considered to be a major significant estimate, an Appropriate Assessment (AA) is undertaken by the regulator to decide on the impact of the LSE and subsequent mitigation and/or consent of the development (migration and biological minimum defined populations are also included in the EIA process).

Displacement and barrier effects to populations are assessed using survey data of abundance of on-water and in-flight birds. From this a proportion of these data are estimated to represent the breeding and non-breeding populations (based on modelling/ demographic approaches). This estimate of breeding birds can then be evaluated in a displacement framework, in accordance with species sensitivity scores of displacement to assess the likely impact to a population. Again, should the OWF be likely to pose an unacceptable risk to a population, further analyses may be requested from consenting authorities or consultees.

In the UK, government scientific bodies work closely with industry and SNCB partners to ensure a high quality impact assessment that follows the precautionary principle, both in terms of each proposed development and cumulative impacts. The collision and displacement modelling has a high prevalence of uncertainty around parameters used. Predominantly, the uncertainty for estimating risk exists as there

is little empirical evidence for impact parameters such as avoidance rates for species, habituation and attraction to windfarms. But there are also knowledge gaps for demographic processes of seabirds, due in part to seabird ecology and associated observational difficulties. Regulation of seabird demography, for example, the way that density-dependence operates in a population i.e. compensation to some demographic rate via competition for resources, such as prey (Furness and Birkhead 1984, Tavecchia *et al.* 2007) is difficult to observe or quantify *in situ* and may either be excluded or be subject to uncertainty surrounding arbitrary estimates used in scenario modelling. Another consideration not captured by assessment is the metapopulation structure of breeding seabird populations. With evidence for emigration and immigration in many seabird species (Oro and Ruxton 2001, Kildaw *et al.* 2005), the absence of connectivity during modelling is considered more precautionary currently, in lieu of empirical estimates of these parameters and additionally upholds the focus of protection at SPA or similarly protected sites. With multiple areas of knowledge gaps both in seabird population dynamics and the quantification of impacts from OWF, updated modelling approaches should seek to increase realism and reduce uncertainty, allowing impacts to be assessed in a framework that is more appropriate biologically and can provide enhanced spatial planning of the offshore wind industry.

1.2 Seabirds in the UK: Background

The coastline habitats of the UK archipelago offer seabirds prospective nesting sites; while regions of high primary productivity in nearshore and offshore waters present foraging opportunities. Consequently, the populations of 25 species of seabirds breeding in UK colonies are considered internationally important (JNCC 2009). In addition, large numbers of birds pass through UK waters out-with the breeding season, either in migratory movements or as members of overwintering populations (Furness 2015). Seabird species can be generally characterised as long-lived animals that exhibit delayed reproduction, low fecundity linked to phylogenetic constraint (such as in the Procellariiformes) and ecological constraints of resource patchiness (Bried and Jouventin 2002), subsequently, species are iteroparous and in many there is evidence of high breeding site-fidelity (Hamer *et al*. 2002, Coulson 2011). These traits mean that anthropogenic impacts may only reveal themselves at population level over extended temporal scales, increasing population susceptibility to undetected decline and extinction. By the same token, due to their low fecundity and, often low fledging success, any variable that may affect individual fitness or survival, such as an OWF could impact upon the reproductive success of individuals and in turn have consequences at population level. Seabird species and their life histories have attracted interest and subsequent research for hundreds of years; from accounts in poetry, such as the seafarer from around 975 AD (Goldsmith 1954), to early 20th century national population counts for single species, like the northern gannet ((*Morus bassanus*) – hereafter referred to as 'gannet') (Gurney 1913) leading to time-series data collection of multi-species assessments such as Operation Seafarer in 1969 (Cramp *et al.* 1974). Seabirds are a unique marine study

system, they spend the majority of time above the sea surface making them easily observable during surveys, the species that occur in UK waters are relatively easily identifiable to species level, many species are wide ranging allowing for large spatial scales to be studied, they utilise a range of marine habitats and they are tied to land for breeding, making them accessible to demographic research at this time (Oro 2014). However, despite their immediate detectability during surveys comparative to other marine organisms, seabirds also prove challenging birds to study. Whilst breeding adults function as central place foragers (Orion and Pearson 1979) and may be relatively easily observed, after fledging, immature birds are transient at sea for many years before recruiting into a breeding colony upon maturity. Given the large geographical range available to many species there is limited information on survival, migration, behaviour and recruitment of these immature life stages for many species.

UK seabird population trends are assessed using data collected from census and annual monitoring at colonies, many of which are SPAs (predominantly adult abundance and productivity data, but at some sites adult survival may also be estimated), additionally at-sea surveys highlight fluctuations in abundance and distributions across species over different spatial and temporal scales (Mitchell *et al.* 2004, MacDonald *et al.* 2015). Individual-based data on vital rates such as adult survival, productivity and recruitment can be derived to characterise the dynamics of a population (Caswell 2001). Assessments of population growth are based on these demographic vital rates. Often denoted by lambda (λ), population growth rate, is an index used to assess the status of the population and subsequently quantify the stability or viability of a population. Much of what we know about seabird demographics comes from constant effort monitoring sites, ringing, and dedicated research groups. Whilst knowledge gaps remain, using long-term longitudinal datasets, both at colony and individual level, processes that have been found known to have negative effects on UK seabird population growth include: climatic stochasticity and oceanographic changes (Burthe *et al.* 2012), fishery practices, including prey depletion and seabird by-catch (Frederiksen *et al.* 2004b, Anderson *et al.* 2011) and pollutant poisoning (Votier *et al.* 2005). As apex predators across a range of marine trophic environments, seabird species may contribute top-down effects to, or conversely be impacted upon, by bottom-up responses of their prey and its availability/quality (Boyd *et al.* 2006, Engelhard *et al.* 2014). Marine trophic webs are dynamic and complex systems and the interplay and subtlety of bottom-up versus top-down processes have proven hard to disentangle, particularly with the addition of climatic and anthropogenic influences. Studies such as that by Horswill *et al.* (2019) are starting to make progress on these variables, using detailed demographic data with covariate analysis in a Bayesian state-space integrated population modelling approach. Long-term colony and at-sea datasets, together with insights from tracking technology, techniques such as stable isotope analysis and advancements in quantitative theoretical approaches are allowing the proximate and ultimate drivers of seabird population dynamics to be identified and consequently indicate that seabirds may be useful in determining and predicting marine effects across a range of spatial, trophic and temporal scales (Cury *et al.* 2011, Frederiksen *et al.* 2013).

1.3 Direct and indirect effects of offshore wind; mortality and sub-lethal impacts

There are several ways OWF may affect seabirds, with multiple reviews in literature documenting a range of effects and responses of terrestrial and marine bird species to such structures (Desholm and Kahlert 2005, Drewitt and Langston 2006, Grecian *et al.* 2010). For the purpose of this introduction, I will divide effects into those described in the UK EIA process: direct and indirect. Directly, OWF can affect birds through collision mortality and through displacement (e.g. from feeding ground) or barrier effects (e.g. to movement: migration, foraging or commuting flight). Indirectly, OWF may affect seabirds via the availability and distribution of their prey (Figure 1.1). Collision directly affects populations via reduced survival. Displacement and barrier effects work at population level by reducing annual survival or reduced breeding success (Fox *et al.* 2006).

There is a great deal of uncertainty surrounding the severity of the risk posed by collision as little empirical evidence has been collected to inform species-specific collision estimates with offshore and onshore wind installations (Stewart *et al.* 2007). Since detection of carcasses in the field is challenging, particularly for structures at sea, collision mortality is calculated from theoretical assumptions dependent on a species' typical flight behaviour, altitude, receptiveness to visual and other sensory cues, foraging behaviour, avoidance and degree of nocturnal activity (often termed nocturnal activity factor, NAF, in EIA) Different species may be subject to differing probability of collision dependent on their typical behaviours. Auk species such as the common guillemot ((*Uria aalge*) - hereafter, 'guillemot') are considered to be at minimal risk of collision with wind turbine blades as they are low, near surface fliers, well below the collision risk height (CRH) of standard wind turbine design. For species that fly at CRH for some or all of their flight pattern it is widely accepted that, faced with an obstacle such as an offshore windfarm some degree of avoidance of the structure in their path will be displayed. This avoidance operates on a continuum but is mechanistically described by the literature as: macro-avoidance, whereby birds will alter their flight path in advance of the structure (macro avoidance may be used as an index for displacement), meso-avoidance, within the windfarm avoidance typically seen as birds flying down the row between turbines to transit through an OWF, and micro-avoidance, again within the windfarm but a last minute evasive action to avoid turbine blades (Cook *et al.* 2012). At population level the death of individuals from collision may negatively affect the growth rates of a population and increase vulnerability, e.g. future colony extinction. A study of a metapopulation of the Egyptian vulture (*Neophron percnopterus*), attempted to assess the collision effects of wind farms to a long-lived species at population level. This study found that when including wind farm collision mortality in a PVA approach, both individual population growth rates and the metapopulation growth rates were significantly reduced, correspondingly the population time to extinction also reduced (Carrete *et al*. 2009). Of seabird species, those most at risk from collision with offshore windfarms include gull spp., gannet and skua spp. (Garthe and Hüppop 2004, Furness *et al.* 2013).

Displacement or barrier effects to individuals from OWF may have energetic associated costs e.g. a reduction in individual body condition, which may be exhibited at population level either via reduced survival or sub-lethally as reduced breeding or fledging success or the quality of the next generation (Fox *et al.* 2009, Masden *et al.* 2010). There is a lack of empirical evidence as to the impact of these effects to seabird populations. An energetics study on common eider (*Somateria mollissima*) found negligible additional energetics required to avoid an offshore installation in Denmark (Masden *et al.* 2009). Theoretically, more efficient gliding species such as the gannet are assumed to have trivial energetic costs to avoidance of nearby installations, for example during foraging trips in the breeding season (Masden *et al.* 2010). Little is known however on the additional effects of environmental factors to collision risk such as wind and flight behaviour or cumulative impacts of additional energetics of avoiding multiple installations, for example during migration. The morphology of some species place them at higher energetic costs of additional flight times; the guillemot for example has large body mass to wing area. Furness *et al.* (2013) found the species likely to be most sensitive to barrier and displacement to be diver species. and auk species. Further to the additional energetics of displacement and barrier effects, during the breeding season, additional time costs to foraging may impact upon chick provisioning rates. Prey species can vary year to year in their distribution and abundance, directly impacting on foraging trip duration of breeding seabirds (Burke and Montevecchi 2009) and breeding success (Frederiksen *et al.* 2005b), this adds another level of unpredictability in trying to quantify any additional impact of offshore windfarms, for example to chick provisioning rates. In lieu of additional impacts from offshore windfarms there remains a lack of understanding as to the severity of these effects alone and in-combination with each other to the persistence of populations.

Indirect effects from OWF are those that operate to affect the prey species of the birds, thus indirectly impacting upon seabird species. There is a paucity of information in the literature regarding evidence of indirect effects, but developments may affect prey either by displacement or habitat loss or conversely, by attracting species to OWF. Russell *et al.* (2014) utilised state-space modelling of telemetry data from two seal species (*Phoca vitulina and Halichoerus grypus*) and found foraging behaviour patterns at wind turbine stances, indicating assemblages of fish at the structures. Lindeboom *et al.* (2011) also found evidence that great cormorants (*Phalacrocorax carbo*) were attracted to offshore turbines as foraging platforms. This suggests that prey species are attracted to the reef-like structure of a development, whilst others have similarly posited the opinion that OWF may attract aggregations of some species, functioning as marine protected areas (MPAs) (Grecian *et al.* 2010). Depending on the habitat there could be potential for developments to displace groundfish and potentially be replaced with reef fish or perhaps the area may be avoided in its entirety by certain prey species. Fish abundance within OWFs may also change as a consequence of the restriction of commercial fishing within OWFs. To which ends there is a call for continued research in this area (Inger *et al.* 2009). If the development attracts aggregations of species, seabirds may be at increased risk of collision as they are attracted to

the area for foraging. If the prey species are displaced from the OWF, the distribution change may impact upon seabird survival or manifest as carry over effects such as reduced breeding success.

1.4 Population impacts from OWF: From the individual to the population

Attributing a population response to single or multiple drivers is critical towards interpreting the subsequent wider ecological inferences of these signals. Detecting these relationships requires an understanding of species' life history, demography and the natural limitations inherent to populations including potential density effects (e.g. crowding or Allee effects): available habitat, inter and intra specific competition and variation, parasite loading, predation and natural mortality (Sutherland 1996). Population studies intrinsically include high uncertainty, with vital rates subject to three major types of variability: demographic stochasticity, individual variation and environmental perturbation. Emergent variability at the population level is best understood at the level of the individual. Parental effects have been recognized as conveying a measure of fitness (Bouwhuis *et al.* 2015), as has the genetic make-up of the organism (Velando *et al*. 2015) and hormonal effects have been found to reduce productivity and development (Rubolini *et al.* 2005, Nelson *et al.* 2015). Such inter-individual variations in physiology, behaviour and the environment will be reflected in individual condition and subsequent breeding success and survival. Consequently, vital rates could vary greatly between individuals even within the same life stage (Cabrelli *et al*. 2009). Abiotic factors such as climate and anthropogenic effects can also affect an individual's condition and survival. Vital rates e.g. age at first breeding, productivity and adult survival are parameters that are derived for a population from individual studies. Depending on the species and the availability of concurrent research on intra and inter population variation, assumptions of the extent in variability of individuals need to be clearly demarked from the outset. Modelling the effects on a population from offshore windfarms whereby the understanding is the species are highly generalised as individuals could likely have different inference than that of a highly specialised population. Inter-population variability within the same species also needs to be considered within assessments and ensuing extrapolation (Frederiksen *et al.* 2005a). Structured matrix models that include parameters (or functions) for vital rates and also stochasticity can be used to assess and interpret the status of a population (Caswell 2001). PVA as mentioned previously, is a quantitative tool designed to evaluate the persistence of a population or group of populations, over a certain time period under certain environmental conditions. These matrices can be utilised to establish the risk of extinction of a population from additional anthropogenic effects (Gerber and González-Suárez 2010). There are two main ways OWF can affect UK seabird populations; through collision mortality and through carry-over effects that may reduce productivity, e.g. by acting as a barrier to foraging grounds. PVA has been

applied as an assessment tool to evaluate the vulnerability of populations to potential negative effects of offshore wind under specific conditions and assumptions across a defined period of time, usually the perceived lifespan of the technology proposed. In the British Trust for Ornithology (BTO) review of the use of PVA to measure impacts of offshore wind (Maclean *et al.* 2007), for 25 species of seabird, 15 were highlighted as having reasonable to excellent scores in terms of availability of demographic data for modelling within the PVA framework. Current research, particularly from tracking studies continues to supply data for species where knowledge gaps are present, for example in emigration and immigration (Sozstek *et al.* 2014).

1.5 Modelling impacts: Assessment approaches and knowledge gaps

Currently the industry adopts a central theme of modelling predicted impacts to closed, single populations. The reason for this approach is that by law, predicted impacts are measured on the protected SPA population in question and despite assumed connectivity, rates of immigration and emigration are unknown (MacArthur Green 2015). The modelling approach varies in terms of the evidence presented, with both PBR and PVA having been favoured as some of the available methods to inform a HRA. The PVA is a projection matrix (Caswell 2001), usually projecting forecasts in a series of 25 time-steps, which is an example of the assumed average working life and consensual basis of a development. These models usually include some form of environmental and demographic stochasticity (although how the former is derived may be arbitrary and how it is implemented may vary) and may be presented both as a linear density-independent version and non-linear feedback term for density-dependence. A review by Horswill and Robinson (2015) presented vital rate estimates for UK seabird species for application to these models. The review included estimates for; age specific survival, age specific productivity, age of recruitment, incidence of missed breeding, natal and adult breeding dispersal. Importantly this review also documented regional variation in these estimates, recognizing spatial variation. Much debate has surrounded the use of density independence or density dependent versions of these models. Since the models exist to assess the additional impacts from an OWF to a population baseline, either approach could be argued to be appropriate. Density independence is assumed to be a more precautionary approach as the feedback mechanism used to include density-dependence is generally reflected on reduced reproduction rates. Reproduction is the parameter targeted for density dependence due to seabird life histories (long-lived, low productivity), in years where conditions may affect adult fitness, seabird species will forego breeding in order to maintain condition (Cairns 1987).

PBR (Wade 1998) was developed to allow for assessment of marine mammals in order to set limits to by-catch and can be utilized with limited or no demographic data (Cooke *et al.* 2012), a benefit when dealing with taxa such as cetaceans for whom information on demographics is lacking. The equation involves three main terms: a minimum population estimate; a maximum net recruitment rate; and a recovery factor. Whilst sensitivity surrounding the population estimates and net recruitment has developed the model to recommended usage of percentile results (60^{th}), the recovery factor (from 0.1-1) – included as precaution, to address uncertainties- has been attributed to the International Union for Conservation of Nature (IUCN) categories of species threat as an index; e.g. 1.0 for populations of 'least concern' or 0.1 for populations of 'vulnerable' and 'endangered' species. The PBR objective is to safeguard the population at the optimum sustainable population (OSP), a range between the carrying capacity (K) and the population size at which maximum net productivity level is obtained (MacArthur Green 2014).

As quantitative techniques get more sophisticated, additional approaches to population-level impacts have been explored in novel and progressive techniques. MacArthur Green (2014) explored immigration rates (the estimation of which would allow for metapopulation analyses, rather than closed, single population; arguably more reflective of reality). Their work took estimates of sub adults, the age class before breeding and applied a constant inflation to replicate recruitment of birds to the breeding population. They trialed a range of inflation values, validating their best fit against the median from apparently occupied nest counts. Recent modelling reviews are beginning to assess the usefulness of integrated state space models within a Bayesian framework and PVA approach for assessing the population level impacts to seabirds from OWF (Freeman *et al.* 2014). Benefits from this approach include applications of predicting decline from posteriors, likelihoods for the count data are combined as an output of the demographic data giving a joint likelihood. This method increases flexibility because the means and variances are not fixed at estimates from capture mark recapture and nest data, but are naturally updated as the model is fitted to these and the census data. These modelling approaches are very intensively computational and care must be taken in setting prior distributions, interpretation of results and applicability of datasets to the species and population in question.

1.6 Modelling impacts: Target seabird species

Three main seabird species will initially form the initial focus of this work. The black-legged kittiwake (*Rissa tridactyla* - hereafter, 'kittiwake'), the gannet and the guillemot, before focusing further investigations solely on the kittiwake. These species have been selected for this work based on their potential vulnerability to offshore windfarms in UK waters in particular (Furness *et al*. 2013), their long-term monitoring and dataset availability- e.g. vital demographic rates across SPAs (SPA abundance, productivity, age at first breeding, adult survival etc.), breeding season diet, tracking studies

and their occurrence across UK SPAs. The three species also follow differing typical foraging behavioural strategies. The main prey species taken in UK waters by seabirds during the breeding season are from Ammodytidae, Clupeidae and Gadidae families (Anderson *et al.* 2014), other species may also be taken e.g. Atlantic mackerel (*Scomber scombrus*). The kittiwake is an offshore surface feeder specializing on a diet of sandeel (*Ammodytes spp.*) specialist and sprat (*Sprattus sprattus*) but will also feed from discards when natural food sources are less abundant, and may take marine invertebrates, especially outside the breeding season (JNCC 2015c). This species is vulnerable to displacement and barrier effects from offshore wind but has recently been argued to have a lowered susceptibility to collision risk due to average flight heights, however more evidence is being sought on flight heights for this species (Johnston *et al.* 2014). The gannet is characteristically a plunge-diving forager, diving from height to depths of up to 20 m but it can also surface-feed and has additionally been found to forage at fishery vessels and where marine mammals such as whales or pinnipeds are shoaling fish (JNCC 2015a). They will forage across all the main prey species as available to them from sandeels to adult herring and mackerel. Gannets are susceptible to collision impacts of offshore windfarms (Furness *et al*. 2013). In terms of displacement or barrier effects, whilst the birds may be subject to such impacts, i.e. re-routing of flight to avoid a development, these impacts may be negligible. As trans-continent migratory species, physiologically they display an energetically efficient flight and as such may be able to effectively buffer against additional foraging distance cost. There may be a cost of barrier effects to chick provisioning rates, but there is a lack of research into these potential impacts. The guillemot (sometimes referred to as 'murre') is an offshore diving species. As an auk, they typically follow a low flight commuting behaviour, but are powerful divers. Considered mainly a sandeel specialist during the breeding season in the North Sea, sprats and juvenile gadids have also been found in dietary analysis, especially in winter (Anderson *et al.* 2014). The species is vulnerable to the risk of displacement and barrier effects of offshore windfarms. These three species are also exhibiting differing population trends in the UK: the gannet has been increasing, the guillemot has had a fluctuating trend of increases and decreases (JNCC 2016), whilst the kittiwake has been in decline and recently placed on the IUCN red-list as vulnerable (Birdlife International 2018).

1.7 UK Seabirds: Population structure

In order to define an impact, first we need to define the population affected. Populations can be described differently across time and space; with an overall definition taken from Lloyd *et al*. (2010) as, "all of the birds belonging to the same species living in a specified geographical area", for example those attempting breeding within a defined study area, such as the breeding population at a SPA or migratory birds passing through UK waters. In general terms during the breeding season, breeding adults of most species are constrained by nesting and chick-rearing requirements and function as central place foragers (Orion and Pearson 1979, Camphuysen *et al.* 2011). Central place foragers are constrained by elevated energetic costs of foraging and flight to and from feeding grounds, which feed back into survival and breeding success of the individual and productivity of the colony as a whole (Camphuysen *et al.* 2011). There are costs and benefits to colonial living for seabirds in the breeding season. Costs of colonialism from conspecifics, such as a negative correlation between prey depletion and colony size as found in kittiwake research (Ainley *et al.* 2003) or intraspecific aggression (Anderson *et al.* 2014). It has generally been suggested that colonial breeding confers benefits of increased protection from predation and social learning advantages (Ashbrook *et al.* 2008). Each breeding colony in the UK SPA network may be described as a single population but there is general acknowledgement that seabird colonies function as a metapopulation network, through prospecting and recruitment and with the extinction and formation of new colonies (Kildaw *et al.* 2007, Coulson and Coulson 2008, Sozstek *et al*. 2014).

The biogeographic population is a commonly used term to describe the overall range of a particular species and in the context of seabird species in the UK, this has been further separated into non-breeding populations that have connectivity to UK waters (Furness 2015). Furness (2015) apportioned the number of species with connectivity in UK waters into temporal scales to include post-breeding migration in UK waters, non-breeding season, migration-free winter and pre-breeding migration in UK waters. Estimates of the numbers of each species are made (dependent on appropriateness of life history of the species) from the contributing connected breeding populations to these defined non-breeding temporal populations and are described as Biologically Defined Minimum Population Scales (BDMPS) for assessment of impacts from development over the smallest practical spatial scales. Winter movements often underpinned by moult and foraging behaviour may vary between and within species (Cherel *et al*. 2006, Harris *et al.* 2010, Frederiksen *et al.* 2012, Tranquila *et al.* 2014), with species' distributions and abundances in UK waters broadly taken from ESAS surveys, or Wildfowl and Wetland Trust (WWT) aerial surveys (Bradbury *et al.* 2014). In general, there is a paucity of data for non-breeding ages and stages as to their survival rates, foraging ecology and habitat use for most species.

1.8 A population model for UK seabirds

A conceptual population model of seabirds in the UK, including the directions of potential impacts of marine renewables is shown in Figure 1.1.

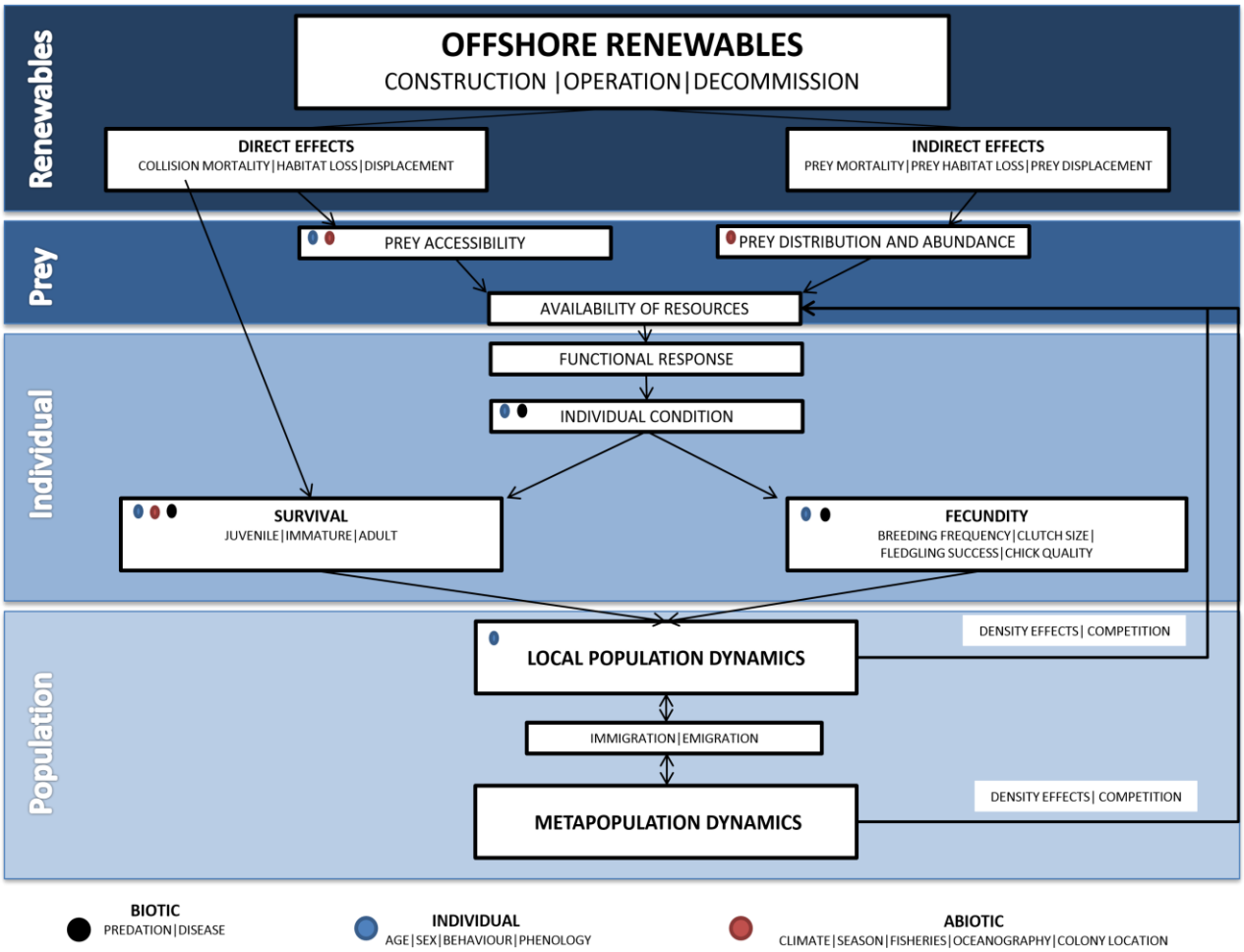

Figure 1.1: Schematic of the relationships between offshore wind and the processes regulating population dynamics of UK seabird populations. Variables affecting processes are colour-coded as biotic, abiotic and individual-based.

Population regulation arises via some factor or factors that can work independently, or interact, to influence the growth of a population, in turn affecting the dynamic carrying capacity. Regulation may be intrinsic, such as via density-dependence which can work, for example, to limit population growth due to competition for resources. Extrinsic regulation of a population may operate, for example, through environmental stochasticity; whereby favourable or unfavourable conditions may enhance or curtail growth in a population.

The availability of prey resources for a seabird is governed by accessibility and the distribution of abundance of the resource. Seabirds' prey distribution and abundance is subject to biotic processes that may affect these two indices of the prey species, such as zooplankton distribution (Alvarez-Fernandez

et al. 2015). Fish distribution and abundance has also been modelled in relation to oceanographic features and environmental variables (Maravelias 1997, van der Kooij 2008), seabird foraging (Ainley *et al.* 1996), predictability and fisheries activity (Patrick *et al*. 2015). Evidence also indicates climate and season play a role in resource availability and abundance (Tasker *et al*. 1999, Cox *et al.* 2013, MacDonald *et al.* 2015). The historical locations of seabird colonies could affect the accessibility of resources, as most species' prey items can be patchily distributed throughout the year and, during breeding seasons, seabirds function as central place foragers. Observations from tracking studies and foraging are imperative to spatial modeling of behavioural movement and habitat preference (Matthiopoulos 2003) and subsequent analyses are important for population-level inference (Morales *et al.* 2010). Evidence for plasticity in intraspecific and interspecific foraging strategies has highlighted that excluding additional environmental stochasticity, costs and benefits of foraging strategies versus colony location may include reduced competition or lower chick provisioning rates with greater foraging distance. Studies using telemetry on gannets have indicated spatial segregation in foraging patches of UK breeding colonies (Wakefield *et al.* 2013). A study of Northwest Atlantic guillemot breeding colonies (Davoren and Montevecchi 2003) showed individuals from two spatially distinct colonies had additional flight costs of lower provisioning rate of chicks and subsequently poorer condition of fledglings in one colony, considered at a greater distance to resources than another. Observations such as these are critical in examining habitat use when considering additional impacts to population indices such as breeding success from offshore windfarms. Carry-over impacts to seabirds from barrier effects of offshore windfarms, such as imposing additional flight times to foraging grounds which may produce costs on an inter-seasonal scale, can be modelled in an energetics framework (Masden *et al.* 2010). Energy acquisition is modelled by the functional response (Holling 1965), the rate at which individual predators consume prey resources if available/accessible. One method of quantifying the functional response is by using time series data such as chick provisioning rate and applying an appropriate framework to modeling the distribution of the functional response in lieu of the uncertainties that surround the data, such as prey abundance (Smout *et al*. 2013). A study of guillemots in the Baltic Sea found a strong negative correlation between provisioning rate and prey size, suggesting adults adapted foraging depending on prey quality (Kadin *et al.* 2016). Seabirds interact with each other and their environment differently across spatial and temporal scales, dependent on their species, age, state and sex. There is also increasing evidence that within populations, individual variation is high within the same life stage (Phillips *et al*. 2009, Votier *et al.* 2010). In structured population modelling approaches, the variation in individuals within a population can be captured using individual based models (IBM) whilst age/stage structured models assume a uniformity of individuals within the ages or stages. Model fit and suitability depends on the questions being asked, intra-stage variation could potentially be captured using a proportional approach to the population or explored using sensitivity analyses in a precautionary approach.

Biotic variables such as disease and predation can affect individual condition and subsequent fecundity or survival rates. These variables can be described as adult survival rates within a population model. The individual's condition determines its ability to survive, compete, and reproduce. Population models are parameterised by ringing observations and recoveries as a capture mark recapture tool for age at first breeding and survival of individuals; observational count data are utilised for estimates of abundance at colonies and productivity. Capture-mark-recapture studies, telemetry insights into movement and behaviour and concurrent advancements in survey design and modelling may improve the frequency of data capture, and the accuracy and precision of the demographic estimates obtained. Continued development of these methods will hopefully allow for inter-seasonal, inter age class population vital rates such as adult survival, productivity, emigration and immigration (Cam 2009) as well as our understanding of variability of vital rates within and between colonies. Together, the information from individuals confers a population's dynamic and each population of individuals feeds into the broader metapopulation network through their connective relationship of emigration and immigration.

1.9 Outline of thesis

The movement to reduce carbon emissions and work towards more sustainable sources of energy is gaining global momentum. Uncertainty in the current EIA modelling process for offshore wind presents a serious challenge to the science-based management and conservation of seabird populations and to the offshore industry through increased cost and restrictions in development. All EU countries are subject to similar legislation as the UK towards elucidating the persistence of wild populations, reflecting potential widespread restrictions in industry.

This thesis aims to empirically estimate processes of seabird population dynamics and evaluate population level impacts to seabirds; appraising current modelling approaches used in industry e.g. PBR/PVA and the applicability of such models to signaling the magnitudes of effects within single, closed populations. I explore patterns in non-breeding age-classes with environmental regulation before culminating in comparing the impact of additional mortality both within a structured metapopulation framework and the single population approach. I parameterise models using existing literature, widely accessible data and build on each chapter's results. By quantifying population regulation, accounting for variation across life-stages and by acknowledging the metapopulation structure of the study species, these models seek to add realism to spatial planning by quantification of demographic processes and their associated uncertainty. Whilst the models allow a platform to unlock new insights into the dynamics of seabird life-history, applying these methods can increase the precision of impact estimates,

providing powerful tools in modern environmental impact assessment and marine spatial planning. Organised as three analysis chapters in paper format, the specific aims of the following chapters are provided below.

Chapter 2: By analysing readily available time-series (of mixed completeness) of three species, from three UK seabird populations, I will:

- Derive empirical estimates of density-dependence and environmental stochasticity and explore the outcome for real seabird populations, following different life-histories, from this regulation under additional anthropogenic mortality;
- Determine if populations are under regulation and if so, describe the predominant regulation detected;
- Assess via PVA, the theoretical precaution in the PBR approach when we consider regulation in assessment, what conditions may exacerbate vulnerability in each species;
- Acknowledging metapopulation structure, but without quantifying connectivity, test theoretically how each population responds to a rescue-effect, under mortality scenarios, examining the implications for industry.

Chapter 3: Regulation by environment may contribute to seabird demography across time and space and there could be several contributing factors. The immature cohort may very well make up a large percentage of any seabird species, however we have often the least empirical information regarding aspects of these life-stages. Using data and literature from a constant effort monitoring site for kittiwake, the Isle of May, Scotland, I will:

- Assess, using a well-studied population, the relationship between regulation and demographic processes, by fitting multiple models to varied environmental time-series that may be influential in regulating demographic processes such as survival of age-classes and productivity;
- Implement and estimate scalar terms across survival at different age-classes to determine relative magnitude of environment regulation and impact across age-classes;
- Evaluate model performance when fitted to commonly available demographic data and when further demographic information not commonly available, adult survival data, is added.

Chapter 4: It is widely accepted that seabird species function as metapopulations and therefore that colonies are not closed, isolated units. Therefore, using a hierarchical model with transfer connectivity conceptually based on a literature review of evidence and using time-series data from the Shetland archipelago breeding sites for kittiwake (including Fair Isle) I aim to:

- Estimate via model fitting, the relationship of transfer connectivity between colonies, simultaneously estimating regulation and other demographic processes;

- Using sampled posteriors from the fully fitted metapopulation model to inform a stochastic PVA approach ask, how might offshore windfarms affect metapopulation structure via additional mortality?
- Compare the outcomes of these PVA scenarios to closed modelling scenarios.

Chapter 2 Preface

The following chapter was reviewed and accepted for publication in The Journal of Applied Ecology 2019. It has been slightly adapted from manuscript form into the chapter for readability. I include the published paper in full in Appendix 2. For publication I am grateful to my co-authors and supervisors, Professor Bob Furness and Dr. Mark Trinder who formulated the original idea, whilst Professor Jason Matthiopoulos and I developed the idea and the approach. I analysed the data and drafted the original manuscript with all authors providing subsequent editorial advice and final approval for publication. I am indebted to our reviewers at the Journal of Applied Ecology for their helpful feedback towards publication and to Professor Des Thompson and Dr Andy Douse for selecting the publication as Editor's choice.

A note on productivity used in this chapter:

Further to examination an error in Equation 2.2 on page 29 was discovered. This equation is described in the original manuscript on page 134 as a postbreeding census and should be: $B = \frac{f}{2} S_a$. The resulting error means that the equation used was: $B = \frac{f}{2S_a}$. Where B is intrinsic productivity, f is highest reported chicks fledged and S_a is adult survival. As such the description of this equation as a post-breeding census has been removed from this chapter. The consequence of such an error is that the calculation of productivity provided to the model is a higher intrinsic value. Further information is provided in Appendix 1: A.1.2. Fixed parameters on page 120.

Chapter 2: The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality

Abstract

The balance between economic growth and wildlife conservation is a priority for many governments. Enhancing realism in assessment of population-level impacts of anthropogenic mortality can help achieve this balance. Population Viability Analysis (PVA) is commonly applied to investigate population vulnerability, but outcomes of PVA are sensitive to formulations of density-dependence, environmental stochasticity and life-history. Current practice in marine assessments is to use precautionary models that assume no compensation from density-dependence or rescue-effects via "re-seeding" from other colonies. However, if it was possible to empirically quantify regulatory population processes, the responses of populations to additional anthropogenic mortality may be assessed with more realism in PVA.

Using Bayesian state-space models fitted to population time-series from three sympatric seabird populations, selected for varied life histories, I inferred the extent to which their dynamics are driven by environmental stochasticity and density-dependence.

Based on these inferences, I conducted an exhaustive PVA across credible parameterisations for intrinsic and extrinsic population regulation, simulated as a closed and re-seeded system. Scenarios of anthropogenic mortality, along a sliding scale of precaution, were applied both proportionally and as a fixed quota using Potential Biological Removal (PBR).

Baseline results from fitting revealed clear environmental regulation in two of our three species. Crucially, I found that for the empirically derived, realistic model parameterisations there are risks of decline to real populations even under very precautionary mortality scenarios. I find that PBR is dubious in application as a sustainable tool for population assessment when we account for regulation. Closed versus re-seeded models showed a large divergence in outcomes, with sharper declines in closed simulations. Fixed-quota mortality typically induced greater population declines comparative to proportional mortality, subject to regulation and re-seeding.

Practitioners using arbitrary formulations of population regulation risk over-precaution (economic constraint) or under-precaution (endangering populations). The demands of increased economic development and preservation of wildlife require that methodologies apply techniques that confer reality and rigour to assessment. The current practice of employing models lacking density-dependence and empirical environmental information imposes limitations in the efficacy of estimating impacts. Here, I provide a method to quantify the conditions that predominantly regulate a population and exacerbate the risk of decline from anthropogenic mortality. It is in the interests of both developers and

conservationists to apply methods in population impact assessments that capture realism in the processes driving population dynamics.

2.1. Introduction

Globally, many species are facing decline and potential extinction from anthropogenic activities (Murphy & Romanuk 2014; Ripple *et al*. 2016). Seabird populations are at risk from additional anthropogenic mortality from by-catch, oiling, harvesting and marine renewables (Croxall *et al*. 2012). The UK coastline hosts internationally significant numbers of seabirds, especially during the breeding season, and several of these species have been assessed as potentially at risk from offshore wind installations (Furness, Wade & Masden 2013). The marine renewables industry (Platteeuw *et al*. 2017) is seeking expansion, incentivised, in part, by internationally agreed sustainable-energy targets (Marques, Fuinhas & Manso 2010). Poorly planned developments may cause impacts such as additional mortality from collision strikes (Johnston *et al*. 2014). Industry, especially in countries bearing a legal requirement for environmental assessment (European Commission 2011), has a responsibility to minimize its impact on wildlife. Assessment approaches vary, but generally contain an appraisal of risk to populations from impacts of additional mortality (Buckland, Goudie & Borchers 2000), following the precautionary principle (Sands & Peel 2012), supported by EU directives (European Commission 2009).

Determining the consequences of additional mortality to a population requires an estimate of population size, an understanding of life history, estimates of demographic rates and how these are affected by regulating influences such as density-dependence and environmental stochasticity (Lande, Engen & Saether 2003). At the point of assessment and more generally in population ecology, there are inherent uncertainties associated with these parameters (Clark 2003). Assessments of inadequately studied populations may use proxy values from populations of the same or similar species for productivity or survival rates (Kindsvater *et al*. 2018). In addition, a lack of empirical estimation of connectivity (immigration or emigration) often leads practitioners to use closed system models (Hanski 1998). Empirical estimates of population regulation across spatio-temporal scales are also deficient. The shape and magnitude of density-dependence is difficult to quantify in wild populations despite its recognized importance for population dynamics (Bonenfant *et al*. 2009; Knape and deValpine 2012). It is also challenging to derive quantitative estimates for extrinsic regulation from environmental stochasticity, especially since it may be confounded with intrinsic regulation in short time series (Engen, Bakke & Islam 1998). Understanding how population persistence is affected by variable combinations of density-dependence and environmental regulation is unknown (Saether *et al*. 2002). To increase the credibility of predicted outcomes from population assessments it is essential to represent biological reality whilst capturing uncertainty in estimates of understudied processes (Saunders, Cuthbert & Zipkin 2018). Failure to faithfully reflect accuracy and precision in predictions leads to one of two detrimental outcomes for human-wildlife conflict; over-precaution due to an inflated estimate of risk may curtail

economically important activities, whilst undetected risks to population viability, could set sensitive populations on a path to extinction.

Reflecting knowledge gaps in connectivity and the ability to capture population regulation, UK seabird populations are modeled in an environmental impact assessment (EIA) assuming no immigration and, often, no density-dependence. The risk of additional mortality to a seabird population from collision is estimated typically across a period of 25 years, the operational life span of a wind farm, and evaluated as to how this estimate will affect the population. Population viability analysis (PVA) (Boyce 1992) and Potential Biological Removal (PBR) (Wade 1998), are among the methods used to evaluate anthropogenic additional mortality on seabird populations under assessment. PVA is an application of projection matrix modelling. PBR, designed initially for marine mammal assessment, is a simple harvest assessment calculating the maximum number of animals that may be sustainably removed from a given population. In EIA, PVA usually contains some estimate of demographic rates, with more recent assessments attempting to include environmental stochasticity by implementing the demographic rates as stochastic processes. Although some models may include a form of density-dependence, there is ongoing debate about the practical justification for its inclusion (Green *et al.* 2016; Horswill, O'Brien & Robinson 2016). In general, PVA has been shown to be sensitive to estimates of parameters, affecting predicted outcomes (Reed *et al*. 2002; Cook & Robinson 2016). PBR requires minimal demographic input, save for an adult survival estimate and the age at first breeding. There is an assumption of compensatory density-dependence included in the model background (Niel & Lebreton 2005). The PBR calculation returns a threshold value of additional mortality to a population above which a decline is expected, it contains no stochastic component and no population projection. PBR has been criticised as a tool for EIA as it fails to quantify potentially serious population consequences which can occur below this threshold (Green et al. 2016; O'Brien, Cook & Robinson 2017).

Environmental signals affecting population dynamics can be explored using time-series data (Leirs *et al*. 1997; Frederiksen, Mavor & Wanless 2007), and density-dependence signals may also be extracted from population time-series (Lande *et al*. 2002; Brook & Bradshaw 2006). For realistic assessment, we should aim to derive empirical values for the strength of density-dependence and the magnitude of environmental stochasticity from such data. Exploring these values in a PVA would provide multiple intrinsic and extrinsic regulatory scenarios against which additional mortality may be assessed. Furthermore, modelling the populations with a rescue-effect (where immigration prevents extinction (Brown & Kodric-Brown 1977)) could help us assess the sensitivity of outcomes to the assumption of closed populations. I therefore aimed to assess how several levels of anthropogenic mortality can impact real seabird populations (both closed and open to a rescue-effect), operating under empirically derived estimates of environmental stochasticity and density-dependence.

I used Bayesian methods to fit a state-space population model to historical data from sympatric populations of three well-studied UK seabird species with divergent life histories: Northern gannet *Morus bassanus*., black-legged kittiwake *Rissa tridactyla*. and common guillemot *Uria aalge* This provided posterior credible intervals for density-dependence and environmental stochasticity for each population. These intervals defined parameter ranges for the strength of density-dependence and environmental regulation, which I explored systematically using my population models, generating predictions of population viability across the entire space of plausible combinations of intrinsic versus extrinsic regulation. To assess risk from additional mortality I utilised PBR as a tool providing a range of values across a precautionary gradient, allowing a general approach to visualising 25-year mortality impact. Populations were modelled both under assumed closedness and under the possibility of annual rescue-effects from immigration.

2.2. Materials and Methods

2.2.1 Demographic Model

High-quality demographic rate and population abundance data were obtained for the sympatric island populations of Bass Rock (gannet) and the Isle of May (kittiwake and guillemot), Scotland.

Both the Isle of May and the Bass Rock are located off the east coast of Scotland, UK. Because each of these species come from the same geographical region of Scotland and have been monitored across roughly similar time periods- this assumes that, broadly speaking, they are likely to have experienced the same environmental conditions. To capture intrinsic growth rate (i.e. maximal growth at low densities), the population model used the highest value of productivity reported across the time-series (see Appendix1: A.1.2).

All modelling and analysis were undertaken in R (R Core Team 2016). A stochastic stage-structured matrix model was developed for each species. The dimensions of the annual transition matrix were based on each species' age-at-maturity. For example, the deterministic version of the model, using rates, for a species with one juvenile and three sub-adult classes would take the form:

$$\begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \\ n_{4,t+1} \\ n_{5,t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & B_t \\ S_{j,t} & 0 & 0 & 0 & 0 \\ 0 & S_{1,t} & 0 & 0 & 0 \\ 0 & 0 & S_{2,t} & 0 & 0 \\ 0 & 0 & 0 & S_{3,t} & S_{a,t} \end{pmatrix} \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \end{pmatrix} \quad (2.1)$$

Where B and S represent the vital rates of productivity and survival, and the subscripts $j, 1, 2, 3$ and a on the vital rates denote juvenile, sub adult and adult age classes respectively.

As a female-only model, productivity was adjusted under the assumption of a 1:1 sex-ratio as the number of female chicks fledged per pair, calculated thus:

Productivity B was adjusted to better reflect the female component of the population, calculated thus:

$$B = \frac{f}{2S_a} \tag{2.2}$$

With f being the number of chicks fledged per pair and S_a adult survival. Equation. (2.2) produces a productivity rate modified by the probability of adult survival (see Appendix 1: A.1.2).

In the stochastic model, the number of chicks fledged and number of animals of each age class surviving were modelled as binomial processes, for all species, including kittiwake. Using the binomial process for fecundity is motivated by the fact that, in the cases of gannets and guillemots, only one egg is laid annually per female and despite the larger clutch sizes of kittiwakes, poor productivity driving declines means that commonly, colonies report on average less than one chick fledging successfully (Coulson 2017). Despite recent elevated kittiwake fledging success on the Isle of May (Newell *et. al* 2016), a Poisson form of demographic stochasticity would have yielded unrealistically high and low annual productivities, affecting the realism of the model, particularly at low population sizes.

Generally, seabirds are characterised as long-lived animals that exhibit delayed reproduction, low fecundity linked to ecological constraints of resource patchiness and there is evidence of compensatory density-dependence in several studies (Horswill, O'Brien & Robinson 2016; Bried & Jouventin 2002). Here I investigate how intrinsic (density-dependence) and extrinsic (environmental stochasticity) conditions work to regulate populations. Deriving estimates of regulation during model fitting, I simulate populations forward to assess their fate under various combinations of intrinsic and extrinsic regulation and additional mortality.

There is evidence across all species that adults forego breeding when extrinsic and intrinsic conditions are sub-optimal to maintain condition (Weimerskirch 2001; Oro & Martinez-Abrain 2004). The model therefore estimates the strength of compensatory density-dependence in productivity alone, under the assumption that this would be the demographic rate most likely to be affected.

I define density-dependence as a limiting factor that reduces a population's growth rate as population density increases, for example through increased competition for resources (e.g. prey or space). Resources such as these are established extrinsically, resulting in an environmentally determined

carrying capacity (k). The model applies a compensatory form of density-dependence to the linear predictor for productivity. Whereby the intercept for productivity reflects the intrinsic (maximum) rate of productivity. Density-dependence therefore operates as a penalty applied to the intrinsic rate for productivity (a set value in these models) by the addition of one unit of density in the population. applied as a function to total population size.

Those populations simulated with weak density-dependence would be characterised as having a close to zero density-dependence and relatively unaffected intrinsic growth rate for productivity- (in the models this is also dependent on environmental stochasticity). Whilst those experiencing stronger density-dependence would incur a greater impact to the realised productivity demographic rate, the compensatory recovery of which is determined by: the slope of the line, the strength of the penalty and the population size relative to k (governed by environment and mortality).

I do not attempt in this model to account for a potential 'floater' population of adults that have the potential to breed but have not.

The probability of fledging female chicks at each time step B_t was modelled as a logit function of a linear predictor b_t. The logit transformation was used to ensure that B_t remained bounded within the 0-to-1 range. The linear predictor took the form,

$$b_t = b_0 - \phi n_{t-1} + \varepsilon_t \tag{2.3}$$

The terms on the right-hand side of equation (2.3) correspond to an intercept b_0, the effect of density (n_{t-1}) on productivity, measured as a penalty to the intercept by a coefficient (ϕ), and the effect of an environmental perturbation term (ε_t) comprising a time series of identically distributed Gaussian terms $\varepsilon_t \sim N(0,\sigma)$. The standard deviation (σ) of this term, was used as our metric for the magnitude of environmental stochasticity acting on the populations. The intercept represented intrinsic productivity, in the absence of density-dependence and environmental perturbations and was derived from female-only reported maximal values of B (Appendix 1: A.1.2) as the inverse logit transformation:

$$b_0 = \log\frac{B}{1-B} \tag{2.4}$$

Environmental variation can affect survival at all life stages (Weimerskirch 2001; Jenouvrier *et al*. 2005; Frederiksen *et al*. 2008; Lewis *et al*. 2009) and I assume that its impact is synchronous to the impact on productivity. In the model, the same fluctuations in environmental stochasticity are therefore also applied to survival, using a scaling term (p) (expressing the relative importance of environmental stochasticity for breeding and the survival rates of different life stages). This scalar was calculated from available time-series of demographic data, specific to each of our study populations (Appendix 1: A.1.1).

Survival for each age class $(S_{*,t})$ was modelled as a logit of baseline survival (s_{*0}) and environmental stochasticity ($p_* \varepsilon_t$). For example, in the case of juveniles, the linear predictor took the form:

$$s_{j,t} = s_{j0} + p_j \varepsilon_{,t} \quad (2.5)$$

The population's initial age and sex structure was unknown, so as a plausible start (assuming equal sex-ratio), I used the population's stable age distribution, derived from the dominant eigenvector (Caswell 2001) of the density-independent projection matrix. This distribution was then scaled using the population starting size to derive numbers for each age class. With a lack of observed data on the number and structure of each population, I utilise the dominant eigenvector, applied only to the first data point during model fit and to the first data point in the subsequent simulated projections to avoid any influence of stationarity. I further avoid any influence of stationarity by fitting across time-series that should allow the model to 'forget' the initial condition.

2.2.2 State space model fitting to derive regulation

The above population model was fitted to the observations of historical population trend data for each species at each colony using the program JAGS (Plummer 2003) interfaced with R via the runjags package (Denwood 2016).

Species and colonies were selected based on the availability of empirical demographic rates and historical population estimates from the colony of choice (Harris, Frederiksen & Wanless 1997, Wanless *et al.* 2006, Horswill & Robinson 2015, Newell *et al*. 2016, JNCC 2017), vulnerability to offshore wind (Furness, Wade & Masden 2013) and varied life history strategies (Hamer, Schrieber & Burger 2001), for example: differing age to maturity, variation in vital rates, foraging ecology, morphology and overall fundamental differences in historic and current population trends. Subsequently, the Northern gannet population from the Bass Rock (increasing growth), Black-legged

kittiwake population from the Isle of May (declining) and the Common guillemot population (fluctuating growth) again from the Isle of May were selected for analyses (Table 2.1).

Table 2.1: Selection criteria for species

Species	Scientific Name	Age at 1st Breeding	Population Analysed	Data quality score (1-6)* Horswill & Robinson 2015	Population counts (Years) (JNCC/CEH)	Conservation score (/18)† Furness et al. 2013
Kittiwake	*Rissa tridactyla*	4	Isle of May	6	24	14
Gannet	*Morus bassanus*	5	Bass Rock	6	5	17
Guillemot	*Uria aalge*	6	Isle of May	6	39	16

* 6 being highest quality of data. † Ranked out of 18, with 18 being greatest concern. Authors conceptualise score based on: status in the Birds Directive, % biogeographic population present in Scotland, adult survival and UK threat status.

Both the Isle of May and the Bass Rock are located off the east coast of Scotland, UK. Because each of these species come from the same geographical region of Scotland and have been monitored across roughly similar time periods- this assumes that, broadly speaking, they are likely to have experienced the same environmental conditions. To capture intrinsic growth rate (i.e. maximal growth at low densities), the population model used the highest value of productivity reported across the time-series (See Appendix1 A.1.2).

There were missing data from years between counts in all the colonies except kittiwake. The datasets for each species were: kittiwake: years=24; estimates across years=24; gannet: years=29; estimates across years=5; guillemot: years=44; estimates across years=39. Observation error was included in the model by allowing for a 1% sampling error in colony counts.

To estimate the regulatory parameters of interest: strength of density-dependence (ϕ) and strength of environmental stochasticity (σ), minimally informative priors were used for the models (Appendix 1: A.1.4).

The density-dependence parameter ϕ (Equation 2.3) was assigned a gamma distribution, restricting density-dependence to a compensatory form. During model fitting, the MCMC chains explored extremely low values for density-dependence in some species. To facilitate computation in these cases I imposed a floor-truncation to this prior at the value 10^{-11}. My models estimated the strength of environmental stochasticity as the precision ($\tau = \sigma^{-2}$) of the stochastic process ε_t. This was assigned a gamma prior (constraining σ^2 to positive values). Models were run until satisfactory convergence,

based on the Gelman-Rubin diagnostic, PSRF (Brooks & Gelman 1997), effective sample sizes for all model parameters and visual inspection of traceplots (Kass *et al*. 1998). The ranges of values for the strength of density-dependence and environmental stochasticity were given by the upper and lower 95% credible intervals of the posteriors for ϕ, σ .

2.2.3 Mortality sensitivity: Population viability analysis

Populations were projected in a PVA analysis using the demographic matrix model outlined in 2.2.1 with ranges of values for density-dependence and environmental stochasticity taken from the posterior credible intervals (2.2.2) obtained from model-fitting. I divided each interval into 51 increments, producing 2601 pairwise combinations of values for density-dependence and environmental stochasticity. For each species, every combination was examined via population projections from my PVA model. In simulations I used a 200-year settling time provides ample time also for the model to 'forget' initial conditions and avoid stationarity. This time-period was decided upon for two motivations, firstly to reduce the influence of initial conditions on the outcome of additional mortality and secondly to allow me to assess impacts of additional mortality to baseline populations that are able to persist through regulatory processes. This informs in two ways, both allowing us to view long-term vulnerabilities to the populations under regulation and also vulnerabilities to the populations under both regulation and additional mortality.

Firstly, to gain a broader overview of the dynamics of these models and to allow comparisons between species, the estimated posterior values for density-dependence and environmental stochasticity were extended beyond their credible values and projected in PVA with no additional mortality. To assess what impact mortality had on populations under different regulation, populations were again projected under each pair-wise combination. After the settling-in period of 200 years, mortality treatment was applied with the PBR derived from the starting population size at the 200-year mark.

PBR (Wade 1998) was developed to allow for assessment of marine mammals in order to set limits to by-catch and can be utilized with limited or no demographic data. Since its original conception, its use has been expanded and it is now used to provide estimates of sustainable harvest in impact assessments of seabirds (Dillingham and Fletcher 2011). The equation involves three main terms: a minimum population estimate $(N_{\min})$; a maximum net recruitment rate $(R_{\max})$; and a recovery factor (FR) (Dillingham& Fletcher 2008). The recovery factor is a precautionary scalar (in the range 0-1, from maximum to minimum precaution) that works by shrinking the PBR threshold. If a population was calculated to have a threshold PBR of 400 at recovery factor 1, for example, a recovery factor of 0.1 would reduce this threshold to 40. The model assumes compensatory density dependence (Niel & Lebreton 2005). The basic PBR calculation takes the form:

$$PBR = N_{\min} \frac{R_{\max}}{2} FR \quad (2.6)$$

Further methodology on the derivation of terms for this calculation can be found in Furness and Trinder (2014). For the mortality sensitivity, treatments of PBR with FR set to 0 (Baseline), 0.1, 0.3, 0.5 and 1.0 (Full threshold) were applied.

Severity of mortality was manipulated by the recovery factor term (FR) in the equation 2.6. The PBR was applied annually as a fixed number, and as a proportion removed annually based on the starting population size at 200 years. In all cases mortality was applied across all age classes in proportion to their annual size. Mortality was applied over a 25-year period, a typical windfarm lifespan.

The mean population size μ_1 across this period, was then calculated and compared to the 25-year population mean μ_0 directly prior to the introduction of anthropogenic mortality. Impact (I) was calculated as a proportional change in population thus:

$$I = \frac{\mu_0 - \mu_1}{\mu_0} \quad (2.7)$$

The comparison of means from 25-years post-mortality treatment with 25-year mean pre-mortality treatment was favoured over other metrics as it better accounts for fluctuations of population size from environmental stochasticity in the model, giving an average view of population impact. For example, a 'favourable' or 'unfavourable' run of stochasticity towards the end of the time-period could mask the impact of mortality treatment across the application period. The 25-year time period also reflects an average industry assessment for a typical lifespan of a windfarm. To further explore the effects of mortality in this system I simulated the PVA analysis under a traditional 'closed' system, where I first assumed no connectivity in the populations and then allowed an annual rescue-effect by the introduction of a female, re-seeding the population and preventing extinction, but not avoiding declines.

2.3. Results

2.3.1 Baseline population change beyond boundaries of empirically derived density-dependence and environmental stochasticity

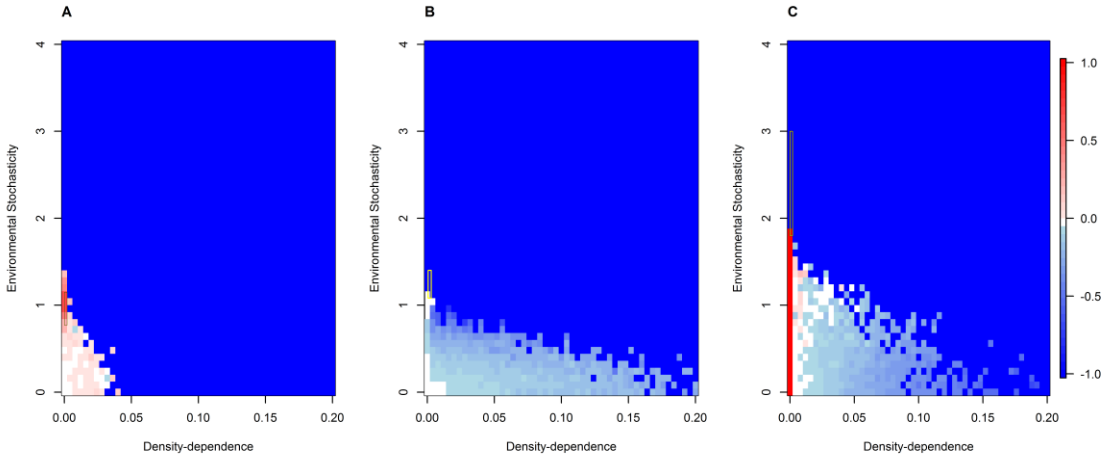

Figure 2.1 Baseline population change when density-dependence (DD) varies between 1e-11 and 0.2 and environmental stochasticity (ES) varies between 0 and 4. Panels A, B and C represent gannet, kittiwake and guillemot respectively, with boxes indicating the posterior boundaries of DD and ES derived from fitting and used in subsequent mortality projections. Pale colours are near-zero changes, pink through to red indicate proportional increases. Light blue indicates small declines through to darker blues indicating greater decline

With no additional mortality, each species displayed declines and eventual extinctions under higher strengths of density-dependence and higher environmental stochasticity (Figure 2.1). All species produced similar qualitative patterns to increased regulation but varied in their response and sensitivity to regulation at lower values. The boxes overlaying plots in Figure 2.1 indicate the fit-derived estimates for density-dependence and environmental stochasticity (Appendix 1: A.1.5). The boxes vary in their shape and limits across each of the species, but all are estimated near the lower limits of the full range of density-dependence explored, where colony persistence is unaffected by density regulation.

2.3.2 Mortality treatment results: Gannet

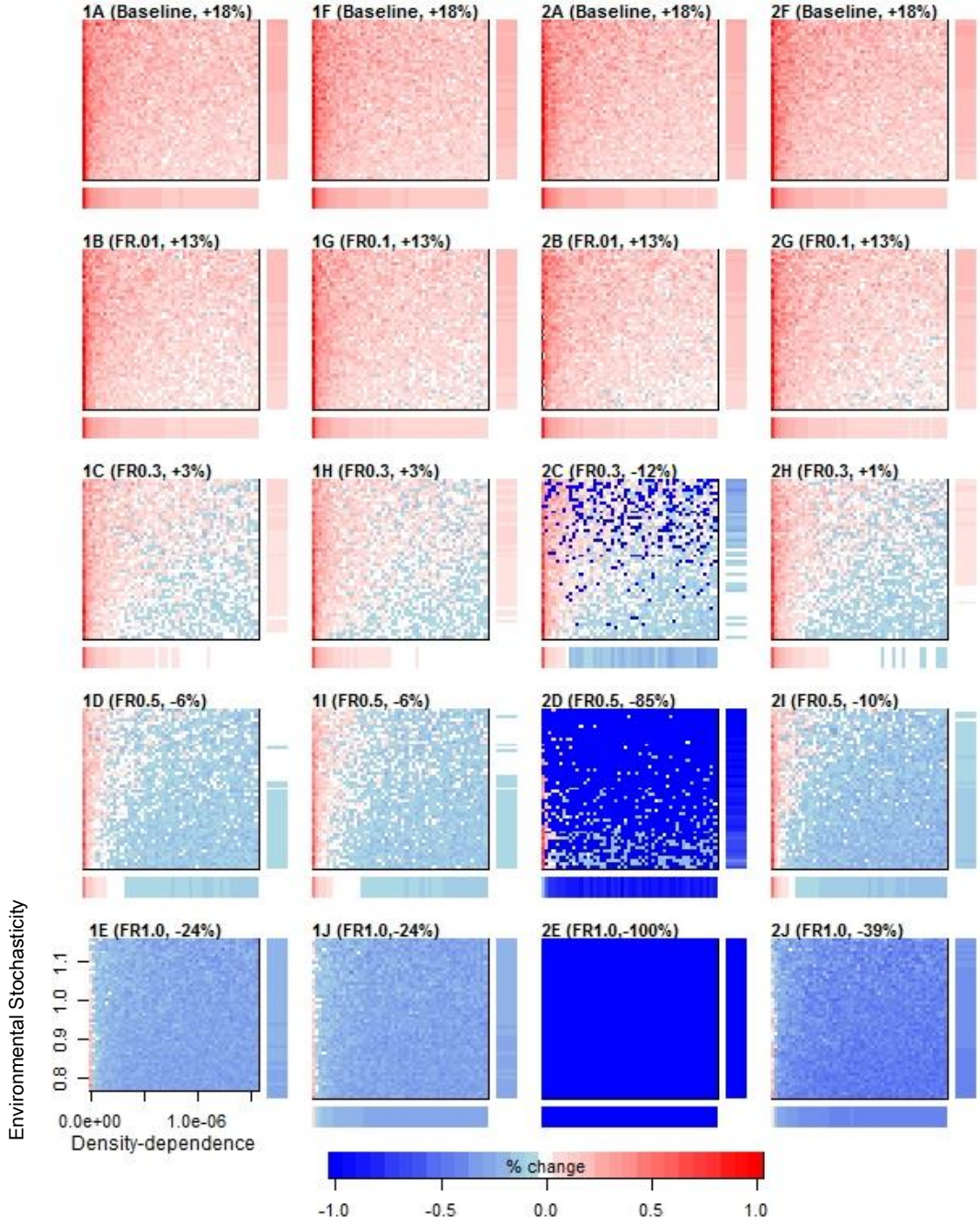

Figure 2.2 Gannet population projections under estimates of strength of density-dependence (x-axis) and environmental stochasticity (y-axis). Closed proportional removal (1A-1E) and re-seeded (1F-1J). Closed fixed removal (2A-2E) and re-seeded (2F-2J). A-J represent different mortality treatments, reporting the corresponding impact (mean population change (%) pre and post mortality) across each plot. The bands to the right and below each plot represent mean % change across rows and columns.A & F- no additional mortality (baseline); B &G- additional mortality with PBR FR of 0.1; C & H- additional mortality with PBR FR of 0.3; D & I- additional mortality with PBR FR of 0.5, E & J- additional mortality with PBR FR of 1.0. Coloration indicates impact. Blues indicate population decline, white indicate zero change and pinks through to red indicate population increases, with darkest reds being any proportional increase of 1.0 or greater.

The gannet baseline, with no mortality treatment, showed no clear pattern of population change regulated by environmental stochasticity, strength of density-dependence or any combination of these. Both closed and re-seeded baseline projections were found to have increased across the 25-year period on average (Figure 2.2, panels 1A, 2A & 1F, 2F). Under a proportional mortality there was no difference in impact between the closed and re-seeded projections. Density-dependence contributed to decline under increased proportional mortality in both (declines seen from RHS to LHS along x-axis), with the full proportional impact causing loss across much of the projected populations (mean -24%) (Figure 2.2, panels 1A-1J). In the fixed mortality analyses results varied between the closed and re-seeded simulations. Increasing mortality resulted in higher vulnerability predominantly under higher environmental stochasticity in the closed analyses (decline seen in populations nearer the upper limit of the y-axis (Figure 2.2 panels 2A-2E)) with decline more prominent under higher density-dependence in the re-seeded versions (Figure 2.2, panels 2F-2J). Closed, fixed take simulations with the highest mortality experienced extinction across density-dependence and environmental stochasticity combinations. In contrast re-seeded simulations under the same conditions averaged -39% change (Figure 2.2, panels 2E & 2J).

2.3.3 Mortality treatment results Kittiwake

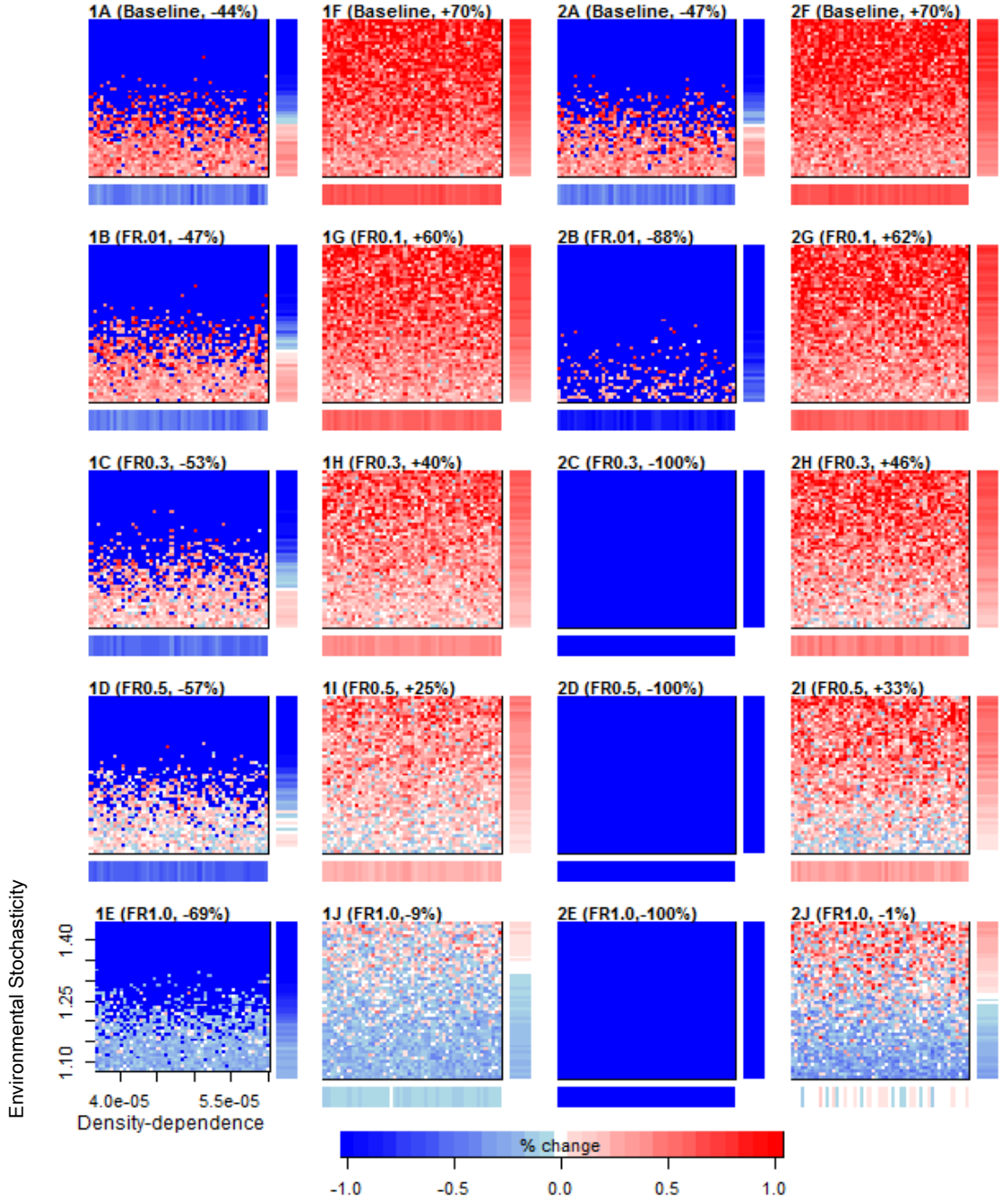

Figure 2.3: Kittiwake population projections under estimates of strength of density-dependence (x-axis) and environmental stochasticity (y-axis). Closed proportional removal (1A-1E) and re-seeded (1F-1J). Closed fixed removal (2A-2E) and re-seeded (2F-2J). A-J represent different mortality treatments reporting the corresponding impact (mean population change (%) pre and post mortality) across each plot. The bands to the right and below each plot represent mean % change across rows and columns.A & F- no additional mortality (baseline); B &G- additional mortality with PBR FR of 0.1; C & H- additional mortality with PBR FR of 0.3; D & I- additional mortality with PBR FR of 0.5, E & J- additional mortality with PBR FR of 1.0. Coloration indicates impact. Blues indicate population decline, white indicate zero change and pinks through to red indicate population increases, with darkest reds being any proportional increase of 1.0 or greater.

The kittiwake closed baseline simulations indicated extinction and therefore regulation by environmental stochasticity to all projections above a clear threshold (Figure 2.3, panels 1A and 2A). Projections below this level showed increases but no pattern was seen from density-dependence. The re-seeded baseline (Figure 2.3, panels 1F and 2F) showed increases in the areas previously declining or extinct in the closed scenarios. Closed baseline scenarios showed a mean population drop across the simulated space, whilst the re-seeded baseline found a mean increase in population change across projections (Figure 2.3, panels 1A, 2A & 1F, 2F). In the closed simulations, as mortality treatment was applied, both proportional (Figure 2.3 panels 1A- 1E) and fixed (Figure 2.3, panels 2A-2E) declined, with the fixed declining to a greater extent than the proportional projections. The re-seeded simulations were found to also decline as mortality treatment was increased, the decline was more gradual than their closed counterparts (Figure 2.3, panels A-J). Different magnitudes of decline were seen between the proportional and fixed re-seeded simulations (Figure 2.3, panels G-J). As mortality increased, those populations facing a proportional mortality reduced more than those under a fixed mortality. Overwhelmingly, re-seeded simulations maintained positive growth (dark red pixels) under high environmental stochasticity, whilst those simulations under increased mortality and lower environmental stochasticity were found to decline (blue pixels) (Figure 2.3, panels F-J).

2.3.4 Mortality treatment results Guillemot

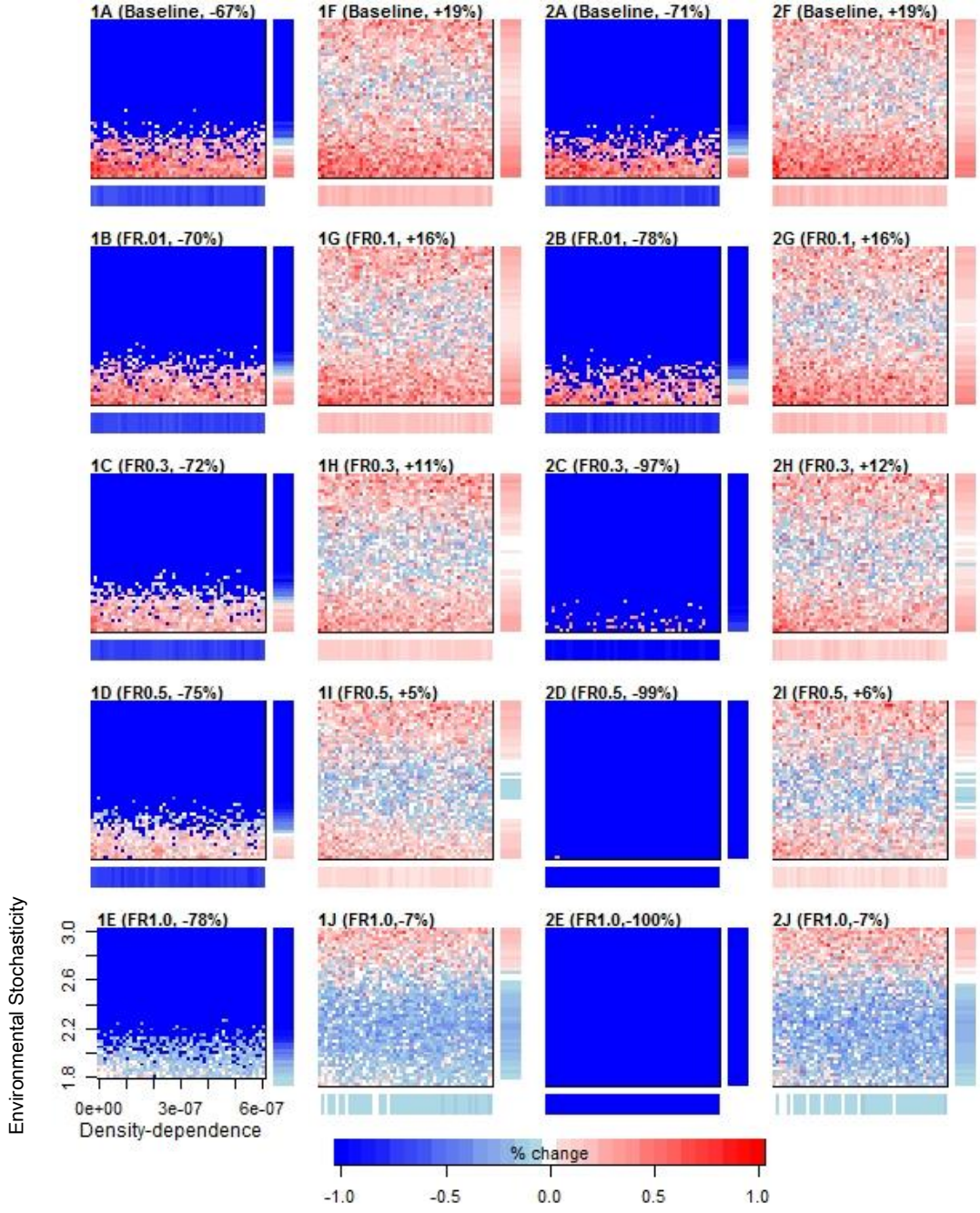

Figure 2.4. Guillemot population projections under estimates of strength of density-dependence (x-axis) and environmental stochasticity (y-axis). Closed proportional removal (1A-1E) and re-seeded (1F-1J). Closed fixed removal (2A-2E) and re-seeded (2F-2J). A-J represent different mortality treatments reporting the corresponding impact (mean population change (%) pre and post mortality) across each plot. The bands to the right and below each plot represent mean % change across rows and columns. A & F- no additional mortality (baseline); B &G- additional mortality with PBR FR of 0.1; C & H- additional mortality with PBR FR of 0.3; D & I- additional mortality with PBR FR of 0.5, E & J- additional mortality with PBR FR of 1.0. Coloration indicates impact. Blues indicate population decline, white indicate zero change and pinks through to red indicate population increases, with darkest reds being any proportional increase of 1.0 or greater.

The guillemot closed baseline projections indicated clear extinction and therefore regulation by environmental stochasticity to all projections above ~ '2.2' strength. The re-seeded populations however reversed this effect, with increases shown (Figure 2.4, panels 1A, 2A, 1F & 2F). In the closed simulations all mortality treatments reported extinctions, with mean values higher than the baseline. However, the risk of decline as mortality increased was reduced in the proportional harvests comparative to the fixed harvest rate (Figure 2.4, panels 1B-1E, 2B- 2E). The re-seeded simulations were found to also decline as mortality treatment was increased (Figure 2.4, panels G-J), the decline was more gradual than their closed counterparts. In the re-seeded simulations a very different pattern was observed than in the closed. Here, under lower mortality those populations experiencing neither intermediate environmental conditions experienced decline (Figure 2.4, panels F-I). As mortality increased, this pattern enhanced, capturing more of the middle band of environmental stochasticity as vulnerable to decline and eventually at the highest proportional mortality causing decline even in those projections with lower environmental stochasticity (Figure 2.4, panels 1G- 1J). There is also a very slight hint at density-dependent risk to decline from the bottom right-hand side of the highest mortality (Figure 2.4 plot 1J &2J) comparative to those projections with lower density-dependence on the bottom left-hand side of the same plots.

2.4 Discussion

Population persistence is a function of quantifiable effects (e.g. mortality from collisions at wind farms), population dynamics (life history, strength of density-dependence, connectivity), and random effects (variable environmental conditions) and these may conspire to cause declines in seemingly stable populations. Quantifying internal and external processes and associated population change are still fundamental problems in population biology and conservation (Elton 1924; Turchin 1995; Matthiopoulos *et al*. 2015).

In my study, exploring extended ranges for the strength of density-dependence and environmental stochasticity allowed a visual comparison of vulnerability between my study species. All three-study species presented extinctions under higher strength of density-dependence (penalized fecundity) and high environmental stochasticity (high unpredictability), but the shape of these effects varied depending on each species' demography. The gannet and guillemot time series I used for model fitting were intermittent. These lower sample sizes and the necessary data-imputation carried out by my model, extended the time necessary for convergence and generated broader credible intervals than one might expect with more data-rich populations (Appendix 1: A.1.5). Hence, my broader ranges of scenarios examined along the environmental stochasticity axis, for these populations, are also the result of greater observational uncertainty.

Under the explicit assumptions of population structure in these simulations, i.e. closedness, and in the absence of additional mortality, the baseline windows derived from the model fitting show kittiwake and guillemot straddle a well-defined threshold separating proliferation and extinction- mediated by environmental stochasticity. Notably, the gannets are not operating close to this threshold, possibly reflecting the fact that although current population growth is slowing down, the Bass Rock population has been increasing and gannets are arguably more robust to environmental perturbations due their life-history (Wanless, Murray & Harris 2005; Montevecchi *et al.* 2009; Garthe, Montevecchi and Davoren 2011). When I allowed rescue-effects, the picture changed for kittiwakes and guillemots. There is a clear indication, particularly for kittiwake, that population re-seeding can offset detrimental environmental stochasticity. The results are similar albeit more stochastic for guillemot where re-seeded simulations also offset the magnitude of decline under certain mortality treatments.

This work highlights several findings of interest to conservation strategists and population assessments. Firstly, the PBR calculation, is questionable in its theoretical sustainability of the population. Results here show clearly that for all species there were some stark reductions from the baseline mean population size under mortality estimated using PBR, exacerbated by regulatory processes. This was seen in both the closed and re-seeded simulations of each mortality type (fixed or proportional), where population baselines were not maintained. Whilst perhaps some lower levels of PBR applied mortality may be considered 'sustainable', a switch in regulation may further reduce a population, potentially

affecting sustainability. PBR has come under criticism from conservationists and industry advisors as to its appropriateness in assessment and is now broadly considered unsuitable for seabird assessment in the U.K EIA process. The results here agree with recent work suggesting it should not be utilised in seabird population management (Green et al. 2016; O'Brien, Cook & Robinson 2017).

Secondly, there is no permissible value of decline to a population under assessment from industry impact. In renewable energy impact assessment, mortality is usually applied as a proportion thereby treating the impact as a per capita effect. Intuitively, one might expect a fixed mortality to have a stronger effect on a declining population and a weaker effect on an increasing population. In most of the treatments the proportional application of mortality conveyed a reduction in mean decline comparable to the fixed mortality. However, my results also indicated different patterns in regulation and risk when the same population baseline was subjected to a proportional or fixed mortality. For example, in the kittiwake re-seeded models, risk of decline from mortality was greater to those projections under lower environmental stochasticity compared to the closed projections; the decline from baseline was marginally greater under a proportional mortality than a fixed when re-seeded. This suggests that regulation from environmental stochasticity can mediate between mortality estimate and population size to either enhance the buffering effects of the re-seeding to decline or effectively absorb the buffering re-seed. In such cases the fixed calculation may be more conservative in application than a proportional, dependent on starting population size, period of mortality and subsequent environmental stochasticity. The closed simulations showed that environmental conditions and a fixed mortality will result in extinctions. This suggests that the population dynamics, starting population size, time-series trend and regulation is crucial to consider when applying a mortality treatment. For example, the gannets at Bass Rock, an increasing population thought to slowly be reaching their carrying capacity (k) (Murray, Harris & Wanless 2015) reflected no difference in results between the closed and re-seeded simulations and a proportional take. Given the inherent positive growth of this population, re-seeding the population has very little influence on the risk of extinction. Density-dependent regulation was clear in patterns from multiple mortality treatments applied to the gannets; this does suggest that, particularly in the case of the gannets that they are likely to be sensitive to regulation from their conspecifics, such that mortality and higher strengths of density-dependence (penalized maximal fecundity) work together to confer decline. My re-seeded models for guillemot and kittiwake returned a band of decline at intermediate and lower environmental stochasticity respectively. This suggests that the guillemot, in intermediate levels of environmental stochasticity are either being simulated with successive 'bad years', lowering k and exacerbating density-dependence penalties to fecundity (reflected as a decline in % change between the means compared across timescales) or hit by successive 'good years' mediated by density-dependence and show no change. For the kittiwake example of more decline in lower fluctuations of environmental stochasticity, two scenarios may be unfolding. In higher fluctuations of successive 'good years' of environmental stochasticity, density-dependence becomes irrelevant and is

over-ridden by radical growth or in higher levels of negative environmental perturbations, re-seeding forces a recovery, biasing our proxy for impact (this % change).

With a paucity of reliable connectivity estimates between populations of the same species, closed system modelling is the preferred precautionary approach to population assessment. There is clear evidence of connectivity through immigration and emigration in many seabird populations (Horswill & Robinson 2015) and low rates of either may impact on colony population growth. My basic theoretical re-seeded models followed classic metapopulation theory where local extinctions have the potential for local increases in the face of connectivity for the kittiwake and guillemot (Hanski & Gilpin 1997). My results show a clear reduction in sensitivity to decline for many projections under this basic rescue-effect, but what it does not reveal is the true spatial population dynamics of connectivity between colonies of each species. For example, the risk of decline and extinction of a colony, one can hypothesize, will be different for those acting as sinks rather than sources within a metapopulation structure (Sanz-Aguilar *et al*. 2016). It would be of benefit to industry and conservation objectives alike to encourage research empirically and theoretically exploring connectivity estimates to examine this dynamic further in the context of regulation and risk.

Thirdly, the ongoing debate around the inclusion or exclusion of density-dependence in population assessment modelling derives from the stance that density-independent models are a more precautionary approach. My results indicate that risk of decline was enhanced by the penalty effect on fecundity at higher strengths of density-dependence under certain conditions upon application of even the lowest mortality. Density-dependence was included as a compensatory mechanism in the models. However, there is a growing literature suggesting other forms of density-dependence may be appropriate to explore in future adaptations of these models, particularly in the case of species such as kittiwake, where severely reduced population sizes can experience enhanced predation, accelerating declines (Horswill & Robinson 2015). Here I explore the effect of direct mortality, but guillemot may suffer displacement (Furness, Wade & Masden 2013). This may manifest a different pattern in impact under regulation, the ecological mechanisms of which are not captured here, but I provide a baseline method against which such effects may also be assessed.

2.5 Conclusions

Seabird populations are dynamic systems, regulated by extrinsic and intrinsic influences. Insights from this work unveil vulnerability in different seabird populations from these influences even in the absence of additional anthropogenic mortality. Assessment in wildlife systems is rarely able to derive estimates for the strength of intrinsic and extrinsic regulation reducing our confidence in PVA predictions. Clearly, as my results show, unpredictability in the environment is key to population viability and subsequent carrying capacity (Lande 1993) affecting density-dependent responses on fecundity. It is understood that extreme weather events may be more frequent, and that climate change is affecting

processes like the synchronicity of breeding attempts with prey availability and changing the accessibility of prey spatially. This approach captures information contained in demography to allow us to theorise about the risk of decline in the future, reflecting how populations may respond to unknown conditions and highlighting how regulation is affected by mortality and the sensitivity of projections to mortality treatment. I show that this method can be applicable to data-limited populations, a benefit of a Bayesian approach. Populations lacking time-series for example would produce larger credible intervals, capturing more uncertainty. Care must be taken in these instances to describe the data-limitation, rather than assume a potential greater effect signal from the process estimated. Complementing current literature, this work determines that PBR is not a rigorous tool for seabird assessment and furthermore I recommend it not be used to facilitate EIA for seabirds. Here I demonstrate that population decline, together with regulation may confer opposing outcomes of risk depending on the population dynamics and the type of mortality applied. My results suggest that populations experiencing higher environmental perturbations, such as unpredictable foraging sources, require enhanced protection from additional mortality. The responses to the rescue-effect in my analyses were interesting to note between our study species and their underlying dynamics. Further exploration of the connectivity in these systems would be beneficial. For example, my assumption that colonies experiencing more environmental dynamism might be more vulnerable is confounded by the knowledge gaps in the mechanisms of connectivity i.e. to what extent is connectivity driven by extrinsic or intrinsic factors and what is the availability of immigrants for species, such as the kittiwake, where multiple colonies are in decline? I should stress that, in the absence of empirical rates of connectivity, precaution remains with the assumption of a closed-system. Resolution of human-wildlife conflict happens at the space between over-precaution and recklessness. This can only be found and navigated with sound quantitative knowledge of the certainties and uncertainties in the systems involved. Adding realism in impact assessment can only improve upon mediating positive outcomes in both conservation, environmental and economic goals.

Chapter 3: Preface

Moving forward, with a focus solely on the red-listed Black legged Kittiwake from the Isle of May colony in the Firth of Forth, the next data chapter progresses on the baseline model of chapter two.

As this chapter is being developed with a view for publication, I am currently collaborating with my direct supervisory team and Professor Sarah Wanless and Doctor Francis Daunt from Centre for Hydrology and Ecology, Edinburgh (CEH). As such, comments received from a first draft of this chapter (in manuscript form) from both Sarah and Francis have been gratefully received in contribution to this chapter.

A note on productivity used in this chapter:

Further to examination an error in Equation 2.2 on page 29 was discovered. This equation should be a postbreeding census, described as: $B = \frac{f}{2} S_a$. The resulting error means that the equation used was: $B = \frac{f}{2S_a}$. Where B is intrinsic productivity, f is highest reported chicks fledged and S_a is adult survival.

This script typo carried over into the analyses in this chapter and as such the description of this equation as a post-breeding census has been removed from this chapter. The consequence of such an error is that the calculation of productivity in the time-series provided to the model is a higher intrinsic value, ranging from an increase of 0.002-0.15. Further information is provided in Appendix 3: A.3.2. Productivity time-series on page 156.

Chapter 3: Partitioning population variability reveals hidden relationship between environment and age.

Abstract

Population forecasting is a common tool for assessment of conservation intervention or anthropogenic impacts on wild populations. Challenges include identifying and quantifying proximate and ultimate causes of population variability, estimating underlying demographic rates and assessing the consequences of regulation to these. Some populations of animals are only reliably observed at certain life stages. Difficulty in detection of the immature cohort or seasonally migrating stages creates uncertainty in estimates such as age-specific survival rates and the relationship of these rates to regulatory environmental processes. The Isle of May, situated off the East coast of Scotland in the Firth of Forth, is a constant-effort research site for a colonial seabird, the Black-legged kittiwake with longitudinal datasets for productivity, breeding numbers and adult survival.

I first fit two naïve Bayesian state-space population models with basic environmental terms to only the productivity and breeding abundance data, reflecting commonly collected data at other colonies of this species. Under the hypothesis that environmental regulation would be differentially experienced by different age-classes, one of these models included age-specific scalars, whilst the other did not. After model selection I continued with the age-specific scalar model structure to fit multiple additional models to the same demographic data, now including additional environmental covariates: a proxy for fisheries effects, and local breeding and wider oceanographic environmental variables. Finally, I again fit the basic environmental scalar model, but this time added in additional demographic information via the time series of estimated adult survival. In every model I estimated posteriors for multiple demographic and regulatory processes simultaneously, with uninformative priors, via Bayesian Monte Carlo Markov Chain methods.

Model fit was improved by the inclusion of age-specific environmental regulation scalars. The addition of environmental covariates captured some of the variability of the environmental perturbation to productivity compared to the basic model, particularly in the case of models containing locally explicit co-variates. There was decreased variability in the survival error in a few models, indicating poor explanatory power. I found consistent patterns in mean estimates of scalars for each age-class across models. First- and third-year birds on average shared a similar impact from environment, whilst second-year birds were on average, less affected. Fourth-year/adult survival was found to have a similar or increased mean magnitude of environmental regulation compared to other age classes. The basic scalar model estimated first- and second-year birds to have the lowest intrinsic survival rate, with third-year

birds having higher estimated credible intervals and a slightly higher mean survival than the fourth-year adults. By recreating vital rates across the time-series I observed stability across the rates over time, but these models do not estimate immigration or emigration. It is environmental perturbation rather than compensatory density-dependence that has a regulatory influence on productivity in this population.

The results highlight the complexities of identifying environmental covariates influential to survival in a wide-ranging, age-structured species where information is lacking on the spatio-temporal distribution of specific ages. Quantifying latent demographic relationships with regulatory forces may allow for increased perception in predicting population consequences in the face of limited empirical information on precise drivers of survival in a wide-ranging, age structured population with a broadly unobserved immature cohort. I provide here a basic framework that performs well in examining the relative effect of environment across age-class survival and a method for capturing (by means of the full posterior) uncertainty in survival estimates of non-adult age-classes. Results suggest that there is a trade-off between increased survival through experience (age) and the costs of reproduction and central place foraging. Accounting for population structure and its likely varied response to regulation, in a simple modelling approach may capture uncertainty in modelling populations of conservation concern and enhance subsequent management.

3.1. Introduction

Wildlife population models are often employed as a tool for evaluation of risk in industrial development (Green et al. 2016), conservation strategies (Van Drunen *et al*. 2017), stock assessment (Brook *et al*. 2018), and population control (Margalida *et al*. 2015, Miller *et al*. 2016). Knowledge gaps in the demographic structure, drivers and rates of many species are caused by difficulties in empirical observation. Spatio-temporal ranges, indistinguishable age classes, sexes or variation in the age of first breeding are some examples of conditions that conspire to add difficulty in assessment of wild population dynamics. Additionally, limitations of detectability or accessibility of individuals, sample size of observations, geographical or temporal scale of data-collection, consistency of effort and ability to estimate intrinsic and extrinsic regulation means that uncertainty permeates our understanding of demography and its drivers in many species, which proliferates through demographic modelling approaches.

Long-lived animals such as seabirds generally exhibit relatively low productivity but high adult survival (Weimerskirch 2001). Due to their delayed maturity, immature or non-breeding age individuals may make up a large percentage of the total population (Saether & Bakke 2000). During the time to maturity individuals may be transient or widely dispersed before recruitment into the breeding population, increasing detection and monitoring difficulties. As birds of the marine environment, adult seabirds return, relatively predictably, to breed on land after maturation, where they function for the duration of the breeding attempt as central place foragers (Orion & Pearson 1979). During this time, because of higher accessibility and visibility many species have been studied at the colony (Croxall *et al*. 2012), where demographic processes such as productivity and adult survival may be monitored through traditional methods, such as capture-mark-recapture and breeding success methodologies (Clobert *et al*. 1985, Walsh *et al*. 1995). However, in the intervening years to seabird maturity (in some species upwards of 12 years) and for adults during the non-breeding season, the pelagic dispersal, migration and distribution of individuals has historically posed a technological challenge to empirical observation of ecological processes. Whilst technologies are advancing in this field, cost and geographical bias of data collection means observations and studies may often only sample a small proportion of a population. Consequently, there is often limited information on sex and age-based survival, distribution, recruitment, diet and behaviour (Campioni *et al*. 2015, Coulson 2011).

Recruitment is driven by the availability and survival of juvenile and immature stages, meaning imperfect knowledge of survival during these stages impedes realism in population assessments (Votier *et al*. 2008, Lewison *et al*. 2012). Philopatry rates vary across species and have been shown to be sex-biased (Coulson & Coulson 2008, Coulson 2016) while prospecting and subsequent recruitment is influenced by habitat quality and productivity, governed by intrinsic and extrinsic regulation (Kildaw *et al*. 2005, Aubrey *et al*. 2009, Coulson 2011, Fernández-Chacón *et al*. 2013). How a population

responds to regulatory processes of density-dependent competition or environmental perturbation may not only influence recruitment, productivity and survival rates of the population across time but may also work to exacerbate decline under additional anthropogenic mortality (Miller *et al*. 2019). Consequently, uncertainty around estimates of stage-specific vital rates, their response to regulatory influences and our ability to capture, empirically, these signals across time, limits our understanding of population dynamics and more critically, our ability to assess the vulnerability of a population to decline (Miller *et al*. 2019).

Seabird life stages may be differentially sensitive to environmental conditions, stimulating or curtailing population growth (Oro *et al*. 2010). Previous empirical studies have found increased vulnerability to oil spill mortality in immature stages of auks (Votier *et al*. 2008) and tagging studies have shown age-related differences in the temporal distribution of shearwaters (*Calonectris diomedea*) during migration, with differences in oceanographic conditions encountered at different ages (Péron & Grémillet 2013). There may be spatial segregation of age classes of seabirds due to competition for food especially in the waters around large colonies where intra-specific competition is likely to result in exclusion of less competitive younger birds (Pettex *et al*. 2019). Some studies have postulated that the combination of breeding costs and the constraints of central place foraging of breeding adults may confer an additional survival cost relative to the unconstrained immature age-classes (Ballance *et al*. 2009, Campioni *et al*. 2015). However, the effect of environmental stochasticity on specific life stages is hard to quantify due to the complexities in capturing and correctly attributing 'noise' in the system to the correct demographic rate in the absence of empirical information, particularly in understudied age classes.

As conservation and industry regulators seek to manage preservation of wildlife by population evaluation, population models need to develop methods that represent biological processes and their associated uncertainty to facilitate the reliability of vulnerability assessments. In species, such as seabirds, the issues of detection during immature dispersal and recruitment and adult non-breeding seasons mean that whole demographic phases of population models are data-deficient. Furthermore, the impact of environmental perturbation on any given population is difficult to identify and quantify in modelling approaches whilst fluctuations in adult abundance counts may be attributable to survival or skipped breeding as many seabird counts record only completed nests (Newell *et al*. 2016). Finally, the contribution of density-dependence to regulation of demography is also hard to observe empirically. Long-term monitoring sites regularly gather information that, combined with advanced computational approaches, can help us quantify some of these unobserved demographic processes.

Widespread across the North Atlantic, Arctic and parts of the North Pacific, the black-legged kittiwake (*Rissa tridactyla,* hereafter, kittiwake) is a small seabird maturing, typically, at age four or five. Colonial and generally site-faithful to the colony of recruitment as adults, the birds return to their breeding colony where one to three eggs are laid on a cliff nest (Coulson 2011). Their physiology limits them to

predominantly surface or shallow dive foraging, preferentially feeding on small fish species close to the surface such as sandeels (*Ammodytes spp.*) in the East Atlantic or capelin (*Mallotus villosus*) in the West Atlantic and Arctic (Furness and Monaghan 1987, Coulson 2011). The Isle of May National Nature Reserve, situated in the Firth of Forth, off the East coast of Scotland is monitored throughout the breeding season. The colony of kittiwakes here has experienced variable breeding success and an overall decline in breeding numbers over the last thirty years (Newell *et al*. 2016). The decline in abundance and the variability in productivity has been attributed both to anthropogenic fishing pressure facilitating the crash of the sandeel fishery in the Forth, a primary resource for the breeding seabirds, and to environmental change (Frederiksen 2004b, Frederiksen et al. 2007b, Frederiksen *et al*. 2008). This reflects a broader pattern in decline at other Atlantic colonies, leading to a red-listed status in the IUCN *Red-List of Threatened Species* (IUCN 2019) but there is still uncertainty over all contributory factors (Coulson 2011). Using colour marked birds, some of known age, adult survival has been estimated across years using modelling approaches (Frederiksen 2004a).

With a focussed interest in environmental perturbation across age-classes, the consequences for vital rates and the relationship of regulation to demography in the Isle of May kittiwake, here I present a method for deriving estimates of key demographic processes that are broadly unobservable in many populations. I first assumed imperfect knowledge of demographic rates and regulatory processes of this population. By fitting state-space demographic models in a Bayesian framework to combined data on productivity, adult abundance, adult survival and environmental (including prey abundance) time-series I aimed, via model selection, to evaluate the contribution of environmental variables against general perturbations of environment on the Isle of May kittiwake demography. By parameter estimation of latent processes of demography (such as immature survival, environmental stochasticity and density-dependence) I aimed to quantify and review the response of productivity and age class survival to environmental covariates. Under the specific assumptions of the method (see sections 3.2.1 & 3.2.2), I aimed to recreate vital rates across the time-series for four key age-stages and conclude with an evaluation of estimates of density-dependence and environmental stochasticity and their regulatory influence on productivity in this population across time. By drawing a comparison of the results of the simplest model with the results of the environmental models and the more demographically informed survival model, I discuss insights from this approach to colonies where productivity and abundance are the commonly monitored data.

3.2 Methods

3.2.1 The baseline demographic model

Despite variation in the age of first breeding in Kittiwake populations in the UK I assume birds mature into the breeding population at age four (Wooller & Coulson 1977). The deterministic version of the model for a species with a first-year (juvenile), second-year (immature), third year (sub-adult) and a fourth-year (adult) class would take the form:

$$\begin{pmatrix} n_{1,(t+1)} \\ n_{2,(t+1)} \\ n_{3,(t+1)} \\ n_{4,(t+1)} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & B_t \\ S_{1,t} & 0 & 0 & 0 \\ 0 & S_{2,t} & 0 & 0 \\ 0 & 0 & S_{3,t} & S_{4,t} \end{pmatrix} \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{pmatrix} \quad (2.8)$$

Where B and S represent per-capita productivity and survival, and the subscripts denote first, second, third-year and adult age classes respectively.

Productivity was modelled to better reflect female chicks fledged, with a modification for survival (see equation 2.2). The number of chicks fledged and number of animals of each age class surviving were modelled as binomial processes, except for the adult age class which assumed a Poisson distribution. The assumptions about productivity and adult survival deserve some further explanation. Kittiwake on average lay more than one egg and in the demographic time-series (before adjustment to female only) there were two years when productivity was greater than 1. Using the binomial process for productivity here is driven by the understanding that whilst biologically, kittiwakes clutch sizes (i.e. chicks from both sexes) can exceed one egg, poor productivity suggests that commonly, less than one female chick fledges on average (Coulson 2017). Therefore, a Poisson form of demographic stochasticity would regularly yield unrealistically high (4+) and low (0) annual productivities for many nests, affecting the realism of the model, particularly at low population sizes. The coupling of the female-only model with concession to binomial, better reflects reality in this population but may need adaptation of approach to populations with higher fledging success.

With regard to the Poisson assumption for adult survival, the reasoning was that many seabird populations operate as metapopulations, recruiting breeding adults into the population from predominantly other natal colonies with low reported philopatry for multiple species including Kittiwake (Coulson 2011, Coulson 2016). Resident colony adults may forego a given breeding attempt if conditions are sub-optimal (Weimerskirch 2001; Oro & Martinez-Abrain 2004). Therefore, I allowed for stochastic variation around the mean adult rate given the knowledge that these processes may work

to vary the number of adults breeding in a population from year to year. By describing the number of adults surviving in the population as a Poisson, I allowed for stochasticity around the mean, because the number of birds present in the population can exceed those produced by a closed system from the previous year. Faced with imperfect knowledge of the frequency of skipped breeding attempts by adults or of the rate of immigration, the Poisson assumption allowed the model to account for some of this additional variability, which potentially contributes to the spread of the abundance data that are recorded. By applying this distribution in this way, I cannot separate and therefore estimate the effects of survival, immigration or missed-breeders in the adult abundance, but I can account for inflation in the numbers of adults from year to year.

There is evidence across the literature for density-dependent regulation of the dynamics of seabirds, including kittiwake (Horswill *et al*. 2017). Typically, negative (compensatory) density-dependence is postulated as being the primary mechanism of regulation in many seabird populations (Horswill et al. 2017). Positive density-dependence (depensation, the Allee effect (Allee 1931)) has also been hypothesised and observed as a regulatory process in some situations and populations (Horswill & Robinson 2015). That form of density-dependence is characterised by suppressed population growth at small population sizes where competition is low, suggesting a link between a fitness trait in one or more demographic rates and a critical population size, through mechanisms such as insufficient defence from predation or compromised detection of resources (Horswill *et al*. 2017). I assume productivity to be the rate most likely to be affected by density-dependence. As long-lived organisms, the life-history of colonial seabirds indicates that they may be expected, in sub-optimal conditions to maximise investment in their own condition over investment in a given breeding event (Monaghan et al. 1989, Saether *et al*. 1993). Initially, I considered the addition of a quadratic term in the linear predictor for productivity (that would capture depensation), however initial modelling approaches in this respect suggested that the time-series abundance did not contain observations of abundance low-enough to capture, empirically, this signal. Therefore, models assumed that any density-dependence detected would be compensatory.

The probability of fledging female chicks at each time step B_t was modelled as a logit function of a linear predictor b_t thus ensuring that B_t remained bounded within the 0-to-1 range. In the baseline model the linear predictor took the form,

$$b_t = b_0 - \phi n_{t-1} + \varepsilon_{b,t} \tag{2.9}$$

Where: b_0 is the intercept; n_{t-1} is the effect of density on productivity, measured by a coefficient (ϕ), and the effect of an environmental perturbation term (e_t) comprising a time series of identically distributed Gaussian terms $\varepsilon_t \sim N(0,\sigma)$. The standard deviation (S) of this term, described the magnitude of environmental stochasticity acting on the population.

Environmental variation may affect survival at all stages (Weimerskirch 2001; Jenouvrier *et al*. 2005; Frederiksen *et al*. 2008; Lewis *et al*. 2009) and the model was developed so that this impact could vary at each life stage. In the baseline model I allocate one environmental term for productivity and an additional, common environmental term for survival at every age class. To establish if inclusion of scalar terms improved the fit of our baseline model (with no additional environmental variables), I produced a non-scalar model that included only the environmental terms as described. In the comparative scalar models, I differentiate between the magnitude of environmental effects on survival at each age class by setting juvenile survival (year one age class) as the comparative environmental term and estimate independent scalar terms to the same environmental perturbation across each of the subsequent age classes. Survival for each age class $(S_{*,t})$ was modelled as a logit of baseline survival (s_{*0}) and the environmental stochasticity (ε_t). For example, in the case of juveniles, the linear predictor took the form:

$$s_{j,t} = s_{j0} + \varepsilon_t \tag{2.10}$$

Where, for other age classes, the linear predictor in the non-scalar model took the form:

$$s_{*,t} = s_{*,0} + \varepsilon_t \tag{2.11}$$

Whilst, comparatively, the linear predictor for other age classes in the scalar model took the form:

$$s_{*,t} = s_{*,0} + c_*\varepsilon_t \tag{2.12}$$

Where c_* represents the scalar for age class two, immature, as a parameter product of the environmental stochasticity (ε_t) shared across life classes. Further environmental variables were supplied to the model additively in the linear predictors (see section 3.2.2) and their effect was scaled by the same age-specific scalar parameter to estimate the overall magnitude of environmental impact on the demography of different age classes (see Equations 3.7-3.11).

The population's initial age and sex structure was unknown, so as a plausible start (assuming equal sex-ratio), I used the population's stable age distribution values, derived from the dominant eigenvector

(Caswell 2001) of the density-independent projection matrix using reported vital rate values from Horswill & Robinson (2015). This distribution was then scaled using the fixed adult population size to derive numbers for each age class at the first time-step. Since the vital rates in the model are time-varying, the model does not assume stationarity in age structure across the time-series from this initialisation process.

3.2.2 The demographic data

3.2.2.1 Integrated population modelling

The approach of supplementing population counts with demographic data is termed integrated population modelling (Schaub &Abadi 2011). This approach can lend power and rigour to analyses of population dynamics, their underlying drivers and improve the parameterisation of forecasting models. However, uncertainty in the form of observation error exists in the empirical data used in these models. As such, appropriate capture of these errors must be incorporated into the analyses, to limit the potential for estimation error, driven by this observational error.

Models were fitted to time-series data from the Isle of May black-legged kittiwake population of 30 annual records for abundance and productivity for each year from 1987-2016 (Walsh *et al*. 1995, Newell *et al*. 2016). I describe the observational error (ε) for the abundance data as a Gaussian distribution (appropriate for over- or under-dispersed error and large counts) with precision $(\tau = 1/\sigma^2)$ derived from an assumed 5% coefficient of variation around adult abundance measurements.

$$\varepsilon \sim N(0, 0.05n_{4,t}) \quad (2.13)$$

The productivity time-series was modelled as a Gaussian distribution with a tau based on standard deviation (0.05) derived from the standard error (0.16) and sample size: years (9) from the reported colony mean (Harris and Wanless 1998).

Annual adult survival estimates were provided by Morten Frederiksen, in collaboration with the Centre for Ecology and Hydrology Isle of May Long-Term Study, based on marked-colour ring return and true adult age as per published methods (Frederiksen *et al*. 2004a) and subsequent application of method (Frederiksen *et al*. 2004b). The time-series had 26 datapoints with four missing: years 2012-2016. Confidence intervals were provided for the available time-series, these were utilised to calculate an implied standard deviation time-series: $SD_t = (upperCI_t - lowerCI_t)/4$. However, due to the missing years I attributed a prior to the implied standard deviation time-series opting for a semi-uninformative Gamma distribution: $SD_t \sim G(1,1)$ which allowed for imputation of observation error around the missing estimate years during model fit. Therefore, the adult survival time-series was modelled as a

Gaussian distribution with tau derived as $1/SD_t^2$. This approach offers a semi-informed method of estimation of survival based on the available data providing the prior for the missing years but in lieu of empirical information. As a result, the model draws on pattern and probability from the previous years to compute these data and their credible intervals.

3.2.3 Environmental explanatory variables

Evidence in the literature suggests the potential for multiple sources of environmental conditions to impact life stages of many seabirds including kittiwake. Wind strengths (Christensen-Dalsgaard *et al*. 2018) sea-surface temperatures (Frederiksen *et al*. 2007a), precipitation, storm strength and prevalence have all been shown to impact seabird distribution, phenology and demographic processes (Schreiber 2002).

In the basic model (with no environmental time-series data) I attribute generic environmental conditions to an epsilon error term, drawing the magnitude from sigma of a normal distribution centred on 0. However, longitudinal datasets exist for environmental variables that have the potential to affect kittiwake productivity and survival at each stage (see Appendix 3 Table A.3.1) (Frederiksen *et al*.2004b, Sandvik *et al*. 2005, Carroll *et al*. 2015, Carroll *et al*. 2017). It is uncertain where individuals of each age class of the colony may be situated at different temporal scales. Previous studies with birds tagged from the Isle of May and other colonies have found 80% of adults from colonies in the East Atlantic wintered in the West Atlantic between Newfoundland and the Mid-Atlantic Ridge (Frederiksen *et al*. 2012). Additional research has observed individuals from the Isle of May in the adult class migrating to the West Atlantic or East Atlantic depending on their breeding success, with additional pre-breeding movements to the mid-Atlantic in male adults in one year (Bogdanova *et al*. 2011). Additional research has found less of a connection to breeding success and movement across colonies, with tagged adult kittiwake from several North Atlantic colonies moving to post-breeding areas in the North Sea, Central Atlantic, Irish Sea and Denmark Strait, whilst other individuals migrated directly to what is considered the main overwintering area in the North-west Atlantic (Bogdanova *et al*. 2017). For other age-classes spatio-temporal distribution is less well known, with data from ringing recoveries overemphasising coastal areas but with some at-sea observational data recorded from ships offering a more oceanic account of distributions, during non-breeding season for all age-classes and in some age-classes year-round at-sea distributions (Coulson 2011). Generally, the Mid-Atlantic is vacated by kittiwakes of all ages from around May, with a redistribution to continental shelves and coasts, apparently linked to dietary switch to increased fish intake. First years come to coastal areas, not to visit colonies but to aggregate and moult, returning offshore at night to feed and rest. Second-year immature birds spend most of the year at sea. Third-year sub-adult birds may return to attempt to breed, arriving later than their older, experienced conspecifics. Many third-year birds will not breed however but may prospect, that is visit, breeding colonies (Coulson 2011). Prospecting kittiwakes exhibit squatting behaviour,

whereby they inhabit nests they did not build or attend chicks they did not produce, much to the chagrin of returning occupants. Prospecting and squatting are considered a behavioural mechanism, providing social and environmental learning for individuals to evaluate their recruitment into a particular colony (Cadiou *et al*. 1994).

Because of the inability to empirically identify suitable temporal-spatial areas to represent all age classes of kittiwake and therefore derive specific location environmental co-variates, I instead chose to include a locally relevant and broader environmental index. Using the chosen environmental indices: sea-surface temperature (SST), an environmental measure from a local area utilised by the birds during the breeding season, (NOAA High Resolution SST (Reynolds *et al*. 2007)) and the winter North Atlantic Oscillation (NAO) (Hurrell *et al*. 2003) – a geographically broad measure for weather conditions during the non-breeding season, I adapt the basic population model to assess the relative importance, if any, of these indices and the population dynamics of the Isle of May kittiwake, during the 30 year time window observed.

Sea-surface temperatures were taken from a similar locale as used by Frederiksen in his 2007 paper (Frederiksen *et al.* 2007a):55°30'-57°30'N & 1°E-3°W. Due to variation in the source grid used there is slight variation in the area analysed: 55°50-57°50 & 0.5E°-3.5W°. In a consistent spatial but lagged temporal approach I assume this locality would mainly influence the demography of the kittiwake colony around the site during the breeding season. Kittiwakes preferentially forage on age class 1+ sandeels during incubation then tend to switch to 0 class (sandeels from the same calendar year) during chick rearing (Lewis *et al*. 2001b). Productivity in kittiwake has been attributed to the abundance and availability of both classes of sandeels (Daunt *et al*. 2008), whilst kittiwake breeding phenology may be shifting to coincide with the emergence of larval sandeel stages (0+ class) (Frederiksen *et al*. 2011, Burthe *et al*. 2012). Survival of adults has also been linked to the availability of 0+ sandeel during the breeding season (Oro and Furness 2002, Frederiksen et al. 2004b) and nutritional stress during this time (affecting body condition) is also linked to survival (Oro and Furness 2002).

In a review of empirical evidence, I hypothesized that sea-surface temperature may be directly (e.g. via recruitment, reproductive investment) or indirectly (sandeel prey abundance) influential for the abundance, quality and availability of sandeel during the kittiwake breeding season and subsequently directly or indirectly affecting demographic processes of the Isle of May population. I observe the following temporal data:

Autumnal sea-surface temperature (Sst_a) is described in the models as a single annual mean value derived from daily temperature means across September to November in the same calendar year. Lagged by two years (1985-2015), this time period is biologically important for reproductive condition/investment of sandeels prior to spawning (Beaugrand 2009, Wright *et al*. 2017, Macdonald *et al*. 2018). Higher temperatures may negatively affect the quality of those sandeels for spawning, (the

0 + age class) in the next calendar year and subsequent abundance and availability for kittiwake of 1+ sandeel in the breeding season of the kittiwake time-series year.

Winter sea-surface temperature (Sst_w) is described in the model as a single annual mean from the previous December to the calendar year March derived from daily temperature means across that time. Lagged by one year, this timeframe (1986-2016) is biologically important for spawning of and subsequent recruitment of 0+ class sandeels, with some evidence of low recruitment associated with warmer temperatures (Arnott and Ruxton 2002, van Deurs *et al*. 2009) and warmer temperatures affecting reproductive investment (Wright *et al*. 2017). This represents the potential abundance and quality of 1+ sandeel available to the colony during the breeding season further to the spawning event.

Breeding season sea-surface temperature (Sst_s) is described in the model as a single annual mean value for the period of April to August of the same calendar year derived from daily temperature means. With no time-lag (1987-2017), this time period is biologically important for emergence and availability in the water column of sandeels of both 0 and 1+ age (1+ sandeels come out of their burrows during the day to forage on planktonic prey in the water, before returning to burrow at night, whilst 0 group are planktonic into May) (Howells *et al*. 2017). This variable represents the availability of those sandeels to breeding kittiwakes (and other age classes such as prospecting third years and the chicks being reared.

Files for all sea-surface temperatures were taken from NOAA open access (NOAA). Data extraction was facilitated by the available online code written by Miller (2014) with this and all subsequent analyses undertaken in R (R core team 2018).

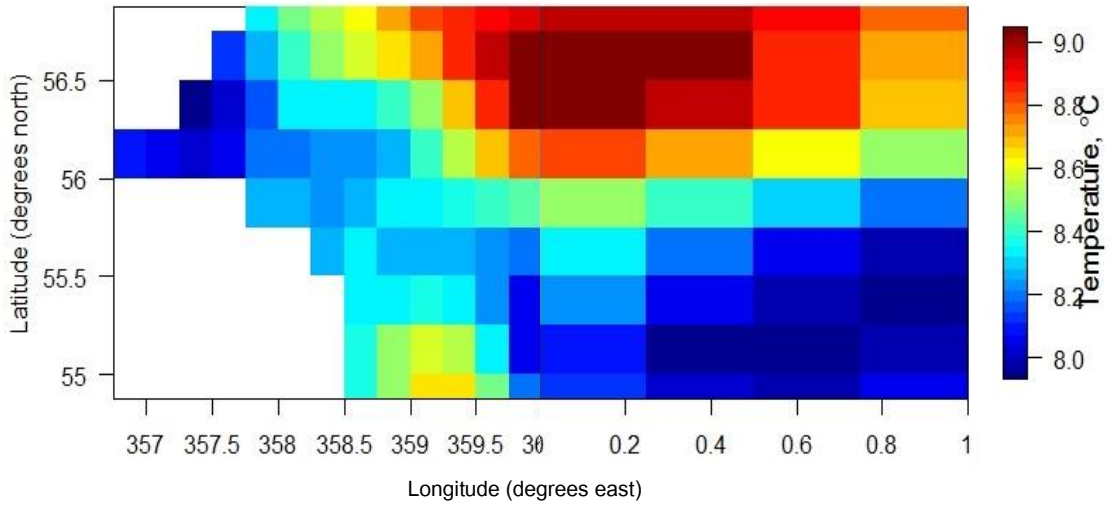

Figure 3.1: An example image plot of the daily mean temperatures extracted from the NOAA data files. The example plot taken from the 25th December 1994.

The NAO influences wind, rain and temperatures in the North Atlantic and surrounds. The index is based on differences in sea-level atmospheric pressure between Portugal and Iceland. Positive winter indices correlate with strong winter storms with generally warmer, windier and wetter winters. Positive values of the NAO index are typically associated with stronger-than-average westerlies over the middle latitudes, more intense weather systems over the North Atlantic and wetter/milder weather over western Europe. Negative are colder, drier winters (Hurrell 1995). There has been weak evidence of NAO winter values, hereafter described as NAO, correlating with seabird vital rates (Frederiksen *et al*. 2004b, Sandvik 2005), suspected due to the link between NAO and SST and corresponding impact on sandeels (Arnott & Ruxton 2002).

Environmental time-series were tested for multicollinearity using variance inflation factors in R. No collinearity was detected.

Environmental variables were incorporated into the baseline scalar model and evaluated by means of co-variates for each variable (Sst_a, Sst_w, Sst_{br}, NAO) with each having a specific co-variate for each term as a contributor to the linear predictor for productivity. Specific covariate terms were also attributed to each environmental variable for survival, shared across age-classes and contained within the parentheses for environmental error described in section 3.2.2 (Equation 3.5). For example the linear predictors for productivity b and survival at juvenile (j, age class 1), immature (i, age class 2), sub-adult (sa, age class 3) and adult (a, age class 4) for a model with winter NAO and breeding season sea-surface temperature would take the respective forms:

$$b_t = b_0 - \phi n_{t-1} + \varepsilon_{b,t} + nao_b NAO_t + sstbr_b SSTBR_t \quad (2.14)$$

$$s_{j,t} = s_{j0} + \varepsilon_t + nao_s NAO_t + sstbr_s SSTBR_t \quad (2.15)$$

$$s_{i,t} = s_{i0} + C_i(\varepsilon_t + nao_s NAO_t + sstbr_s SSTBR_t) \quad (2.16)$$

$$s_{sa,t} = s_{sa0} + C_{sa}(\varepsilon_t + nao_s NAO_t + sstbr_s SSTBR_t) \quad (2.17)$$

$$s_{a,t} = s_{a0} + C_a(\varepsilon_t + nao_s NAO_t + sstbr_s SSTBR_t) \quad (2.18)$$

3.2.3.1 Prey abundance

In addition to the chosen environmental indices I also add in a direct prey abundance co-variate. Several studies have linked prey abundance to survival (Reiertsen *et al*. 2012) and productivity of black-legged kittiwake, particularly in the Isle of May productivity (Frederiksen *et al*. 2004b, Daunt *et al*. 2008) This additional model, to complement the specific sandeel-driven SST hypotheses, took total sandeel biomass (TSB) data time-series from ICES (2018). Whilst these data are modelled on appropriate regional area designations some of the region may be outwith the foraging range of Isle of May kittiwake adults when they are functioning as central place foragers, but the dynamics of the sandeel stock over the whole defined region is considered to be coherent (ICES 2018). Previous research has indicated an on/off fishery effect to kittiwake productivity in the local area around the Isle of May (Frederiksen *et al*. 2004b). Here, I utilise the TSB sandeel dataset for the region to encompass generally available prey abundance in the area, and do not attempt to transform this data into a fishery effect by modelling catch per unit effort. Instead I assume a broad relationship between the regional available stock biomass and some underlying fishery and other contributing effects e.g. environment. The time-series was missing 6 years of data at the beginning of the study period. To recreate these data, I calculated the trend in the first ten years of available data (rather than across the whole time-series as estimated TSB post 2004 would be affected by a fishery moratorium and depletion of the stock in general from fishing effort in the previous years). Using this trend, I estimated the earlier time-series values. This method may provide a conservative estimate of total sandeel abundance for the recreated years of 1987- 1993, however, given that the sandeel fishery in the North Sea expanded rapidly in the 1980s (Greenstreet *et al*. 2006), using the trend from 1994-2004 should confer plausible estimates of total sandeel stock biomass, however I acknowledge the limitations of recreating time-series in lieu of empirical data. To manage these limitaitons and the limitations in general of sandeel estimates, to allow for error in the TSB time-series I attributed an arbitrary but plausible 20% error in reported TSB. This was then described in the model as:

$$sandeel[t] \sim N(sandeelTSB[t], 1/0.2sandeelTSB[t]\wedge 2).$$

3.2.4 Models: prior specifications and construct

Inference was performed using JAGS (Plummer 2003) and the runjags package in R (Denwood 2016). To explore the four additional environmental variables, 16 models of combined variables were implemented. All models were fitted by running two Monte Carlo Markov Chains (MCMC) to convergence (usually requiring $6e^{+05}$ to $8e^{+05}$ iterations), with decimation thinning applied to save memory. Mixing and convergence of the MCMC posteriors was evaluated for each parameter by assessing the Gelman-Rubin statistic, psrf, traceplots and effective sample size (Brooks and Gelman

1997, Kass *et al*. 1998). Model selection was carried out by the deviance information criterion (DIC) (Speigelhalter *et al*. 2002).

Table 3.1 Parameters and Prior Information

Term	Descriptor	Prior (jags)
β	Intrinsic productivity rate	0.5+0.4*dbeta(10,10)* Mean=0.7, var=0.2
S_1	Intrinsic rate juvenile	0.5+0.4*dbeta(10,10)* Mean=0.7, var=0.2
S_2	Intrinsic rate immature	0.7+0.2*dbeta(10,10)* Mean=0.8, var=0.1
S_3	Intrinsic rate sub-adult	0.75+0.24*dbeta(10,10)* Mean=0.87, var=0.12
S_4	Intrinsic rate Adult	0.8+0.1*dbeta(10,10)* Mean=0.85, var=0.1
$\varepsilon_{b,t}$	Environmental influence on β	dnorm(0,1/ σ_1^2)
$\varepsilon_{*,t}$	Environmental influence Survival	dnorm(0,1/ σ_2^2)
C_8	Scalar term for each life stage after juvenile	dgamma($4e^{-04}$,0.04) (Mean 0.01, sd=0.5)
σ_1	Environmental perturbation of β	dgamma(4,4) Mean=1, sd=0.5
σ_2	Environmental perturbation Survival	dgamma(4,4) Mean=1, sd=0.5
nao$_*$	Coefficient for winter NAO (productivity/survival)	dnorm(0,25)
sstx$_*$	Coefficients unique to each sea-surface temperature (productivity/survival)	dnorm(0,25)
sand$_*$	Coefficients unique to sandeel TSB (productivity/survival)	dnorm(0,25)
φ	Compensatory density-dependence	dgamma($1,1e^{+06}$) Mean= $1e^{-06}$, var=$1e^{-12}$

* Here the prior for the intrinsic rates uses a scaled beta distribution as a conjugate prior for the binomial. Intrinsic vital rates use a specific mean and variance as the boundaries for the distribution described as a product of the probability density of the beta, given as (10,10) for each term.

3.3. Results

3.3.1 Environmental regulation of vital rates

The addition of environmental covariates to both the productivity and survival rates was intended as an investigation of whether these covariates or their combinations resulted in a reduction in the basic error term (Figure 3.2, model rank 3) standard deviation (sigma) and thus detect an environmental signal by capturing some of the variability in the demographic rates. Table 3.2 shows the DIC results of both the non-scalar basic model with the scalar basic model (rank 3) and the rank of all scalar models. Model fit was improved upon inclusion of the scalar term (Table 3.2), thus subsequent plots do not include the non-scalar model. Figure 3.2 shows the estimate for the basic scalar model, number 3 on the DIC rank (Table 3.2). In productivity, several model combinations reduced the sigma error estimate to a similar value from the baseline (rank 3). This suggests, in those models some or all of the environmental co-variates relate to productivity observed each year. Models that did not reduce the DIC were the model ranked 2nd, the basic model plus NAO and the model ranked 12th, the basic model with additional adult survival time-series. This suggests the NAO covariate offered little explanatory power towards annual productivity as described in this model, whilst the addition of adult survival data for the model offered little explanatory power in observed productivity. In the survival plot panel (Figure 3.2), the basic sigma estimate of model 3 was reduced by the sandeel model, ranked 1st; the NAO model ranked 2nd; the winter and breeding sea-surface temperature model, ranked 4th and the 5th ranked model with NAO and autumnal and summer sea-surface temperature. The addition of the environmental co-variates increased the noise in all other model combinations from the baseline model (3). The sigma estimates from all models for both productivity and survival had overlapping credible intervals, suggesting no clear determination of statistical significance.

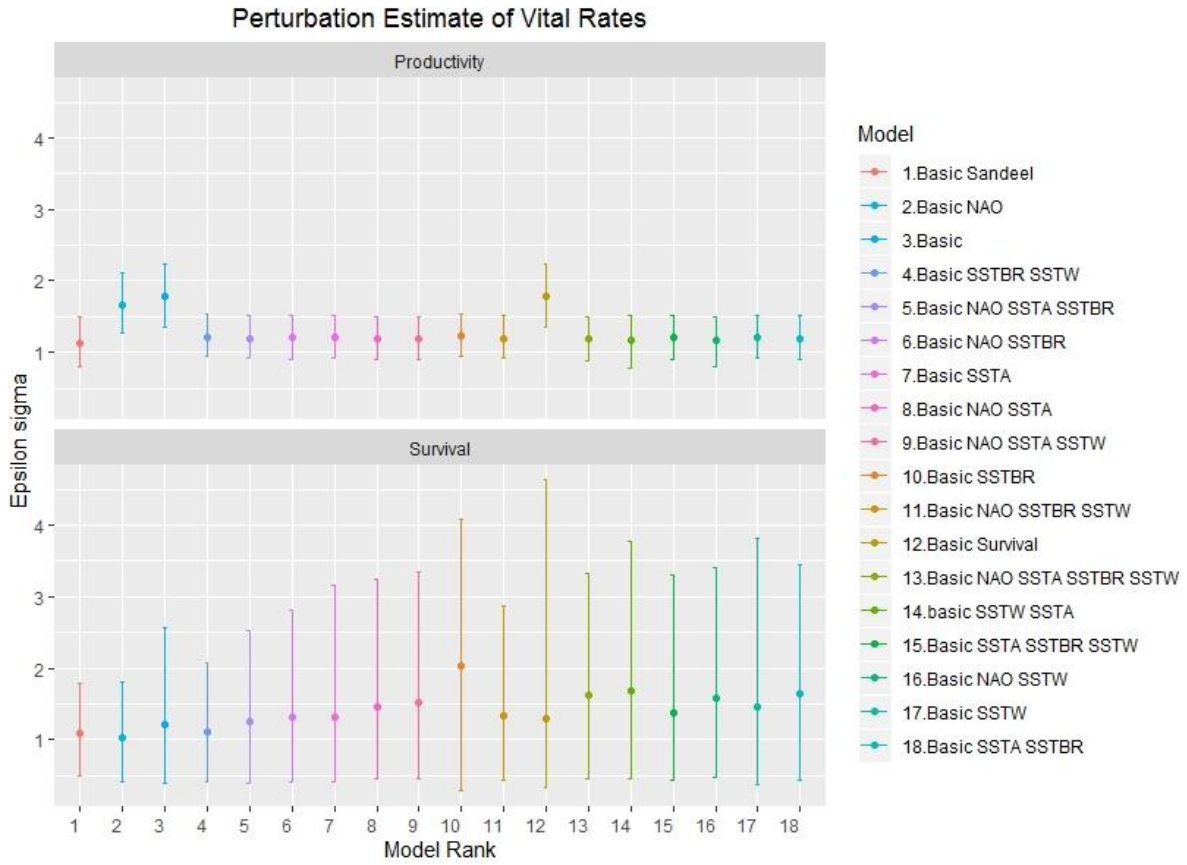

Figure 3.2: Model rank based on DIC versus epsilon sigma estimate for productivity and survival. Number 3 is the baseline model with no additional environmental predictors. Not pictured the comparative non-scalar model.

Table 3.2: Model fit: ordered by rank of DIC. *Note the survival model is additional demographic data not additional environmental and retains the uninformative basic epsilon.

MODEL	MODEL NAME	RANK	G-R	MEAN DEVIANCE	PENALTY	PENALIZED DEVIANCE
NO SCALAR						
ε_t		NA	1.01	417	53.2	470
SCALAR MODELS						
$\varepsilon_t + sandSANDEEL_t$	BASIC SANDEEL	1	1.01	288.4	43.5	331.9
$\varepsilon_t + nao_w NAO$	(BASIC NAO)	2	1.02	410.5	55.2	465.7
ε_t	(BASIC)	3	1.03	410.6	55.18	465.8
$\varepsilon_t + sst_w SST_{w,t} + sst_s SST_{s,t}$	(BASIC SSTW SSTBR)	4	1.06	410.5	55.48	466
$\varepsilon_t + nao_w NAO + sst_s SST_{s,t} + sst_a SST_{a,t}$	(BASIC NAO SSTA SSTBR)	5	1.06	410.2	55.98	466.2
$\varepsilon_t + nao_w NAO + sst_s SST_{s,t}$	(BASIC NAO SSTBR)	6	1.05	410.2	56.09	466.3
$\varepsilon_t + sst_a SST_{a,t}$	(BASIC SSTA)	7	1.09	410.2	56.3	466.5
$\varepsilon_t + nao_w NAO + sst_a SST_{a,t}$	BASIC NAO SSTA	8	1.07	410.4	56.84	467.3
$\varepsilon_t + nao_w NAO + sst_w SST_{w,t} + sst_a SST_{a,t}$	BASIC NAO SSTA SSTW	9	1.1	410.7	57.35	468.1
$\varepsilon_t + sst_s SST_{s,t}$	BASIC SSTBR	10	1.08	412.6	56.22	468.8
$\varepsilon_t + nao_w NAO + sst_w SST_{w,t} + sst_s SST_{s,t}$	BASIC NAO SSTW SSTBR	11	1.09	413	73.76	486.7
ε_t *	BASIC SURVIVAL*	12	1.02	688.5	170.5	859
$\varepsilon_t + nao_w NAO + sst_w SST_{w,t} + sst_s SST_{s,t} + sst_a SST_{a,t}$	BASIC NAO SSTA SSTW SSTBR	13	1.08	999.9	25716	26716
$\varepsilon_t + sst_w SST_{w,t} + sst_a SST_{a,t}$	BASIC SSTA SSTW	14	1.05	1974	34706	36680
$\varepsilon_t + sst_w SST_{w,t} + sst_s SST_{s,t} + sst_a SST_{a,t}$	BASIC SSTA SSTW SSTBR	15	1.08	969.6	45088	46057
$\varepsilon_t + nao_w NAO + sst_w SST_{w,t}$	BASIC NAO SSTW	16	1.07	1123	56294	57418
$\varepsilon_t + sst_w SST_{w,t}$	BASIC SSTW	17	1.04	767	79791	80558
$\varepsilon_t + sst_s SST_{s,t} + sst_a SST_{a,t}$	BASIC SSTA SSTBR	18	1.08	1965	152982	154947

3.3.2 Environmental impact across age-class

Figure 3.3 shows the results of estimating scalar values for the effect of environmental perturbations across different age classes. Estimates suggest that juveniles (age class 1) and sub-adult birds (age class 3) experience a similar impact from environmental effects with several models reporting a mean of around 1 for the 3rd Year age class (Figure 3.3, middle panel). Some of the models returned a mean above one, suggesting potential for an elevated impact of the environment to third-years comparative to juveniles, whilst one model (ranked 11) had a mean reduced from 1, suggesting a decreased magnitude of impact. Across the majority of models, including the baseline (rank 3), the adult age class (4th Year, Figure 3, bottom panel) had overall a scalar near to or elevated from 1, suggesting a similar or increased effect to adults from environmental perturbation comparative to juveniles. In the second-year age class, the immatures (Figure 3.3 top panel), the scalar for environment was reduced from 1, by almost half, across many of the models. This is suggestive that the immature (2nd Year) age class does not experience the same magnitude of environmental perturbation compared to the other age classes analysed.

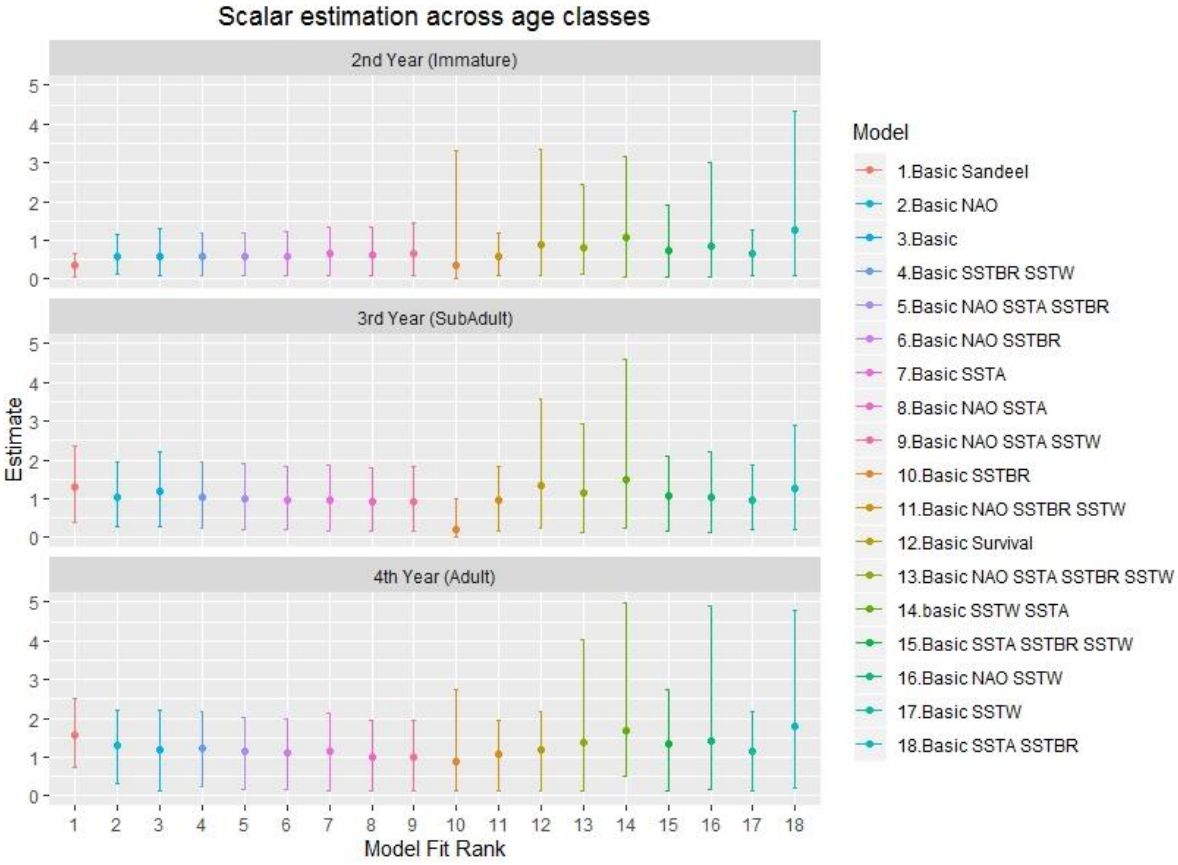

Figure 3.3 Results of scalar estimation across age-classes. Not pictured is 1st Year, Juvenile age-class which was hard-wired to a scalar of 1, against which these additional age -classes may be compared.

3.3.3 Estimating intrinsic vital rates

Results from the baseline model for estimating vital rates showed a shift in both productivity and juvenile survival from the prior distributions (Figure 3.4). the productivity posterior intercept greatly reduced comparative to the prior, but the resulting posterior mean describing the mean recorded productivity data. Juvenile survival converged across an increased range of estimates from the prior. In all of the other survival classes there were slight reductions in credible interval estimates in the posterior, immatures (age class 2) indicating an elevated lower limit, whilst both sub-adult (age 3) and adult (age 4) classes had a reduced upper limit (Figure 3.4).

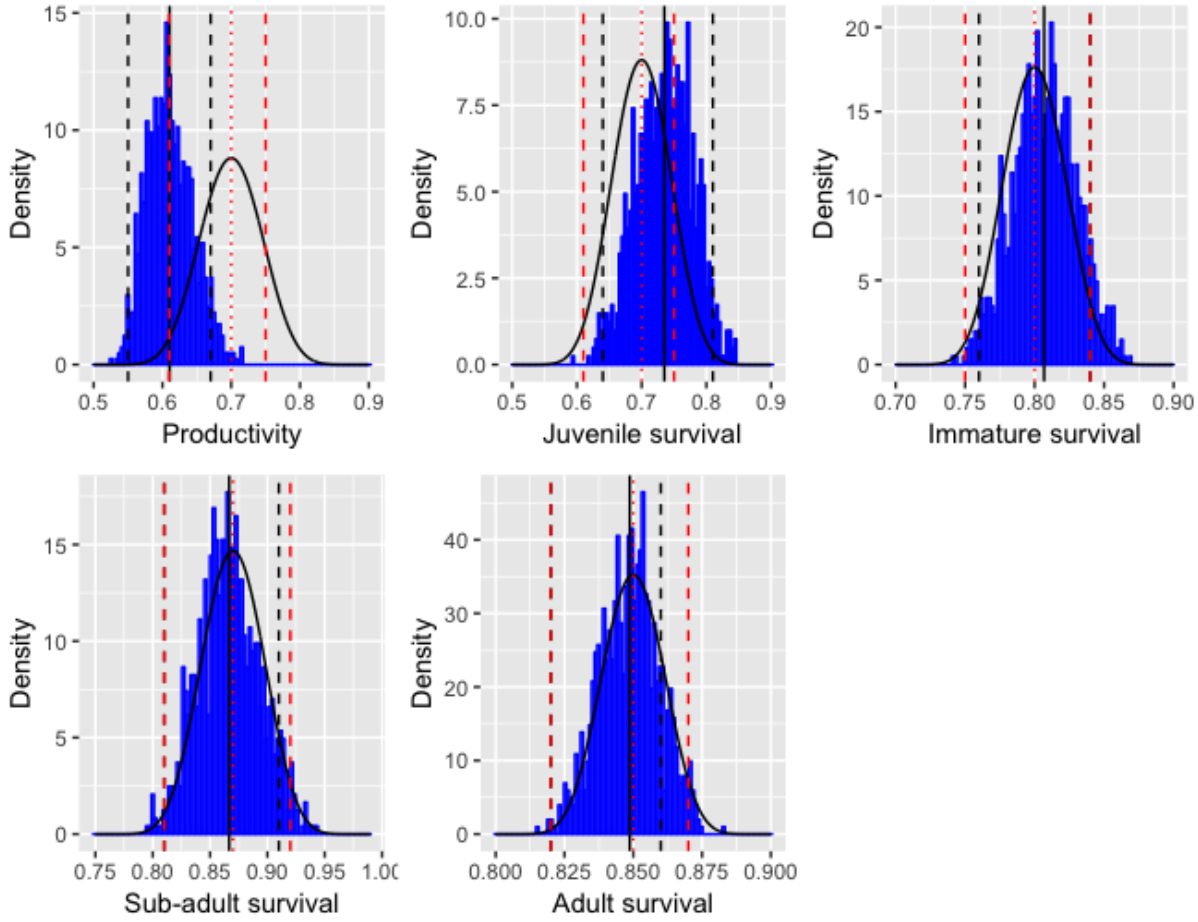

Figure 3.4: The sampled posterior (blue) against the prior density curve for each vital rate. Prior mean (red dotted line) and 95% credible intervals (red dashed lines). Posterior mean (solid black line) and 95% credible intervals (black dashed lines). Where only one colour of credible interval lines is seen there is an overlap in value.

3.3.4 Time-series and vital rate estimation

Both Plot A and Plot B of Figure 5 suggest a good fit of the baseline model to the abundance and productivity data respectively, observing a notable exception in the abundance fit during a steep drop in observed breeders in 1994 and then a sharp rise in nests the following year (1995). In plot C of Figure 3.5, the recreated vital rates for survival of each age-class at each year show no obvious negative or positive trends (no significant trend detected in regression). Productivity, the red line, follows the time-series fit highlighted in plot B, where a negative initial trend becomes more variable and then increases again towards the end of the time-series.

To confirm the predictive power of the estimated time-step vital rates for each age-class I took the initial value for the time-series adult abundance and projected the population forward using the mean estimated values for productivity and survival for each age class at each time-step in a simple matrix model in R. The results of that are shown below in Figure 3.6 alongside the observed data.

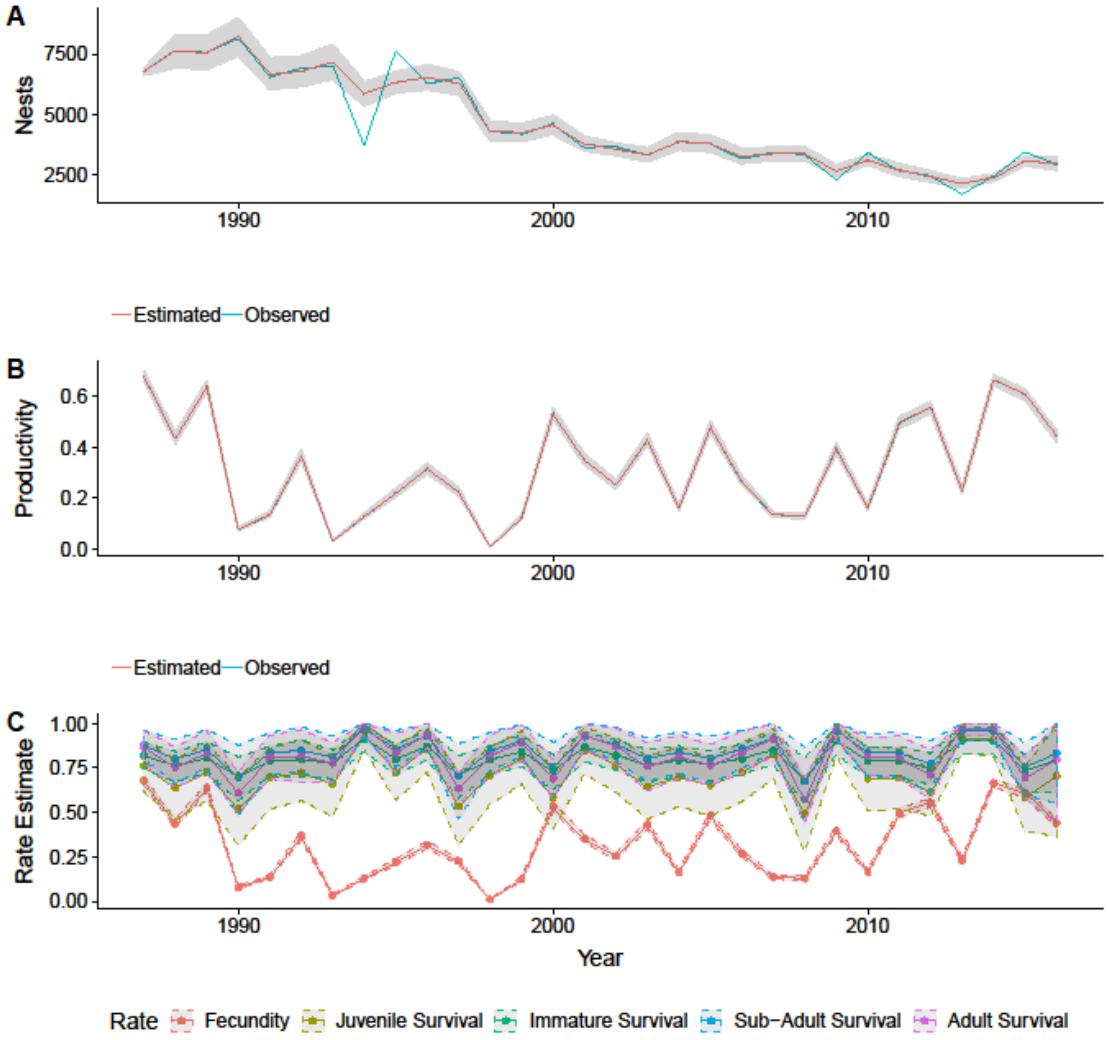

Figure 3.5: Panel A shows the model fit (red mean and grey 95% credible interval shading) against the adult breeding abundance time-series (blue). Panel B is the model fit for observed (blue) and estimated productivity (red) with grey shaded 95% credible intervals. Panel C shows the recreated realised vital rates across the same time series with shaded 95% credible intervals.

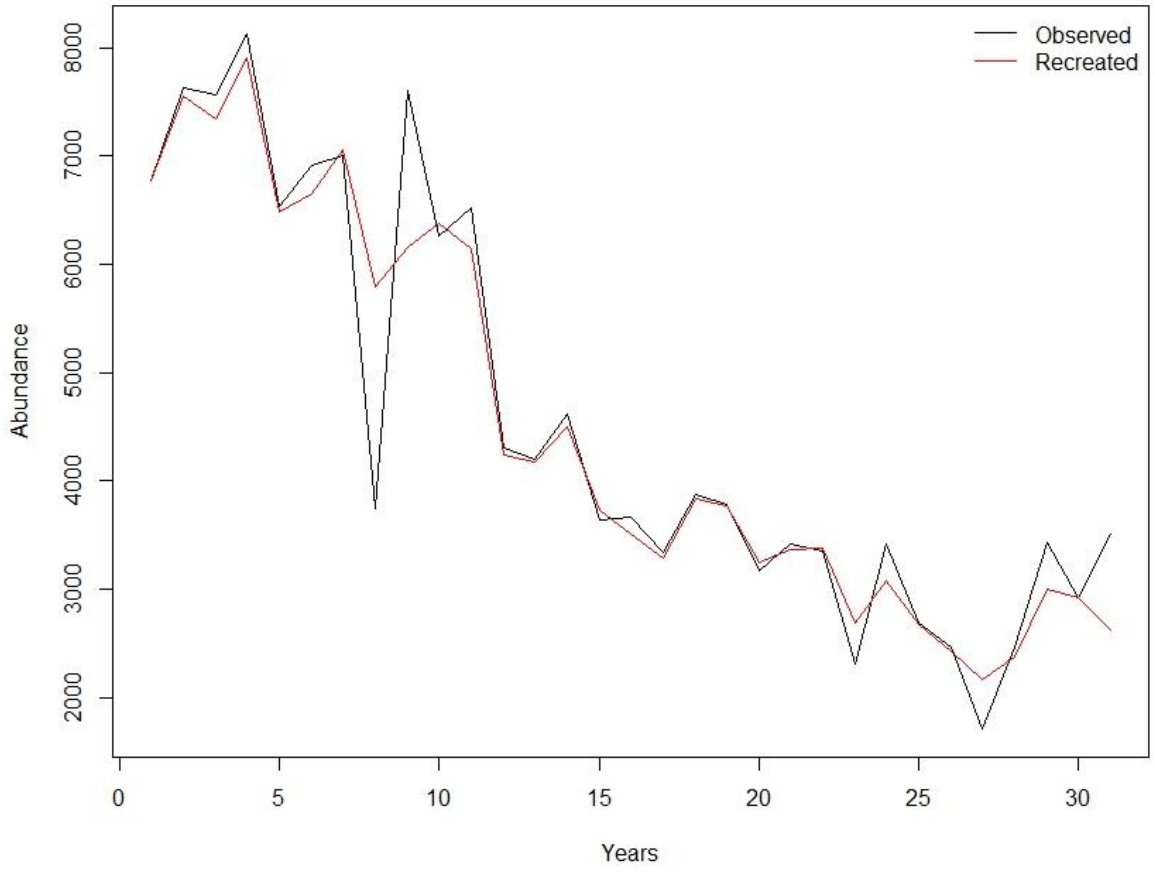

Figure 3.6: The recreated time series produced from the time series starting value and the mean vital rate estimates from modelling (red) against the observed data of breeding adult abundance (black).

I also examined how the model fit to the survival estimates provided from capture mark recapture modelling (Figure 3.7). This model, ranked 12th in the model selection, showed a poorer fit to the data (Figure 3.7) in comparison with the model that included only productivity and adult breeding abundance data (Figure 3.5). Whilst survival estimates or their credible intervals did overlap with the confidence intervals of the provided data, uncertainty was quite high in both the observed and the estimated data (Figure 3.7, panel C). The credible intervals of the adult breeding abundance estimates (Figure 3.7, panel A) were greatly increased compared to the simpler model (Figure 3.5, panel A). The fit to the productivity time-series broadly followed the same signal but with elevated estimates and reduced overlap (Figure 3.7, panel B).

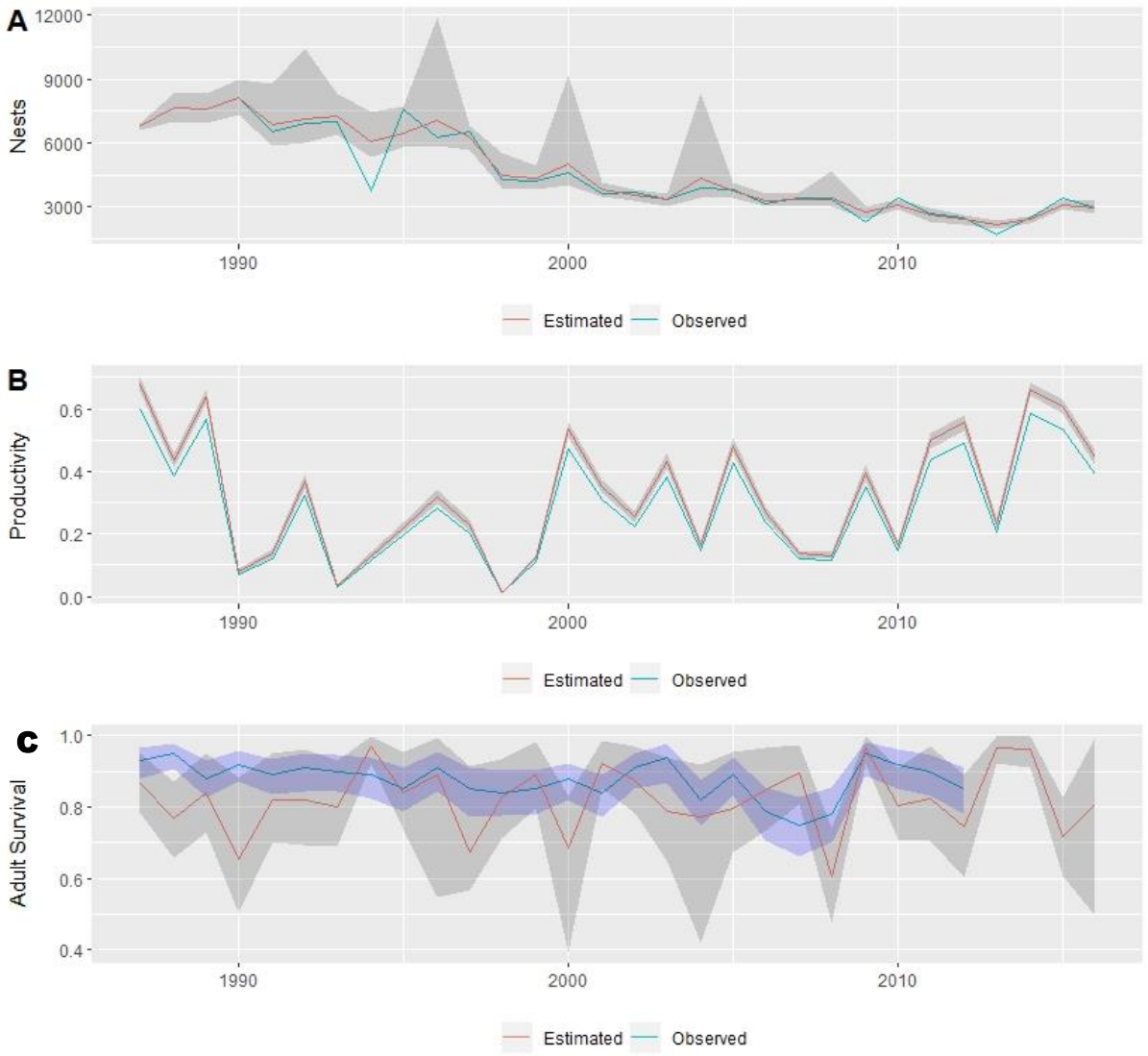

Figure 3.7: Panel A shows the model fit (red mean and grey 95% credible interval shading) against the adult breeding abundance time-series (blue). Panel B is the model fit for observed (blue) and estimated productivity (red) with grey shaded 95% credible intervals. Panel C shows the model fit for observed adult survival (blue), with blue shaded 95% confidence intervals and estimated adult survival (red) with grey shaded 95% credible intervals.

3.3.4 Regulation and productivity

Figure 3.8 presents the estimates (and their associated credible intervals) of environmental and density-dependence regulation to productivity during model fitting, set within the context of the productivity value (colour) and population size (shape size) for each datapoint.. The resulting plot indicates that productivity appears regulated predominantly by environmental regulation. There is a clear trend in the colouration from high to low productivity corresponding to the y-axis value of environmental perturbation. As expected, there is a signal of increased density-dependence when the abundance of breeding population is larger i.e. a greater magnitude of density-dependence (larger spots are further to the right-hand-side of the x-axis) and vice-versa. There appears to be no obvious pattern in breeding

abundance and productivity, with both larger and smaller populations achieving similar productivity values depending on the environmental perturbation. Whilst the credible intervals indicate very small values of density-dependence possible (truncation was applied to permit computation at low values) and therefore we cannot completely discount very low or even zero values of density-dependence in this population, the credible intervals and mean values estimated suggest there is the potential for density-dependence, however as the primary observation of datapoints is along the y-axis, environmental stochasticity is the predominant regulator to productivity in this population.

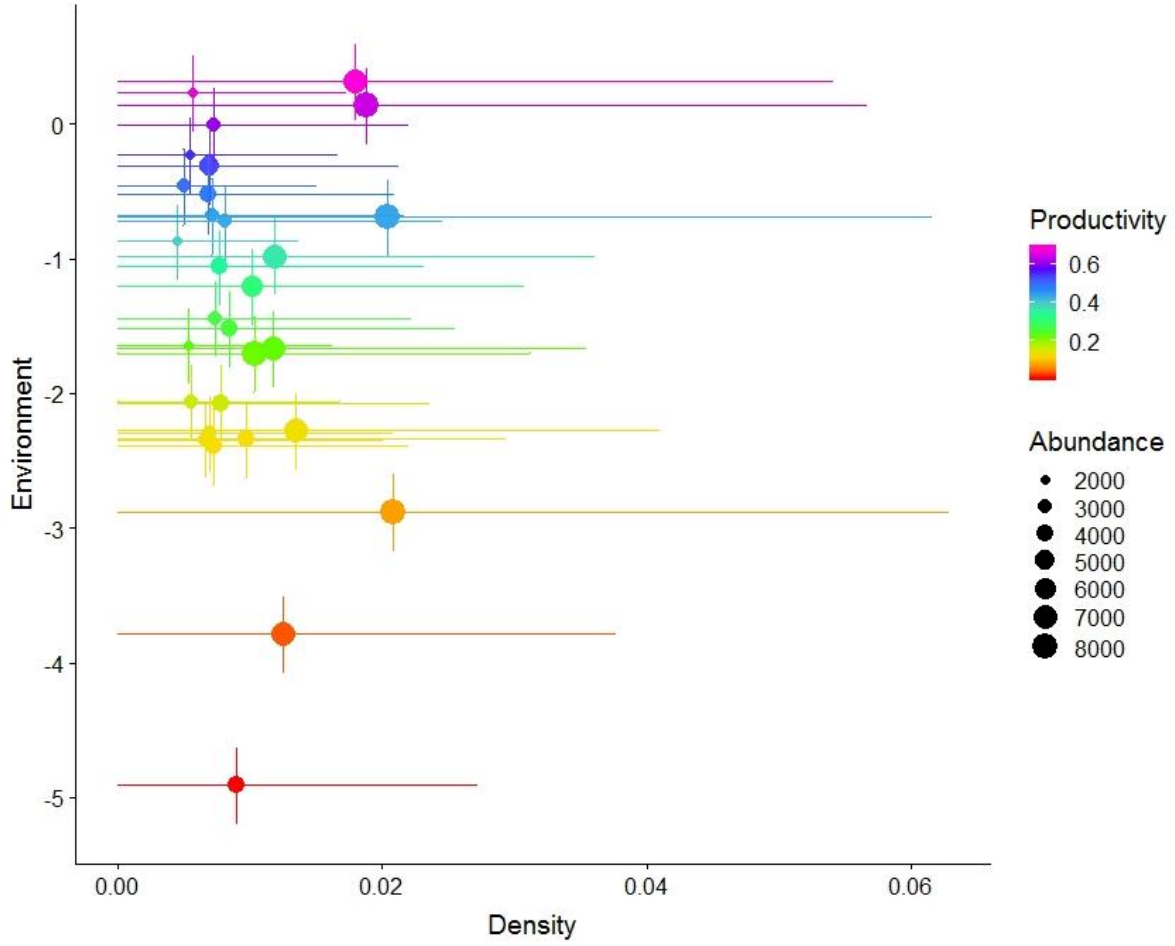

Figure 3.8: The relative contribution of density-dependence (x-axis) and environment (y-axis) to productivity across the model time-series. Each spot is coloured based on the productivity record of that year (reds being low productivity, through the spectrum of yellows, greens and blues, with purple and pinks indicating higher productivity) and sized according to the abundance record for the same year, with larger spots indicating larger populations. The cross-hair lines through each spot represent the credible intervals for density-dependence (horizontal) and environmental stochasticity (vertical).

3.4. Discussion

Unravelling the complexities of life-history and quantifying latent population processes contribute collectively to our effective understanding of population vulnerability and conservation management. If our goal is to predict or forecast population change, we must seek to understand how a population

responds to changing conditions, over time, at the level of the demographic trait. In evaluation of models I find the model of total sandeel stock biomass displays, diagnostically, the best fit. Recreation of vital rates suggests a stable population dynamic, under the assumptions of the model (i.e. connectivity not fully described), whilst estimates of regulation suggest productivity in the population is predominantly regulated by environmental stochasticity. The method used here unlocks information in a long-term dataset to identify a relationship in age-specific demographic rates with environmental regulation, previously unreported.

In the Isle of May kittiwake, there is a clear reduction from the mean environmental error for productivity upon addition of the environmental variables, with the most notable reduction in those models that included sandeel abundance and SST. This reflects published ecological understanding of the influence of sea-surface temperature and the quality and availability of sandeels during the breeding season (Lewis *et al*. 2001b, Frederiksen *et al*. 2005b, Wanless *et al*. 2007). None of the models reduce the baseline environmental error beyond the credible intervals (which might suggest significance of a contributing variable), however the basic model plus the NAO and the model with the survival estimates did not reduce the mean error from the baseline as effectively as those models with SST included. This suggests that NAO and adult survival has less explanatory power comparative to SST and prey abundance in the environmental perturbation of productivity as it is expressed in the model.

Conversely, environmental variables in the survival predictors show more variation, with only four models reducing baseline environmental error and the remainder displaying an increase in noise against the baseline. Mortality across all age classes can be broadly attributed to depreciation in condition, usually from lack of resources and or disease. There are clear indications that prey abundance in the region reduces the error in the baseline survival. Here, we mainly view a local proxy for resource quality and availability in the SST time-series and a coarser index of weather conditions in the NAO. In the non-breeding season resources may be less predictable, extreme weather events may be more common and a bird's ability to maintain condition may depend on their previous condition, age /experience and distribution. The NAO model did reduce the baseline error in survival, but unlike the presumed assumption of sea-surface temperature affecting prey, the composite indices of the NAO make it difficult to establish which aspects of the index affect survival. Since we know that wind may affect kittiwake distribution, return to the colony and subsequent foraging and breeding attempts (Coulson 2011) the warmer, more positive NAO values have the potential to confer some negative response to kittiwake survival, or perhaps NAO conditions may affect kittiwake prey or foraging efficiency. I did not attempt to assess for carry-over effects on survival, which accrue to affect condition and survival in an individual (Golet *et al* 1998, Harrison *et al*. 2010). Research by Reiertsen *et al*. (2012) found adult survival was related to prey abundance in breeding and non-breeding areas for adult kittiwakes. As was found here, their prey abundance models performed better than both SST and NAO explicit models. They suggest that the species' ability in non-breeding ages and stages to cover large geographical ranges

may buffer from direct conditions, but fishery effect and indirect climatic impacts on the abundance, rather than spatio-temporal distribution of prey may be important for survival. The complexities in these results was not altogether unexpected as Oro (2014) advises upon the difficulties and intricacies in understanding the mechanisms underpinning climate indices and demographic rates. Despite this, the models reveal a convincing consensus in estimation of the relative impact of environmental perturbations across all model combinations. We see consistently in the estimated scalar terms that juveniles and sub-adults (age three) experience environmental perturbations on or near the same scale, adults experience environment to a similar or greater degree than juveniles (age 1) and immature (age 2) birds have a reduced impact comparatively.

It is biologically sensible to assume that in long-lived birds such as the kittiwake, experienced mature birds may be buffered from environmental conditions comparative to non-breeding ages (Lescroël *et al*. 2009), however the scalar results suggest that this is not necessarily always the case. Results may be indicative of a trade-off between laying down the resources for breeding, the toll of the breeding itself and the flexibility of movement of those non-breeding ages that are not so tied to investment in maintaining pre, during and post breeding condition. In the black-legged kittiwake there is evidence of differing spatial and temporal distributions of age classes and sexes of individuals (Coulson 2011). First year and third-year life stages are attracted back to coastal regions around the breeding season, for differing reasons. Many first-year birds may loosely aggregate at the coast when they begin moult, whilst third years spend more time associating with and prospecting for colonies. It is believed that second-year birds are more oceanic in distribution at this time (Coulson 2011). Those non-breeders associated with coastal waters or colonies will also fly offshore every night. It is potentially a combination of flexibility in distribution (reduced competition/increased foraging range), additional foraging experience comparative to first years, minimal costs of prospecting and no cost of breeding that results in our signal of reduced magnitude of environment to second-year birds. Campioni *et al*. (2015) suggested ecological differentiation between adult breeding stages and non-breeding age-classes of two species of seabird were likely related to the cost of functioning as a central place forager and the energetic demands of the breeding attempt. Meanwhile, Reiertsen *et al*. (2012) suggest flexibility of movement may buffer against climatic influence, perhaps indicative of the reduced impact observed in the more transient second year age class in this study.

The results of the intrinsic productivity and survival estimates found that juveniles have the lowest survival rate, followed by second-year immatures, with adults also having a slightly reduced survival comparative to third year birds. There is overlap between the estimates and those available in literature, but with altogether lower mean values in the posterior for productivity, and slightly higher values in the posterior estimates for juvenile survival. Overall, these estimates reflect generally our understanding that the risk of kittiwake mortality is highest in juvenile and immature stages during the non-breeding season and whilst buffering of environmental impacts may be enhanced by the absence of the confines

of central place foraging in these age-classes during the breeding season, increased experience overall is probably more influential towards survival than the ability to relocate from detrimental environmental conditions. Multiple studies have observed both differential spatial and temporal movements of younger seabirds and use of more predictable food resources such as fronts/shelves by adult birds, suggesting the importance of learning and experience towards increased survival (Riotte-Lambert & Weimerskirch 2013, Péron & Grémillet 2013, Fayet *et al*. 2015, Votier *et al*. 2017). In productivity there is a shift in the posterior from the prior. Here, the posterior converges near the mean of the observed data during fitting, shifting from the naïve prior that was attributed to the model.

Assessment of the role of density-dependence and environmental stochasticity on productivity gave a clear picture of stronger environmental influence of productivity. Evidence of environmental effects on breeding success here and elsewhere has been documented (Frederiksen *et al*. 2005b, Frederiksen *et al*. 2007a, Hatch 2013). Compensatory density-dependence appeared to have only a weak regulatory signal on regulating productivity across time for this time series (during which breeding numbers changed only slightly). Testing for and modelling a signal of depensatory density-dependence is impeded by implementing the full observed population size from the island, as population sizes never get small enough to empirically observe any quadratic relationship. Often island populations in some species may be fragmented due to availability and preference for cliff-nest sites. For example, there is potential for depensation to be influencing productivity on reduced spatial scales, possibly through increased predation in areas of lower nest density. Teasing apart this signal from data-collection methods and analytical approaches, remains problematic.

Estimating the vital rates for this population across time shows that it is possible to recreate the trend in adult abundance (decline) and whilst the estimated vital rates follow a relatively stable trajectory, as expected in stable population dynamic theory (Lotka 1922). One perhaps surprising result from the model was that the addition of survival estimates did not improve model fit or time-series estimates of adult survival. There was considerable variation in the estimates of both the capture-mark-recapture and the model fit survival estimates, resulting in an overlap but no improved fit of the model as might have been expected. This model also had much larger pulses in credible intervals around the adult abundance fit and generally slightly increased productivity estimates. This could indicate an incongruence with the population breeding abundance estimate, potentially confounded with the inclusion of environmental terms which were not explicitly included in the mark-recapture estimates (Frederiksen 2004a).

Whilst I used a Poisson distribution to infer variation in the adult cohort allowing for inherent immigration and floating, non-breeding adults, I was unable to quantify these individually. There is also no mechanism for emigration defined in the model and subsequent fit. As such, the model does not adequately capture non-breeding adults that persist in the population, nor dispersal or recruitment processes that are known to operate within seabird metapopulations, particularly kittiwake (Lebreton *et*

al. 2003, Breton *et al*. 2006, Kildaw *et al*. 2008, Coulson 2011). One outcome of this is clearly seen in the model estimate of abundance on years 1994 and 1995, where there was a marked non-breeding uptake, which recovered the year after. Therefore, I suggest caution in assessing demographic rates as a mechanism for observed decline in adult abundance when the assumptions of the population model do not capture complete demographic processes. Whilst it is likely demographic interrogation at a meta-population level that includes regulation may indicate demographic drivers of decline, only a few colonies with multiple monitoring programmes have attempted to derive plausible rates due to historical limitations in data, funding and technological capability to assess such queries on a larger scale.

Finally, whilst Bayesian integrated population modelling is a powerful approach that reduces or at least captures uncertainty in the posterior distributions, some of the results here suggest replicated designs of this study should consider broadening the assumptions of error in the observation part of the model. For example, the error associated with productivity is perhaps too conservative and should be widened to better represent the potential here for error. Not fully allowing for errors in integrated modelling approaches can lead to further inaccuracies or miscalculations, for example- does the performance of the survival model (that includes a better accountability of observation error) improve when we widen our observation error potential of productivity(which has an arbitrary and arguably conservative error)? Another area of adaptation in future versions of this model should include wider prior limits for the distributions of the vital areas- as we observe a shift along the axis of productivity and quite a tight fit to some of the more conservative priors. Relaxing these may confer further information towards more robust estimates of the vital rates and help eliminate any potential influence of the priors in contribution to scalar patterns, conclusively.

3.5 Conclusions

Here, I present a method for unlocking information in demographic processes using data from multiple breeding seasons. I establish the informative capabilities of environmental indices to demographic models as explanatory variables and show that, overall, the uninformative model with simple epsilon term performed well, fitting to time-series of productivity and abundance comparative to those with additional information. From this approach I also highlight a method for structuring and subsequently quantifying the relationship between environmental perturbations and age. This approach more realistically describes the trade-off between age and flexibility of foraging with experience, particularly during the breeding season (scaling) and non-breeding season (survival). This work highlights the ability to estimate regulatory processes empirically, although I recognise potential difficulties in modelling fragmented sub-populations within a larger population. I suggest future advances on this approach could include some metric for prey in known wintering areas, whilst continued or increased capture mark-recapture studies may improve survival data fit.

Chapter 4 Preface

In this chapter I take the foundation models of chapter two and the advances made in chapter three models to estimate metapopulation dynamics of kittiwake populations in the Shetland region. Acknowledgements must go to Doctor Luca Nelli, in assisting me with mapping my results in R and providing me with shapefile maps and code for R. Thanks also to Helen Moncrieff for an evening discussion on breeding kittiwake in the Shetlands and Orkneys.

A note on productivity used in this chapter:

Unlike the previous two chapters, productivity supplied to this model was not adjusted to account for a post or indeed a pre-breeding census. Productivity was adjusted by *0.5, to represent a female only modification for productivity under the assumption of a 1:1 sex ratio. More information is provided in Appendix A.4.3 on page 164.

Chapter 4: Estimating connectivity and vulnerability in a metapopulation: a case study of Shetland Black-legged kittiwakes (*Rissa tridactyla*).

Abstract

Seabird colonies have long been acknowledged as forming metapopulations, but due to difficulties in effort, technology and accessibility, the underlying connectivity between them has not been empirically measured.

Due to this knowledge gap, as part of a precautionary approach, environmental impact assessment evaluates the viability of single colonies as if they were closed populations. However, following metapopulation theory, we understand that connectivity may enhance viability of populations or conversely dynamics such as source-sink may confer overlooked vulnerabilities to sub-populations in a network. For example, those populations that are sinks, may be negatively impacted should their source population/s be subjected to additional anthropogenic mortality, such as from an offshore renewable development.

Using hierarchical Bayesian state-space modelling, I provide a method of theoretical quantification of the connectivity in a regional metapopulation of black-legged kittiwakes (*Rissa tridactyla*) in Shetland, UK. Here, I estimate connectivity as an annual per-capita probability of transition between two colonies, based on the relationship between density-dependent productivity at the natal colony, versus productivity at other colonies in the network as a function of distance. Results from model fitting to time-series of demographic variables, estimated mean connectivity as a decay curve moderated by distance. This inferred that the probability of transfer from one colony to another was moderated both by distance, breeding success and regulation from density-dependence.

Subsequent metapopulation projections under several additional anthropogenic mortality scenarios found spatial disparity in the persistence of colonies under closed and metapopulation simulations. Applying mortality treatments to Special Protection Areas identified Fair Isle to be influential in contribution to other colony sizes in the metapopulation, providing emigrants to many colonies in Shetland. Under most treatments, Fetlar was the only SPA to display positive growth under current conditions. This work provides the first evidence of its kind of estimates of a regional metapopulation derived from empirical data and highlights, via sensitivity to additional mortality, key component populations that are influential to colony persistence across the region.

4.1 Introduction

Spatially structured metapopulations, follow a dynamic in which there is some connectivity or transfer of individuals from one population or 'patch' to another (Levins 1969, Hanski 1999). Patches in the classic theory may be considered broadly homongenous in quality, with extinction and re-colonisation events stabilising and allowing for a robustly persisting metapopulation. Persistence of any singular sub-population within a network may be subject not only to forces of extrinsic and intrinsic regulation but also to net recruitment from connected sub-populations, driving population growth and subsequent continuance (Pulliam 1988). Because population patches may vary in quality, 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 a population where the growth rate is positive at low densities may be key in persistence of sink populations, where the growth is negative at low densities and in the absence of immigration (Thomas and Kunin 1999). Pseudosink populations may be observed exhibiting traditional sink dynamics in the presence of the source population but can enable metapopulation persistence in the event of source extinction via maintaining a reduced carrying capacity (Holt 1985, Watkinson and Sutherland 1995, Thomas and Hanski 1997). The origin of immigrants may come from one or more source sub-populations within the network (Holt 1997). Those populations that become extinct may, in time, become recolonised again by immigration (Hanski and Gilpin 1997). Source colonies are key to metapopulation persistence if in the long-term the pseudosink populations cannot maintain survival (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 1997). 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. Understanding the mechanism of dispersal: an individual's decision to leave (emigrate) or the decision to settle from elsewhere (immigrate), be it social, environmental or through some other informed process remains to be fully answered for many species.

Wildlife populations are often assessed for vulnerability to anthropogenic impacts in environmental impact assessments during development planning. For example, in the UK offshore renewables industry, developments in proximity to Special Protection Areas (hereafter, 'SPAs') designated for breeding seabird species or assemblages are legally required conduct an assessment of their potential impact to the integrity of the SPA (Birds 2009/147/EC Birds Directive). During assessment, populations are described as closed (i.e. having no immigration or emigration effects in their population dynamics), however it is widely accepted that seabirds live in spatially structured metapopulations (Klomp and Furness 1992, Cam *et al*. 2004, Coulson 2011, Votier *et al*. 2011).

Seabirds are long-lived, slow-maturing and wide-ranging animals with often low reproductive output (Bried and Jouventin 2002). Many species are ubiquitously found in breeding colonies around the UK and the wider Western Palearctic (JNCC 2009). Observations of marked breeding adults of many species often present high nest-site fidelity, however marked pre-breeders from many species have been found to recruit (settle to breed) into breeding colonies other than their natal one. The degree to which both philopatry (the recruitment into the natal colony) and emigration (the recruitment into a colony other than the natal colony) operate varies both interspecifically and intra-colony within a species (Coulson 2016). For example a study of Black-legged kittiwake (*Rissa tridactyla*) (hereafter, 'kittiwake') from North Shields colony in the UK reported 9% female and 36% male philopatry in recruits born in that colony (Coulson and Coulson 2008), whilst studies of other species such as the Great skua (*Stercorarius skua*) report a very high philopatry of >90% (Klomp and Furness 1992). Meanwhile studies of ring recoveries reported ~60% philopatry in kittiwake (Wernham *et al*. 2002). The spatial migratory and dispersal range of seabirds is vast. For example, a kittiwake study found individual birds recruiting to colonies up to 1000km from the natal colony (Coulson and Coulson 2008). However, much of the research into kittiwake dispersal and recruitment in UK colonies indicates a potential bimodal decay curve, reflective of a relatively local dispersal followed by occasional greater dispersal distances (Coulson and Neve de Mevergnies 1992, Coulson 2016) (Appendix, Fig. A.4.1). This ability to disperse widely after fledging combined with the large scale of colonies available to recruits, implies unfeasibly high mark-recapture effort for direct estimation of dispersal distances (particularly for the extreme tail of that curve). Therefore, in the absence of the ability to quantify connectivity directly, precaution has retained the assumption of closed-ness.

Immature dispersal and subsequent recruitment is a key driver of demography in seabirds and many studies are offering insights and evidence towards identifying the mechanisms that may underpin a seabird's decision to leave or emigrate and that which may affect its decision to recruit and immigrate into a particular colony. In the years before maturity, evidence increasingly suggests pre-breeding individuals of many species may 'prospect' several breeding colonies, before ultimately recruiting (Hatchwell and Birkhead 1991, Klomp and Furness 1992, Boulinier *et al*. 1996, Coulson 2011, Bicknell *et al*. 2014). The understanding is that social, qualitative information is received by the prospectors, assisting them in recruitment decisions. Several studies have suggested the mechanisms of decision making in recruitment to a particular colony. Conspecific attraction (Stamps 1988, Reed and Dobson 1993) is thought to offer information as an initial visual cue of recognising a potentially suitable patch (Kress 1983, Kress 1997, Danchin *et al*. 1991, Parker *et al*. 2007). Conspecific attraction has been found also in nocturnal seabirds via audio cues (Major and Jones 2011) and attraction to other recruits (Szostek, Schaub and Becker 2014). There is evidence that individuals may then gain further information on the attributes of a patch by observing conspecifics in an adaptation of public information theory (Valone 1989, Valone and Templeton 2002, Danchin *et al*. 2004). Indeed, Cam *et al*. (2004)

found colonies of Audouin's gull (*Larus audouinii*) attracted more dispersing breeders via conspecific attraction, but additionally they also found the probability of movement was also influenced by productivity, indicative of observing conspecific success and subsequent attraction. Other studies have indicated that the breeding success of conspecifics may be an indication of habitat quality, mediated by environmental conditions and density-dependence (i.e. food availability, predation, and parasitism) (Danchin *et al*. 1998, Doligez *et al*. 2003, Boulinier *et al*. 2008).

Availability of mates (Gauthier, Milot and Weimerskirch 2010) has also been found to influence recruitment decisions, whilst nest-site availability, neighbour aggression and position within the colony affect both competition to settle and attraction for settling (Birkhead and Furness 1985, Porter and Coulson 1987, Coulson 2011). How then do new colonies form in such clearly gregarious species such as seabirds? Why would a pair of individuals or group decide to settle somewhere 'new'? Forbes and Kaiser (1998) suggest that in order to break the 'information barrier' of a new site (N.B. the site may have historically been occupied) there must be a trade off in the cost of recruiting at an existing site exceeding that of forming a new colony. A study in a Pacific colony of kittiwakes found that the quality of established colonies was influential as to whether or not new colonies would form (Kildaw *et al*. 2005). Once a new colony formed they saw higher productivity despite the probability that most of the recruits were likely inexperienced birds (Kildaw 2005). Recolonisation events have also been documented at those colonies that have been managed for predator eradication (Ratcliffe *et al*. 2010). After recolonisation, growth may be slow and eventually crowding may ultimately diminish habitat quality (Fretwell 1972, Ratcliffe *et al*. 2010). Most seabird species will display high nest-site fidelity after they have recruited into a population, however, although posited to be rare, movement of adult breeders has been found with decline in habitat quality, sustained declining trends, low productivity and colony size (Oro and Ruxton 2001, Tims *et al*. 2004, Kildaw *et al*. 2005, Fernandez-Chacon *et al*. 2013).

Arguably, there are probably several mechanisms functioning in dispersal decisions depending on the species, the region, the general population size, prevailing local stressors (disturbance, parasitism, predation, environment), sex-bias in movement and availability of resources. Unravelling these components in a wild system is complex. Ponchon *et al*. (2015) showed that populations were differentially vulnerable to metapopulation processes and stochasticity. They found philopatric or random dispersal models of kittiwake metapopulations suffered extinction, whilst informed or semi-informed dispersal maintained those metapopulations. In a study of demography of several kittiwake colonies in the Atlantic and Pacific, net recruitment was inferred from modelling growth rate against survival and productivity data from the colonies studied. The colonies studied showed distinct variation in demographic rates and, in particular, one colony on the metapopulation periphery was found to have net recruitment requirement to sustain growth (sink), whilst another probably had net emigration (i.e. acted as a source)(Frederiksen *et al*. 2005a).

If a population under assessment for the impact of additional mortality, is a particular sub-population within a metapopulation process and is evaluated as a closed system we may confer erroneous results that may conflate or negate the precautionary approach meant to safeguard from decline and extinction. Depending on the dynamic of the metapopulation there may be several ways that connectivity proliferates through the system adding complexity towards a true evaluation of extinction vulnerability and impact from additional mortality (Ponchon *et al*. 2015). For example, if following a source-sink dynamic, sink populations may become extinct if the immigration they rely on to persist is halted, for example via additional mortality to a source population. Perhaps transfer of individuals in a metapopulation is uniform, therefore perhaps additional mortality would impact across a metapopulation and depending on the size of the population or magnitude of the additional mortality this again may potentially affect sub-population persistence. Finally, if colonies do exist in isolation there may be a threat from extinction from high philopatry, which under regulation may become an ecological trap, inducing decline or extinction (Ponchon *et al*. 2015).

Here, I fit a Bayesian state-space hierarchical model to time-series data (1986-2017) of adult abundance and chicks fledged from monitored nests across 84 kittiwake colonies in the Shetland archipelago (including Fair Isle). With evidence from literature, I assume a relationship between productivity at colonies and distance to be a potential mechanism of dispersal between colonies. I aim to use this model to ask:

Can we estimate connectivity and if so, what is the relationship of connectivity in our metapopulation fit? Are colonies uniformly transferring individuals across distance, existing in isolation or is there transfer as a function of productivity and distance? Can I estimate this connectivity by fitting the model to indirect information (i.e. population counts)?

Using the results of these initial investigations I then restructure the metapopulation model into a PVA. I simulate the Shetland region (including Fair Isle) with no additional mortality both as a metapopulation and the industry standard closed assumption. I aim to evaluate ifthere are differences in outcomes for the region between simulations.

By applying additional mortality scenarios in decreasing precaution to protected SPA colonies I then aim to evaluate by comparison of treatments if there is any evidence of source-sink dynamics, net emigration or net immigration in the metapopulation. For example, how does additional mortality from key kittiwake colonies impact upon SPA colonies and the regional population as a whole?

It is important to note that this case study is of the Shetland kittiwake metapopulation as it was during the study period. The case study was selected because the historical data were suitable for analysis, and not in order to make predictions about the future of this particular population (which in practice is not subject to offshore wind farm impacts as there are no offshore wind farms in Shetland waters).

In discussion of the outcome of these questions, I summarise their context for seabird population ecology, offshore development and impact assessment.

4.2 Methods

4.2.1 Defining a metapopulation

In order to define an area to describe as my metapopulation I had to consider the specifications of connectivity within the evidence and context of my species.

The JNCC seabird monitoring programme (SMP) (Walsh *et al*. 1995, JNCC 2018) hosts over 1000 kittiwake colony entries across the UK. Faced with an unknown definition of the kittiwake metapopulation, as a start I focussed my potential metapopulation region based on a feasible distance of transfer between colonies 50-150km apart, capturing the local decay curve in previous empirical studies (Appendix 4: Fig A.4.1) (Coulson and Neve de Mevergnies 1992, Coulson 2016). To select a region, I chose an identifiable productivity cluster taken from the work of Frederiksen *et al*. 2005b. They found spatial cluster patterns in the breeding success of kittiwakes in the UK, linked to sandeel aggregations in identifiable regional aggregations (Frederiksen *et al*. 2005b). One of these regions, Shetland (including Fair Isle), has 84 registered kittiwake colonies on the SMP including six master sites designated by law as Special Protection Areas, hereafter SPA. In general, the Shetland region has seen a decline in adult kittiwake abundance almost halving from the 1980s to the 1990s (Heubeck *et al*. 1999), with decline linked to sandeel availability (Beaugrand 2004) and increased predation by great skuas (*Stercorarius skua*) (Oro and Furness 2002, Votier *et al*. 2002).

Philopatry rates vary in the literature with issues of bias and effort and variation between colonies (Wernham *et al*. 2002, Coulson 2016). I do not, in this model specify a specific mechanism for philopatry, rather, I assume that philopatry rate is contained in the transfer probability as estimated during model fit. For example, if the model estimates no transfer probability then we may assume complete philopatry, resulting in a closed system with colonies operating in isolation.

Colony co-ordinates were uploaded and analysed in R (R core team 2018). Kittiwakes would not commonly travel ‘as the crow flies’ over landmass, therefore by use of land masking tools, colony distances along the coastline from the i^{th} colony to the j^{th} colony were calculated in km and stored in an 84 by 84 matrix: $(d_{i,j})$. The metapopulation colonies and associated SPA are presented in Figure 4.1.

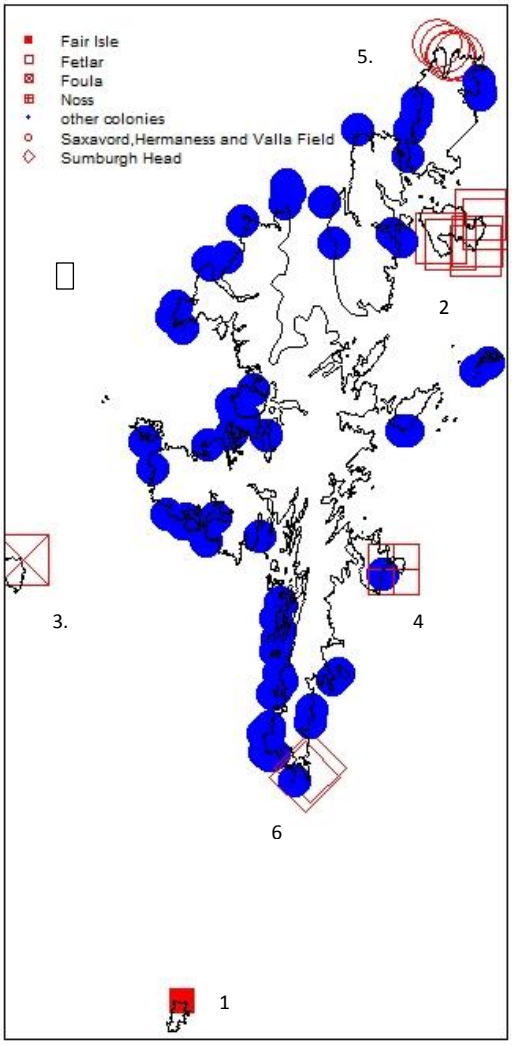

Figure 4.1:The 84 colonies of kittiwake recorded on the SMP database to be modelled as the metapopulation. The legend shows symbols for all colonies (blue circles) and those considered to be part of a parent SPA (red shapes). There are 6 SPAs: 1.Fair Isle, 2.Fetlar, 3.Foula, 4.Noss, 5.Saxavord Hermaness and Valla Field, and 6. Sumburgh Head.

4.2.2 The demographic metapopulation model

The model assumes in general that kittiwakes mature at calendar year four (Wooller & Coulson 1977) giving each population an age structure that follows first-year (juvenile), second-year (immature), third year (sub-adult) and a fourth-year (adult) class taking the form for each population:

$$\begin{pmatrix} n_{1,(t+1)} \\ n_{2,(t+1)} \\ n_{3,(t+1)} \\ n_{4,(t+1)} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & B_t \\ S_{j,t} & 0 & 0 & 0 \\ 0 & S_{i,t} & 0 & 0 \\ 0 & 0 & S_{sa,t} & S_{a,t} \end{pmatrix} \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{pmatrix} \quad (4.1)$$

Where B and S represent per-capita productivity and survival, and the subscripts denote first (j), second (i), third (sa) and fourth-year (a) age classes respectively (juvenile, immature, sub-adult and adult).

This is a female-only model, assuming a 1:1 sex ratio. Productivity and survival for years 1-3 were modelled as binomial processes (adult survival was modelled differently: see equation 4.5). The productivity part of the model is a combination of fecundity and chick survival. Hence, although kittiwakes often lay more than one egg, I use the binomial for productivity here because reduced productivity over many years in the UK populations means that normally fewer than one female chick fledge (Coulson 2017). In tests, modelling this as a Poisson process, I observed unrealistically high and low annual productivities. I therefore believe the binomial captures realism in the system more effectively.

If we assume that the intrinsic regulatory mechanism in this metapopulation is competition for resources (Ashmole 1963, Lewis *et al*. 2001a), we may infer this by estimation of a regional density-dependent parameter. From evidence across literature of the likely form and shape of density-dependence in many seabird populations, including kittiwake, I apply a compensatory density-dependence term to the linear predictor for productivity. From spatial clustering evidence in the literature (Frederiksen *et al*. 2005b), I assume that, in general, for this region the density-dependent mechanism that serves to regulate productivity may be similarly experienced by all sub-colonies, but its relative impact will be dependent on the size of each colony. I make a similar assumption that the environmental perturbation to productivity and survival will be the same across sub-populations based again on the work of Frederiksen *et al*. (2005b).

The probability of fledging female chicks at each time step (B_t) was modelled as a logit function of a linear predictor for each colony $(b_{i,t})$ thus ensuring that B_t remained bounded within the 0-to-1 range. In the baseline model the linear predictor for each colony took the form,

$$b_{i,t} = b_0 - \phi n_{i,4,t} + \varepsilon_{b,t} \quad (4.2)$$

Where: b_0 is the intercept; $n_{i,4,t}$ is the effect of adult density at each colony on productivity, measured by a coefficient (ϕ), and the effect of a productivity specific environmental perturbation term ($\varepsilon_{b,t}$) comprising a time series of identically distributed Gaussian terms $\varepsilon_t \sim N(0,\sigma)$. The standard deviation (S) of this term, described the magnitude of environmental stochasticity acting on the metapopulation.

I apply a generic error term for environment common to survival at each age-class. In my previous chapter, I established the possibility for each age-class to differentially experience environmental effects (Chapter 3.3: Results). Taking this into account I apply a scaling to the survival rates with priors for each being taken directly from the posterior results of the basic model estimates from chapter 3 (see Chapter 3, sections: 3.2 Methods & 3.3 Results).

Survival for each age class at each colony $(S_{*,t})$ was modelled as a logit of baseline survival (s_{*0}) and the environmental stochasticity $(\varepsilon_{s,t})$. For example, in the case of juveniles, the linear predictor took the form:

$$s_{j,t} = s_{j0} + \varepsilon_{s,t} \quad (4.3)$$

Whilst, the linear predictor for other age classes took the form:

$$s_{*,t} = s_{*,0} + sc_* \varepsilon_{s,t} \quad (4.4)$$

Where sc_* represents the respective scalar for age classes two, three or four as a parameter product of the environmental stochasticity $(\varepsilon_{s,t})$ shared across life classes.

Established adults may forgo breeding in any given year (Weimerskirch 2001). To allow for some recognition of these 'floater' non-breeding adult birds, those that have survived but are not breeding or counted in any given year, I model adult survival as a Poisson process, with mean and variance thus:

$$A_{i,t} \sim Poisson(S_{a,t}(n_{i,4,t})) \quad (4.5)$$

Where $A_{i,t}$ is the number of adults attempting to breed at each colony at each time-step described as a Poisson distribution of the survival predictor $S_{a,t}$ (derived from equation 4.4) multiplied by the number of adults in a colony $(n_{i,4,t})$.

4.2.3 Recruitment

I assume that productivity is an indicator of colony quality, mediated by strength of density-dependence and colony size and environment and I also assume that the likelihood of recruit transfer from natal colony to recruitment colony works as a function of this 'quality' and distance. This can then be described as an adaptation of a gravity model thus:

$$T_{i,j,t} = \exp(C_1(-b_{i,t} + b_{j,t}) - C_2 d_{i,j}) \quad (4.6)$$

Where: $T_{i,j,t}$ is the unnormalized (i.e. pairwise) transfer rate between the ith and jth colonies at time t expressed as a function of the difference in productivity of the colony of origin $(b_{i,t})$ and the productivity at the candidate destination colony $(b_{j,t})$. This is modulated by the distance $(d_{i,j})$ between the two colonies as calculated in section 4.2.1. The relative importance of differential productivity and distance for the transfer rate are governed by the two parameters C_1 and C_2 (both of which will be estimated during model fitting). Ultimately describing the relationship between productivity, distance and colony transfer, the equation is expressed as the power of the exponent $(\exp)$ to allow computation, should productivity fall to zero.

After calculation, the transfer rates $(T_{i,j,t})$ are transformed into probabilities by:

$$P_{i,j,t} = \frac{T_{i,j,t}}{T_{i,\sum 1:84,t}} \quad (4.7)$$

Here, $P_{i,j,t}$ now describes the probability of transfer between the ith and jth colonies at each time-step, normalised from the proportion of the likelihood between the transfer array $(\boldsymbol{T})$ ith and jth colony at each time-step divided by the sum of the likelihoods from all the colonies (84). In the resulting probability array $(P_{i,j,t})$, the ith rows will allow calculation of the redistribution and the jth columns at time (t) allow calculation of the number each colony gets.

To adapt the matrix model to include this relationship, I firstly describe the survival of the third-year age class from each colony at time t expressed as a binomial:

$$I_{i,t} \sim binomial(S_{sa,t}, n_{i,3,t}) \quad (4.8)$$

Where $I_{i,t}$ is the number of surviving recruits expressed as a binomial distribution of the survival predictor for the third year age-class at each time-step $(S_{sa,t})$ and the number of third year birds at each colony at time $(n_{i,3,t})$. To then calculate how these available surviving birds may recruit as adults into colonies, I express the recruitments to each colony in two steps. First, I adjust the probability array $(P_{i,j,t})$ calculated in equation (1.7) into an array of potential recruits $(PR_{i,1:84,t})$ by multiplying the summed columns of the array by the number of surviving third years that are now available thus:

$$PR_{i,\sum 1:84,t} = P_{i,\sum 1:84,t}(I_{i,t}) \quad (4.9)$$

Then I calculate the number of individuals recruiting into each colony $(R_{i,t})$ as a count across the rows of the potential recruits array, summing the numbers received by every other colony at each time-step thus:

$$R_{i,t} \sim Poisson(PR_{\sum 1:84,i,t}) \quad (4.10)$$

Finally, with $(R_{i,t})$ describing survival and now recruitment of third years into the fourth year class, for each colony, at each time-step, they are added to the estimates of the survival of the fourth year class (Equation 1.5) to describe the adult population size of each colony at each time-step as:

$$n_{i,4,t+1} = R_{i,t} + A_{i,t} \quad (4.11)$$

4.2.2 The demographic data

Models were fitted to time-series of data from the JNCC Seabird Monitoring Programme (Walsh *et al*. 1995, JNCC 2018) database for the Shetland region, including Fair Isle for 31 years from 1986-2017. In total 84 colonies were registered for the Shetland region, of which there were six master SPA sites: Saxavord Hermaness and Valla Field, Fetlar, Noss, Foula, Sumburgh Head, and Fair Isle. Recorded

time-series data for nests sites monitored for productivity, numbers of chicks fledged from these nest sites and colony-abundance nest counts were available in varying completeness across each defined site. This metapopulation considers an unbalanced effort across sites, but also the potential for kittiwake to have been present but not observed at each site, the model includes all site time-series, from across the same period, regardless of completeness. In this way, the hierarchical processes within the model work to recreate the missing entries based on the information from the demographic process and observation model trends as it simultaneously estimates likelihoods across the metapopulation structure. All starting population sizes are generated by a prior- which draws on sensible/realistic predictions in keeping with the regional trends and later observations at the same site. To avoid using this data would be throwing away information, which fails then to represent the metapopulation potential.

Summary information is available in Appendix 4, Table A.4.1.

I describe the observational error (ε) for the abundance data as a Gaussian distribution (appropriate for over- or under-dispersed error and large counts) with precision $(\tau = 1/\sigma^2)$ derived from an assumed 5% coefficient of variation around adult abundance measurements. $(\sigma = 0.05n_{4,t})$.

The data on fledged chicks were firstly multiplied by 0.5 in keeping with the female-only aspect of the model. The numbers of chicks fledged for each colony $(x_{i,t})$ were described by a Poisson distribution with the mean and variance taken from the product of the linear predictor of productivity for each colony $(b_{i,t})$ and the number of nests monitored at each colony $(y_{i,t})$. The observations of chicks were assumed to have some unknown observer error, with a conservative assumption made that observers may over-estimate the numbers of chicks successfully fledging in a given year, from the numbers of nests counted. As such, the Poisson distribution used to describe productivity is drawn from the equation 4.12 where it is penalized by 0.9. Conferring a 10% reduction in the mean/variance of each annual productivity thus*:*

$$x_{i,t} \sim Poisson(b_{i,t} y_{i,t} 0.9) \quad (4.12)$$

4.2.3 State-space model fitting

The demographic model was fitted to the entire time-series trends of each demographic series for each of the 84 colonies using the programme JAGS (Plummer 2003) interfaced with R via the runjags package (Denwood 2016). There were missing data from years in every colony either in the productivity

counts of nests and chicks fledged or from years between counts. This information is summarised in Appendix 4 Table 4 A.4.1.

4.2.3.1 Population starting size

I lacked information on both population age structure at all colonies and, often, starting adult abundance for many colonies (if no counts were recorded at the first time-step). To facilitate the model fitting I inferred both of these knowledge gaps in two ways. Firstly, in order to facilitate recreation of plausible starting population sizes I assigned the starting population size a gamma prior with mean of 1 and a variance of 100:

$$n_{i,4,t_1} \sim gamma(0.01, 0.01) \quad (4.13)$$

This allowed for those data-deficient starting time-steps to be sensibly informed (in keeping with expectations of starting population size from other colony time-series and following the general trend of the region), but allowed for those colonies with starting values (e.g. Fair Isle in the tens of thousands) to be represented without a distorted influence to the greater region i.e. overinflating starting sizes. Secondly, in order to establish a process to initiate the model with an intital assumedage-class structure, I used the dominant eigenvector (from a matrix model paramterised with regional vital rate estimates (Horswill and Robinson 2015)) to establish an initial stable age distribution that was applied to each recreated or observed population starting size. As the vital rates in the model are time-varied the model does not assume stationarity.

Several parameters of interest were estimated or monitored during fitting, each given biologically appropriate but naive priors or minimally informed priors based on previous chapter results. For example, the density-dependence parameter Φ (shared across colonies) was given a negative sign and a magnitude selected from a gamma distribution, hence restricting it to compensatory form, with a truncation to facilitate computation and prevent extremely low values being explored by the chains. The floor-truncation was specified at the value 10^{-11}. The full prior specification is given below in Table 4.1.

Mixing and convergence of the MCMC posteriors was evaluated for each parameter by assessing potential scale reduction factor (psrf), traceplots and effective sample size (Brooks and Gelman 1997, Kass *et al*. 1998). Because of the computer intensive nature of this model, adaptation and subsequent sampling were slow. Nevertheless, the model achieved convergence for all parameters although the effective sample size of the C_2 parameter was lower than desired (>400). Extended runs of the model showed the effective sample size of this parameter to be increasing. Due to time-constraints for the thesis the posterior results used for subsequent PVA simulations were taken after a burn-in of 1000 and a sample of 6000 (extended at 1000 intervals) with a thin of 10 (i.e. 60,000 iterations post-burnin), at which point the model was deemed to have converged and the effective sample sizes deemed adequate.

The author recognises the need out-with this thesis for the model to run to full satisfactory diagnostic end in order to present results for peer-review.

Table 4.1: Parameters and prior information

Term	Descriptor	Prior (jags)
β	Intrinsic productivity rate	0+0.6*dbeta(10,10)* Mean=0.3, var=0.3
S_1	Intrinsic rate juvenile	0.49+0.44*dbeta(10,10)* Mean=0.71, var=0.22
S_2	Intrinsic rate immature	0.65+0.3*dbeta(10,10)* Mean=0.8, var=0.15
S_3	Intrinsic rate sub-adult	0.67+0.33*dbeta(10,10)* Mean=0.83.5, var=0.16.5
S_4	Intrinsic rate Adult	0.6+0.4*dbeta(10,10)* Mean=0.8, var=0.2
$\varepsilon_{b,t}$	Environmental influence on β	dnorm(0,1/ σ_1^2)
$\varepsilon_{s,t}$	Environmental influence Survival	dnorm(0,1/ σ_2^2)
sc_i	Scalar term for 2nd Year birds (immatures)	dgamma(1.2,2) (Mean=0.61 , var=0.3)
sc_{sa}	Scalar term for 3rd Year birds (immatures)	dgamma(2.916,2.7) (Mean=1.08 , var=0.4)
sc_a	Scalar term for 4th Year birds (immatures)	dgamma(4.2632,2.92) (Mean=1.46 , var=0.5)
σ_1	Environmental perturbation of β	dgamma(4,4) Mean=1, sd=0.5
σ_2	Environmental perturbation Survival	dgamma(4,4) Mean=1, sd=0.5
C_1	Constant for transfer probability in productivity relationship	dnorm(0,25)
C_2	Constant for transfer likelihood as a function of distance	dnorm(0,25)
φ	Compensatory density-dependence	dgamma(1,$1e^{+06}$) Mean= $1e^{-06}$, var=$1e^{-12}$

4.2.4 PVA Simulation treatments

After fitting, the returned runjags results object was sampled using the R package CODA (Plummer *et al*. 2006), extracting 100 estimates from each of the parameters of interest from a random sub-sample of the joint posteriors. These values were then substituted back into the metapopulation matrix model (outlined in section 4.2.2) in R and projected forward for 25 years. Each colony starting population size was based on the joint posteriors coda values, also sampled 100 times. Each colony was then simulated 50 times for each of the 100 estimated values of parameters across the 25 years.

I applied several experimental treatments to the metapopulation simulations in order to explore the regional metapopulation dynamics and assess the vulnerability to decline or extinction. I began by

projecting the metapopulation as a whole with 1) no additional mortality, 2) additional mortality at every colony of 1%, 3) additional mortality at every colony of 5% and finally, 4) additional mortality at every colony of 10%. Mortality treatments were applied to every age-class. To establish any differences between the metapopulation approach and the currently industry preferred closed-system approach I, removed the connectivity terms from the matrix model, assuming now a closed system. I then applied the treatments (1-4) to simulations of each colony, but this time with no connectivity. As SPA colonies are legally protected and subject to arguably the most scrutiny in an assessment of anthropogenic threats to wildlife, their influence both singularly and collectively to the metapopulation dynamic required further examination. Each of the six SPA master site colonies were individually subjected to mortality treatments 2-4, but now an additional treatment 5) complete mortality (i.e. extinction) was also applied. Finally, I subjected all SPA colonies concurrently to treatments 2-5.

Using the 50 repeat simulations of the 100 subsamples I account for stochasticity in the simulations by collating the results across the entire possibilities simulated. Mean starting population size and mean end population size for each colony under each treatment after 25 years was calculated as the mean of each of the 50 repeats of the 100 values. Mean growth rate for each colony was inferred using the results for the mean start and mean end population size ((end-start)/start). Probability of extinction for each colony was calculated by counting the number of times a population went extinct by year 25 divided by the number of simulations (5000).

4.3 Results

4.3.1 Results of metapopulation model fitting

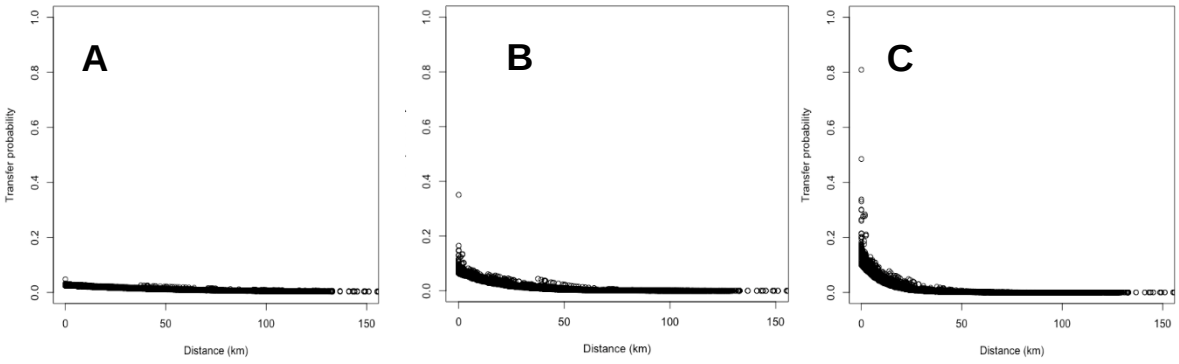

Figure 4.2: Results of estimation of connectivity in the model fitting. The y-axis on each panel represents the probability of transfer (as a function of productivity), while the x-axis is distance (km). Panel A shows the results of the lower 95% credible intervals from model fitting. Panel B shows the mean results from model fitting. Panel C shows the upper 95% credible intervals from model fitting.

Figure 4.2 shows the results of the transfer of recruits, described as recruitment probability as a function of distance as estimated during model fitting. The lower 95% credible interval of the posterior fit, depicted in Panel A, indicates limited distance/recruitment relationship between colonies with very slight decay curve indicating recruitment probability of up to 5% available recruits between colonies 0-100 metres apart. Panel B in Figure 4.2 takes the mean of the posterior fit and shows a maximum recruitment of ~ 35% of available recruits to either the home colony or nearby colonies that decays to zero by around 50km distance- suggesting higher 'sharing' of recruits to nearer colonies. Panel C in Figure 4.2 depicts the transfer probability from the upper 95% credible interval of the posterior fit. Here the transfer curve shows a maximum transfer of 80% of available recruits at shorter distances decaying to zero around 30km.

4.3.2 Comparison of metapopulation with closed population (no additional mortality)

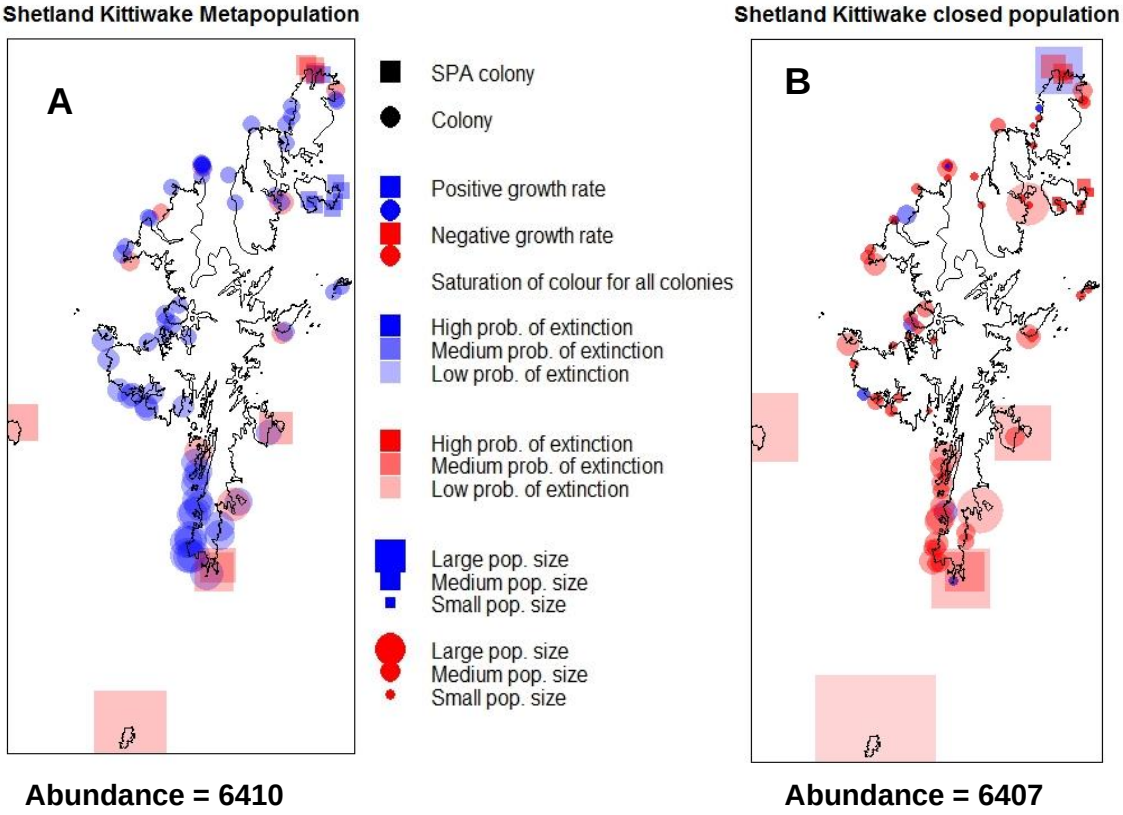

Figure 4.3: Panel A depicts the results of the Shetland colonies projected as a metapopulation over 25 years. Panel B depicts the Shetland colonies projected over 25 years as a closed system. From the legend, shape defines SPA colonies (square) and additional colonies (circle). The colour of each shape relates the colony growth rate, comparing the end population size with the starting population size. The size of each shape indicates the square root of the end population size divided by ten. Saturation of each shape indicates the probability of extinction during simulations. Numbers below each panel show entire population abundance at the end of 25 years.

The results of the PVA simulation clearly show that when connectivity is present several colonies are able to persist and also increase in size, including Fetlar SPA (Figure 4.3, panel A, blue circles and blue

square- Fetlar) compared to when the PVA is simulated as a closed system, however we do see a contingent of the Saxavord SPA increase as both a closed and meta-population (Figure 4.3, panel B, red circles and squares). We also observe that several of the metapopulation colonies have a low probability of extinction (lightly saturated colour, Figure 4.3 Panel A). Overall, we see in the closed PVA, those colonies with larger starting population sizes, such as many of the SPA colonies decline but retain higher population numbers than if we allow for connectivity (Figure 4.3, panel B, red squares & panel A, red squares). We also observe a clear reduction in size of several of the west coastal colonies in a closed system, comparative to the metapopulation simulation (Figure 4.3, panel B, panel A).

4.3.3 SPA additional mortality treatments

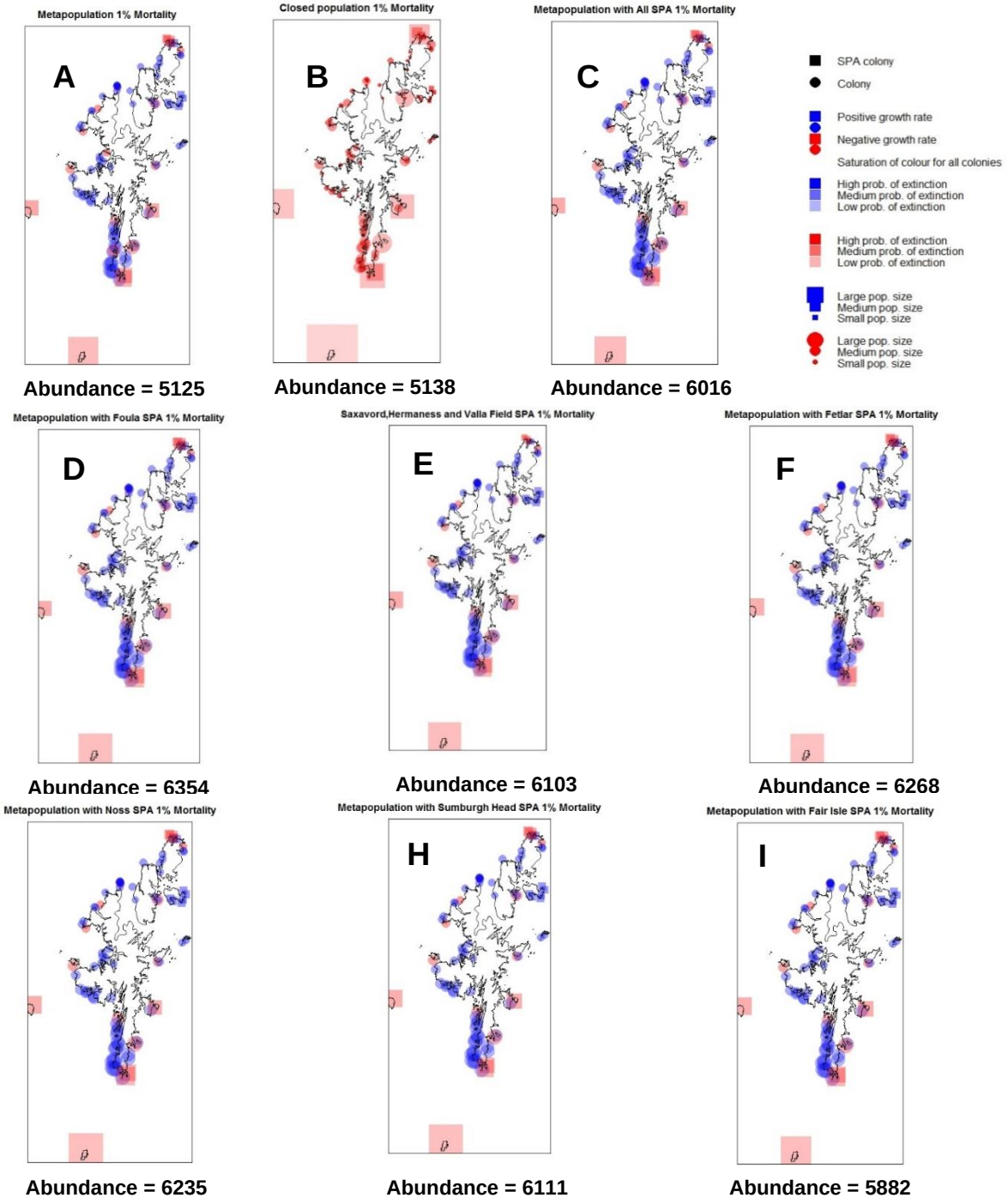

Figure 4.4: Panels A-I depict 1% mortality treatments applied to the whole metapopulation, closed system, all SPAs, then each of the 6 SPA colonies annually across the 25 year PVA. From the legend, shape defines SPA colonies (square) and additional colonies (circle). The colour of each shape relates the colony growth rate, comparing the end population size with the starting population size. The size of each shape indicates the square root of the end population size divided by ten. Saturation of each shape indicates the probability of extinction during simulations. Numbers below each panel show entire population abundance at the end of 25 years.

Figure 4.4 shows the results of applying 1% additional mortality across the entire metapopulation (Fig 4.4, panel A) and then to each colony as a closed population (Fig. 4.4, Panel B), then to all SPA colonies in a metapopulation (Fig 4.4, panel C) and then to each SPA in turn (Fig 4.4 panels D-I). Applying 1% additional mortality across the entire metapopulation network (Figure 4.4 Panel A) appeared to noticeably change the pattern in colony decline, with several colonies along the West coast and southern mainland Shetland turning from blue to red with regional abundance reduced by 20% from the baseline represented in Figure 4.3, panel A. The 1% additional mortality treatment as applied to closed colonies (Figure 4.4, panel B), shows clear reduction in shape size (colony size) from the baseline in Figure 4.3 (panel B) as well as a reported drop in abundance from 6407 individuals to 5138, a drop of 20%. As we apply mortality to each SPA respectively, we begin to see some patterns emerge. If we compare panels D and F in Fig. 4.4 we can see no discernible difference between the application of 1% mortality to Foula SPA (Figure 4.4, panel A) and when we apply 1% mortality to Saxavord SPA (Figure 4.4, panel E), Fetlar (Figure 4.4, panel F),Noss SPA (Figure 4.4, panel G) and Sumburgh Head SPA (Figure 4.4, panel H) the unaffected colonies appear to hold the same pattern, albeit with reduced colony size at the colony affected by the mortality. However, if we examine Figure 4.4 panel I we see that upon application of 1% mortality to Fair Isle SPA, a large drop in total regional abundance (8%) than when any other single SPA is perturbed with Fair Isle hosting a large proportion of the overall baseline abundance. When all SPAs are simulated with a 1% mortality (Figure 4.4, panel C) the population size is reduced by around 6% from the metapopulation baseline simulated with no mortality (Figure 4.3 Panel A). With regards to the total abundance recorded as each SPA is simulated under mortality we see less impact to entire metapopulation abundance when Foula, Fetlar and Noss (Figure 4.4, panels D, F, G) are simulated with mortality comparative to a further reduced abundance reduced abundance when Saxavord, Sumburgh Head and Fair Isle (Fig.4.4, panels E, F and I) are simulated with 1% mortality. This may be due to the size of the population at each colony influencing compensatory mechanisms on productivity as mortality reduces the density- perhaps for example, reduction in 1% at Foula may stimulate productivity to a relatively greater extent than a 1% mortality at Fair Isle. It could also be an outcome of the connectivity, or lack thereof of each SPA as it donates or receives immigrants.

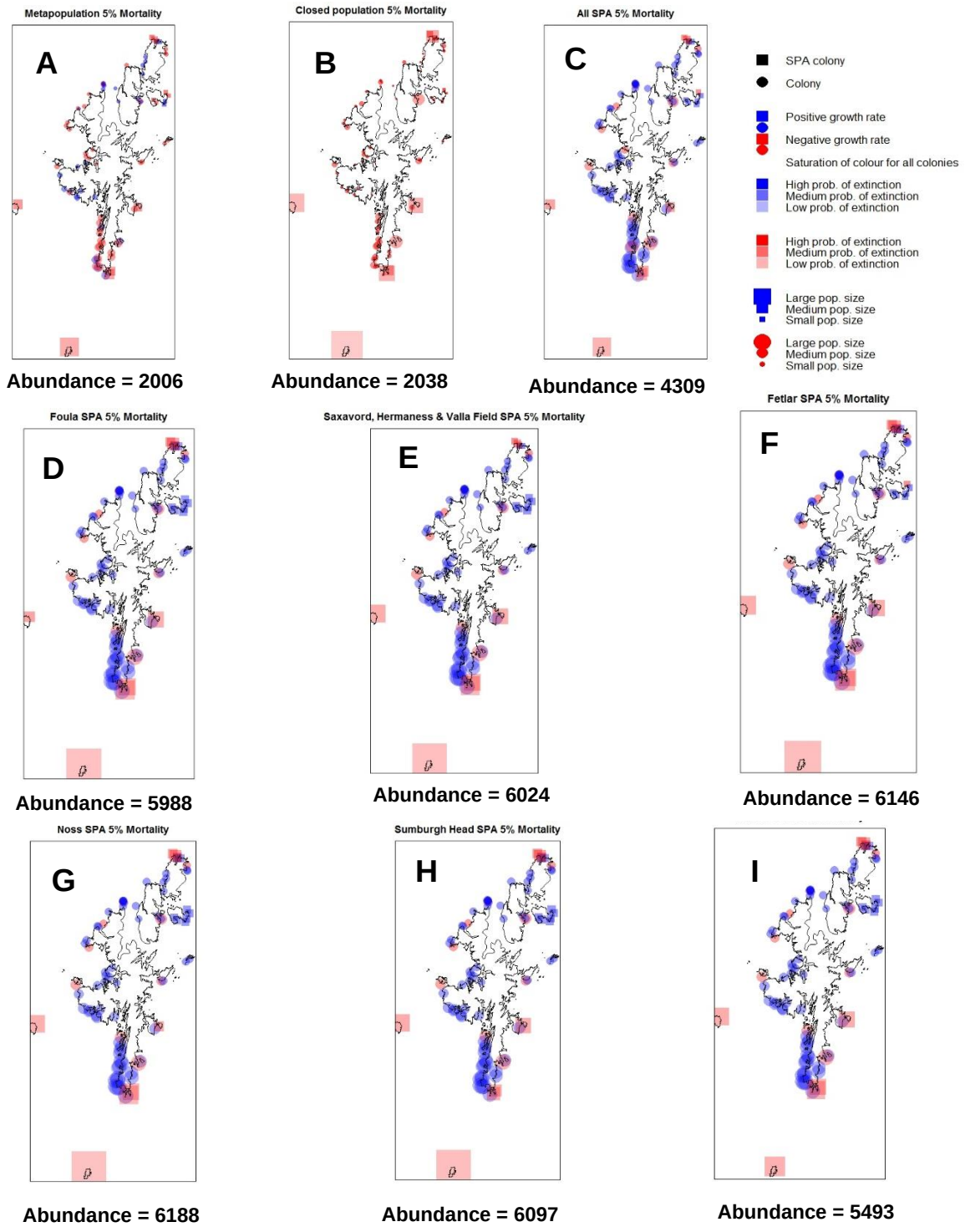

Figure 4.5: Panels A-I depict 5% mortality treatments applied to the whole metapopulation, closed system, all SPAs, then each of the 6 SPA colonies annually across the 25 year PVA. From the legend, shape defines SPA colonies (square) and additional colonies (circle). The colour of each shape relates the colony growth rate, comparing the end population size with the starting population size. The size of each shape indicates the square root of the end population size divided by ten. Saturation of each shape indicates the probability of extinction during simulations. Numbers below each panel show entire population abundance at the end of 25 years.

Figure 4.5 shows the results of applying 5% additional mortality across the entire metapopulation (Fig 4.5, panel A) and then to each colony as a closed population (Fig. 4.5, panel B), then to all SPA colonies in a metapopulation (Fig 4.4, panel C) and next to each SPA in turn (Fig 4.5 panels D-I). As 5% additional mortality is applied across the entire metapopulation (Fig.4.5, panel A) we see a large reduction in colony size (shape size) a notable reduction in the number of blue colonies (positive growth) and a 69% reduction in entire regional abundance from the no additional mortality baseline (Fig. 4.3, panel A). Notably Foula and Fair Isle, whilst declining remain larger in size than other colonies (Fig. 4.3, panel A). When 5% mortality is simulated to each colony as a closed population (Fig.4.5, panel B), we see again a reduction in shape size (population size) at many of the mainland colonies. Many colonies are observed as declining with fewer 'blue' colonies. Those that retain relative larger shape size (population size) we can assume initially had larger starting population sizes relative to the other colonies. Regional population size is slightly higher (1.5%) when mortality is simulated under the closed system compared to the metapopulation (Fig. 4.5, panels A, B).

As I apply mortality independently to SPAs (Figure 4.5 panels D to I) we observe very little obvious differences in the unaffected colonies as each SPA is perturbed. Abundance reduces the most across the metapopulation when Fair Isle is individually perturbed (14% from the baseline in Figure 4.3, panelA) followed by Foula (6.5%). When all SPAs are perturbed the population is reduced by around 33% from the metapopulation with no mortality applied (Figure 4.3, panel A). In terms of regional abundance, as each SPA is modelled with mortality, we see little difference in regional population size between simulating Sumburgh Head SPA with 1% (Fig. 4.4, panel H) and 5% mortality (Fig.4.5, panel H).

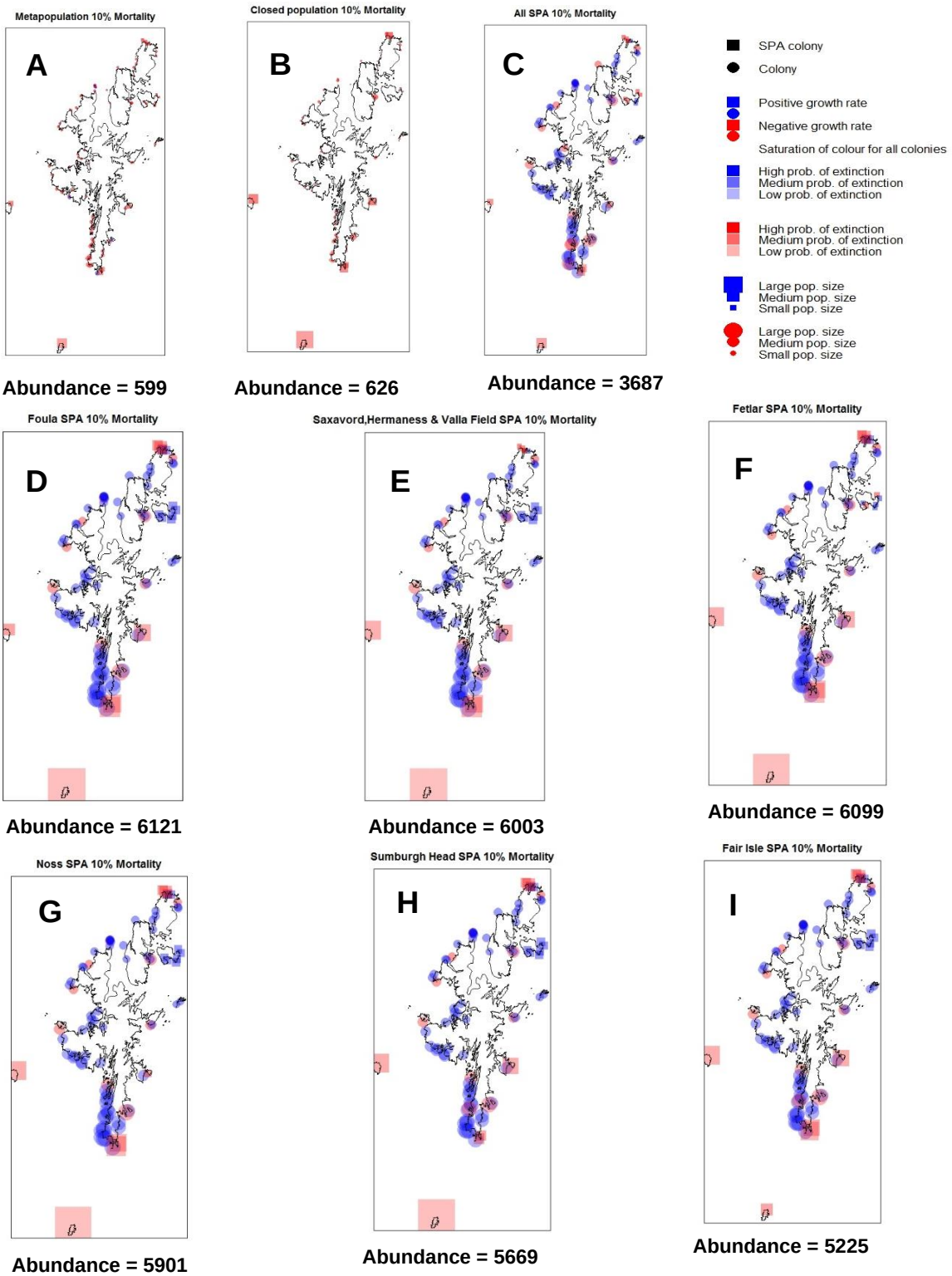

Figure 4.6: Panels A-I depict 10% mortality treatments applied to the whole metapopulation, closed system, all SPAs, then each of the 6 SPA colonies annually across the 25 year PVA:. From the legend, shape defines SPA colonies (square) and additional colonies (circle). The colour of each shape relates the colony growth rate, comparing the end population size with the starting population size. The size of each shape indicates the square root of the end population size divided by ten. Saturation of each shape indicates the probability of extinction during simulations. Numbers below each panel show entire population abundance at the end of 25 years.

Figure 4.6 shows the results of applying 10% additional mortality across the entire metapopulation (Fig 4.6, panel A) and then to each colony as a closed population (Fig. 4.6, panel B), then to all SPA colonies in a metapopulation (Fig 4.6, panel C) and then to each SPA in turn (Fig 4.6 panels D-I). As 10% additional mortality is applied across the entire population, we see massive reduction in colonies (Fig. 4.6, panel A). The change from the baseline population size for the region declines by 91% (Fig. 4.3, panel A). Similarly, under a closed mortality simulation to each population we see an overall similar regional abundance compared to the metapopulation mortality (90%, Fig. 4.6, panels A and B). However, using shape size, we can see larger colonies are retained comparative to the metapopulation simulation (Fig. 4.6, panels A and B). Mortality added to Foula, Saxavord, Fetlar and Noss SPAs (Figure 4.6, Panels D to G) do not appear to noticeably influence the resulting patterns seen in any of the unaffected colonies. Mortality application to Sumburgh Head and Fair Isle (Figure 4.6, Panels D, H & I) show decline in an additional southern Shetland colony, not seen when other SPAs were perturbed. When mortality is applied to all of the SPAs (Figure 4.6, panel C) we see a decline of 42% in total population size comparative to the metapopulation simulation with no additional mortality (Figure 4.3, panel A). When the mortality is added to each SPA independently, we see the greatest decline from the baseline regional population size (Fig. 4.3, panel A) when Fair Isle is simulated with 10% additional mortality (Fig. 4.6, panel I), reducing the population by ~18%.

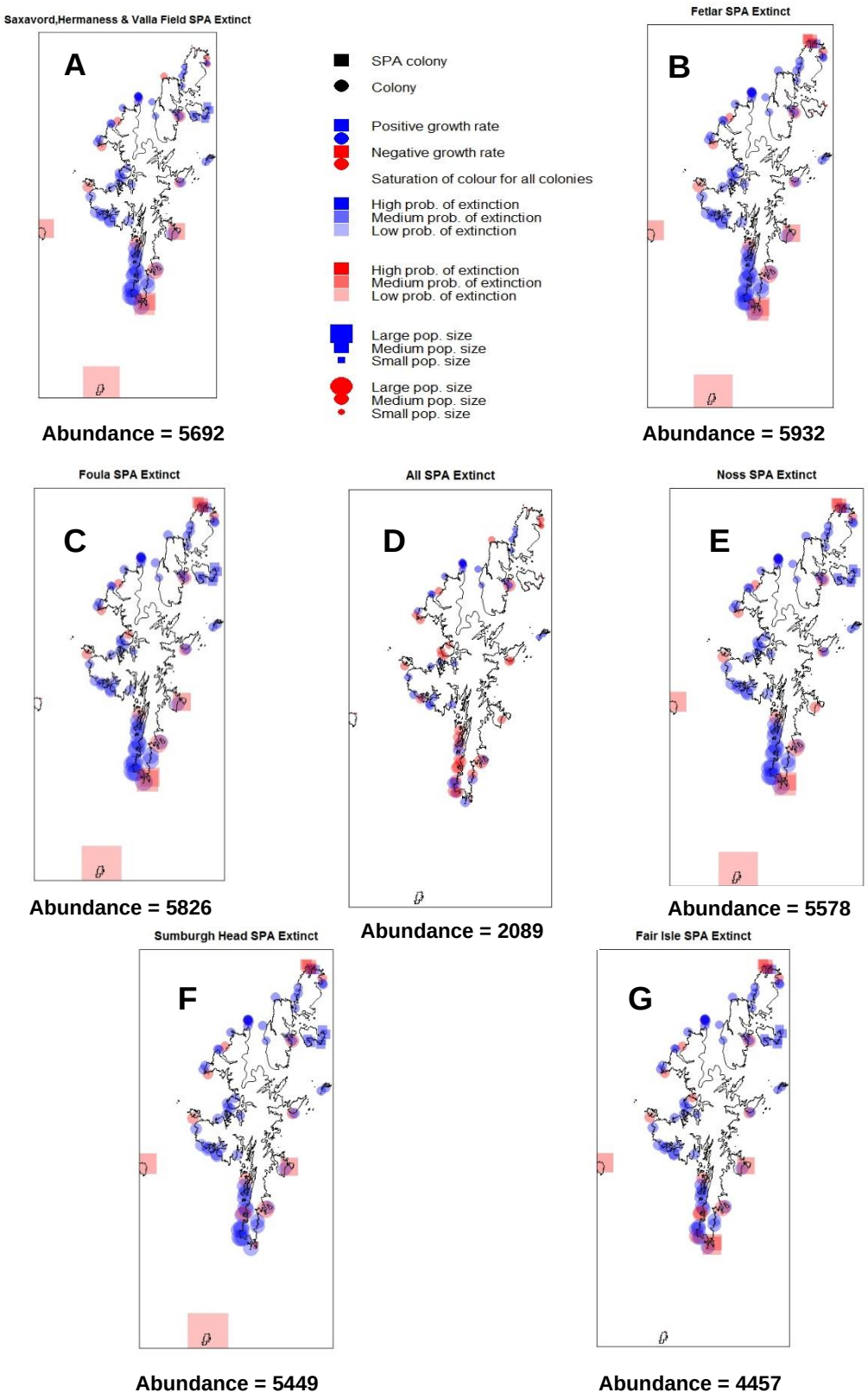

Figure 4.7: Panels A-G depict 100% mortality treatments applied to each of the 6 SPA colonies annually across the 25 year PVA. From the legend, shape defines SPA colonies (square) and additional colonies (circle). The colour of each shape relates the colony growth rate, comparing the end population size with the starting population size. The size of each shape indicates the square root of the end population size divided by ten. Saturation of each shape indicates the probability of extinction during simulations. Numbers below each panel show entire population abundance at the end of 25 years.

Figure 4.7 shows the results of applying 100% mortality (i.e. extinction) to each of the SPA in turn (Figure 4.7, panels A-C, E-G) and then to all SPAs simultaneously (Figure 4.7, panel D). When Saxavord SPA is, 'knocked- out', we see a decline in a colony to the south-west of where Saxavord had been (Figure 4.7, panel A). As extinction is applied to Fetlar SPA and also Noss SPA we see little overall change in the colony patterns comparative to most of the other SPA extinctions (Fig. 4.7, panels A, B, C, E). When Foula is removed (Fig. 4.7, panel C) we observe a colony on the west of mainland Shetland turn from blue to red. Upon the extinction of Sumburgh Head we see additional declines in a southwest colony of the mainland (Figure 4.7, panel F) and a notable reduction in colony size around the southern mainland. Similarly, when Fair Isle is removed we see an obvious reduction in colony size (circles) both blue and red and an additional red colony comparative to Sumbugh Head removal (Figure 4.7, panel F) and increased red saturation (probability of extinction) at colonies on the southern east and west Mainland of Shetland (Fig. 4.7, panel G). Removal of any one SPA reduced the regional baseline population (Fig. 4.3, panel A) from 7% with the removal of Fetlar (Fig. 4.7, panel B), to 30% upon the removal of Fair Isle (Fig. 4.7, panel G). Removing all SPAs, reduced the regional population from the baseline (Fig. 4.3, panel A) by 67% (Fig.4.7, Panel D).

4.3.4 Summary of SPA simulations

Table 4.2: The estimated abundance of SPA population size after 25 years, simulated as both closed and metapopulations, under zero additional mortality and subsequent proportional additional mortality treatments. Mean starting population sizes in parentheses.

SPA	Closed Zero	Closed 1%	Closed 5%	Closed 10%	Meta Zero	Meta 1%	Meta 5%	Meta 10%
Fair Isle (1842)	1778	1416	564	173	653	520	205	58
Fetlar (78)	52	61	23	7	214	181	66	19
Foula (614)	589	475	186	57	168	134	52	15
Noss (402)	386	312	124	38	135	107	41	12
Saxavord Hermaness & Valla Field (409)	404	327	129	40	254	202	78	24
Sumburgh Head (637)	617	493	196	61	349	279	108	31

The results of Table 4.2 show the resulting population size of each SPA after 25 years, simulated as closed or metapopulation and in the presence or absence of additional mortality. All scenarios decline from the initial population starting size (in parenthesis) except Fetlar, which increased in a metapopulation simulation comparative to closed. In the closed models we can see that all the populations decline under additional mortality and without mortality. In the metapopulation the populations decline, comparative to the no mortality metapopulation upon addition of mortality. Fair Isle, Foula, Noss and Sumburgh Head reported reduced absolute population sizes in the metapopulation model under zero additional mortality compared to in the closed scenarios.

4.4 Discussion

Estimating dispersal patterns and subsequent vulnerabilities in a regional metapopulation can enhance evaluation of potential outcomes for population persistence and vulnerability to anthropogenic activities across space and time. Here I find evidence of connectivity in a regional metapopulation and observe through simulation changes in population distribution but not population size. This finding suggests more spatial realism in assessment approaches may provide additional considerations for our metrics of viable or impacted populations to anthropogenic mortality.

The model results for estimating connectivity parameters indicate across the mean and credible intervals, signals of connectivity in various forms. Firstly, on the lower end of the estimate, I find a low transfer probability between colonies within 0-50m distance, followed by a mean decay curve of a higher transfer over slightly increased distance, whilst at the upper end of confidence I observe an estimate of greater transfer at a local scale. Overall the estimates suggest evidence of distance dependent connectivity. By substituting random samples from the posterior values for transfer parameters and other key demographic estimates (density-dependence, intrinsic vital rates, environmental perturbations, and the magnitude of environmental impact to survival rates) in simulations as a metapopulation I found a mixed regional pattern of declines and increases, with varied probabilities of extinction. This is perhaps fairly typical of what one might expect in a connected system under regulation from density-dependence and environmental stochasticity (Lande *et al*. 2003). For example, since the measure of density-dependence across the region is compensatory in effect to productivity, the population size of any colony may be larger than a neighbouring colony, eliciting a reduced productivity comparative to a similar colony with a smaller population size operating on density-dependent compensation. As such, one could imagine transfer between these colonies, the magnitude of which depending on where along the joint posteriors the values were sampled from, broadly represented by the results of section 4.3.1, Figure 4.2. The saturation of colonies is indicative of the highly stochastic nature of the modelling and the sensitivity of this species to environmental perturbation and subsequent, decline to extinction and the relative contribution of connectivity. We know this region is suffering long-term declines, which are captured in part in the time-series the state-space model was fitted to. Broadly speaking therefore, by comparison of the metapopulation with the closed system estimates, we can see there is little difference in overall regional abundance, but spatially, colonies diminish that had lower starting population size. If we consider these closed simulations as representing 100% philopatry (which we know is likely not the case in reality (Coulson 2016) we can see individual colony extinctions are highly probable, with only larger colonies persisting under additional mortality treatments.

Since mortality from a single proposed development is likely to be assessed against one or more colonies with which it may have potential connectivity, applying mortality with increasing impact to

one or more SPA colonies offered insight into how mortality may proliferate throughout a system from the affected SPA. I report several observable relationships between effects to other colonies from mortality to single SPA treatments, but none is more obvious than the effect of Fair Isle SPA on the Shetland Region. Results indicate this colony is operating with net emigration to the Shetland archipelago, particularly obvious in the size of colonies across the region once Fair Isle additional mortality hits 10%. Fair Isle cannot be considered a true 'source' population however since it is observed to be in decline. Conversely a few SPA colonies appeared to be inconsequential to the persistence of surrounding colonies (Saxavord, Noss). However, this initial investigation could be improved upon by further sensitivity experiments detailing metrics of change of more discrete sub-population scales, as we see in Table 4.2 indications that other SPA may be operating like Fair Isle (with net emigration) based on their abundance comparative to closed modelling. Interestingly, Fetlar appears to be the only SPA colony reporting positive growth in the metapopulation simulations, but superficially doesn't appear to be influential in the patterns of neighbouring colonies, suggesting a net gain in immigrants, however we cannot easily distinguish their origin, without further analyses. Experimental adjustment of the colonies around the north might allow for greater understanding of Fetlar's net intake of recruits and the local scale dynamics driving growth there. Notably, under a closed PVA, Fetlar declined. Crucially, the simulations of both closed and open models were parameterised by posterior values fitted under metapopulation assumptions, perhaps fitting as closed populations to derive parameters for closed simulation would confer an appropriate additional comparison.

Cumulative impacts are those that may contribute to an impact to wildlife from existing operational, consented and in development or consented undeveloped infrastructures (Busch *et al*. 2013). Collectively the environmental impact assessment of existing or planned developments must be evaluated. From my model we can see that when you apply mortality to all the SPAs simultaneously, the reduction in regional population size is notable. Since cumulative impacts are likely to be assessed over a particular spatial scale (for example, west coast SPAs might not be included in a cumulative development to the east of Shetland), it would be interesting, moving forward, to evaluate patterns of change when SPAs on one coast are impacted. Perhaps then we might see a differentiating pattern in the persistence, size or vulnerability in neighbouring colonies, not seen when applying mortality to just single or all SPAs. Although many assessments would likely focus on SPA colonies, one would consider it reasonable to assume that the other colonies in spatial proximity to a potential impact could likely suffer relative to the presumed impact on the SPA. As such it would be of considerable value to unpick via sensitivity and further exploration the population dynamics of the other colonies and their role or vulnerability in the system as a whole. Of course, here I model the metapopulation based on a relatively 'local' distance relationship, when in fact there is the potential for other colonies across the species' range to be influential in the transfer of recruits (Coulson and Neve de Mervegnies 1992). As such we cannot rule out other connectivity, which merits further exploration. Shetland seabirds have

suffered decline, thought to be induced in part by a regime change in the North Sea (Beaugrand 2004), and fishery policies (Bicknell *et al*. 2013). Recent years have seen improved breeding success across kittiwake colonies. Both 2018 and 2019 seasons in Shetland have seen increased kittiwake productivity (Miles & Mellor 2018, pers. comm. Helen Moncrieff, Shetland RSPB). The continued monitoring of colonies is key to modelling population dynamics and informing assessments.

If precaution is thought to lie within a closed modelling approach, I find the results here interesting in that the metapopulation as a whole reduced in size on a similar scale as the closed population but what differed was the spatial vulnerability. Indeed, we see that in the absence of additional mortality several of these SPA return markedly smaller population sizes when simulated as a metapopulation than as closed populations. We can assume, judging from the increases in other colonies, including Fetlar that transfer from Fair Isle to colonies in the archipelago is redistributing recruits through the metapopulations network. In my introduction I discuss the ability for pseudosinks or extinction-recolonization events to maintain a metapopulation at reduced carrying capacity (Thomas and Hanski 1997), particularly in lieu of a source population becoming extinct. Given the multiple known pressures enacting on our seabirds as well as anthropogenic developments (climate change, prey regime changes, predation, and extreme weather events), there is a credible argument towards exploring these dynamics further and appraising them for sensitivity to additional mortality and other threats such as climate change or regime change (e.g. how likely is extinction recolonization on spatial scales and how is climate or prey driving this?). This work uniquely combines estimates, derived from empirical data, of major demographic processes and regulation allowing a blueprint for further examination of the subtleties of metapopulation structure and the assessment of vulnerability. The incompleteness of the abundance and productivity time-series reflects the very real conditions of wildlife population monitoring and patchy data. Whilst the process and observation model work in tandem to recreate, sensibly, estimates of these gaps any further information provided to the model can help reduce uncertainty in the results of using incomplete time-series. Further manifestations of this model may seek to improve the informative of time-series with gaps by providing further information. For example, local recorder and expert opinion may provide information on the maximum number of birds a site could physically provide space for. This would both provide information to check the maximum numbers being recreated at each site and also prior information for localised density-dependence effects.

Whilst clearly some refinements, depending on objectives, would improve upon this work, this framework which uses freely and publicly available datasets and literature-based assumptions for this species as to the potential nature of the connectivity structure we estimate (productivity/distance) could be broadly adapted to other species, spatial scales and assessments.

Conclusion

The results here indicate that in the short-term at least, projecting populations as closed populations may give a starkly different spatial outcome comparative to modelling as a defined network. If we are aiming in conservation to identify risk or in impact assessments to establish anthropogenic threats to a baseline, focussing on single populations and our subsequent mitigation actions may be negligible at best (in preventing a decline of a focus population) or deleterious to population persistence at worse (e.g. by overlooking management strategies for colonies across the network that may provide stability in the network). Here, we provide empirically derived estimates of connectivity mediated by density-dependent penalised productivity and distance. We clearly see a declining abundance of kittiwake in the region as a whole, but spatial disparity in growth rates as a metapopulation indicates unseen patterns in the structure and subsequent vulnerabilities in the Shetland Region. Reducing uncertainty in conservation objectives allows for a clearer range of predicted outcomes, which can be harnessed by policy makers and conservation managers to make effective decisions. Evidence based approaches that reflect more reality in a system should be built upon to ensure best practice in balancing the demands of industry and the identification and protection of vulnerable wildlife.

5.0 General discussion

The research in this thesis aimed to investigate seabird population dynamics from real populations in the UK with a view to empirically quantifying estimates of demographic processes and discover patterns or scenarios of sensitivity to additional mortality both to single populations and to entire metapopulations. Reflecting on results, I highlight in the sections that follow the key concepts from the results, particularly the importance of considering demography, life history and spatial structure in impact assessment if we are to avoid over- or under-precaution. I discuss the appropriateness of methods for predictions of impacts and provide suggestions for improvements in these models and the future avenues of interest that they provide the necessary framework to explore.

5.1 Life-history and impact assessment

I found varying patterns of regulation, population growth and consequently, vulnerability of three different species of seabird. Consider the underlying ecology and historical population trends of these species in the UK, gannets: a generalised predator with an increasing population, guillemots: a pursuit diving species that may forage on a range of prey, though not quite generalist, has a fluctuating pattern of growth and finally, kittiwake: a surface feeder preferring sandeel, red-listed due to multiple declines across colonies (JNCC 2015 a,b,c, Birdlife International 2018). In chapter two, via model fitting to time-series of abundance, I obtained estimates of density-dependence and environmental stochasticity for each of these species' populations. I use the entire range of these empirical estimates to then evaluate

population response to combined effects of this regulation. As a theoretical exercise in evaluating life history trade-offs we see a clear indication that in the gannet population at the Bass Rock (Figure 2.2), density-dependence does not regulate this population in my baseline model (when unaffected by additional mortality). This makes sense, the population has been increasing with positive colony growth across the UK, probably as a function of their generalist attributes and their physiological ability to forage further with minimal energetic costs. Everyone loves a success story, but the gannet increases around the UK are a relatively modern phenomenon, occurring in a time of fairly active monitoring and counts, allowing us to capture this trend in numbers as, presumably, the UK population heads towards its carrying capacity (Murray *et al*. 2015). Space is running out on the Bass Rock and recently the Bass gannets suffered a breeding season with notably late or failed breeders, thought possibly to be driven by storms early in the breeding season and additionally a notable lack of substrate for nest structures (seaweeds) (Maggie Sheddan pers comm.). Consequently, the resilience of the gannet population to environmental pressures (storms and substrates) and potentially future intrinsic regulation from density-dependence (competition for nest-sites) may work in tandem with potential anthropogenic mortality from offshore wind to threaten the future growth of these colonies. The continuation of monitoring schemes to provide data with which to update demographic models will be key in developing our understanding of both population processes nearing carrying capacity and the subsequent evaluation of how regulation works alone or in-combination to affect population growth.

Meanwhile another well-studied enigmatic species, the common guillemot at the Isle of May colony was found to be predominantly regulated by environmental stochasticity. This finding is probably attributable to factors influencing vulnerability in this species such as oil spills and winter wrecks. Whilst there are indications that increased density has a positive correlation with breeding success at colony level (Birkhead 1977), perhaps at this particular colony there is no evidence of a strong estimate of density-dependence operating, especially to penalise against breeding success. The guillemot is well adapted as a pursuit diver but is energetically speaking, inefficient in flight. Whilst I have predominantly focussed on the effect of additional mortality to guillemots, their ecology suggests that they may be more vulnerable to indirect effects like displacement, having to forage or travel further could impact productivity (and also potentially survival via carry-over effects into non-breeding seasons). I suggest the model of chapter two be updated to perturb productivity in a sensitivity analysis of this species, to represent the potential outcome for populations under environmental stochasticity, density-dependence and displacement.

Similar results of sensitivity to environmental regulation were found for the declining species, kittiwake- environmental regulation which is reflected in correlations with decline in preferred prey, breeding asynchrony with prey presumably from sea-temperature changes and increased predation. For both the guillemot and the kittiwake, exploring the breadth of credible intervals for their regulation shows that these species, heavily regulated by environment and unaffected by additional mortality can

exist somewhere on the plane of proliferation in population or complete extinction, which we might expect for an r selected species but not for k selected seabirds. This leads to interesting follow-on questions regarding population structure and persistence, such as is this pattern replicated in other populations of the same species? Does inclusion of immigration and emigration impact the dynamic of population persistence and environmental perturbation? How much has environmental change influenced the resilience of kittiwake and guillemot populations and can we identify scenarios that may indicate recovery or conversely those that may initiate extinction?

I did not explicitly inform the model with emigration or immigration- rather I introduce a rescue-effect, which induces a band of decline in the guillemots that bridges persistence at lower and upper environmental stochasticity- suggesting a threshold of persistence under regulation that can be navigated under higher magnitude beneficial conditions with the inclusion of token immigration. Indeed, as the rescue-effect is applied to kittiwake results indicate an interplay between additional mortality, environmental perturbation and immigration, where upon additional mortality requires higher environmental stochasticity to buffer against declines- the catch being the higher stochasticity would need to be advantageous to population growth. As we know, both guillemot and kittiwake are subject to climate change impacts (Finney *et al*. 1999, Frederiksen *et al*. 2007a, Wanless *et al*. 2009), how their life history, population structure and potential vulnerability from added effects of offshore wind influence population persistence remains to be fully understood.

The niche each species occupies reflects its sensitivity (or robustness) to both competition from conspecifics and the environmental factors that impact directly and indirectly on their life-history. Before the application of additional mortality, I presented the relative effect of regulation to each of these colonies. Whilst difficulties remain in identifying the proximate and ultimate drivers of some of this regulation, my first model introduces a quantifiable method for generic regulation, which may be useful as an initial step towards identifying the patterns of competing pressures that are influential in population changes but against which I test for the impact of additional mortality. In my chapter 2 result plots (Figures 2.1-2.4) I display an entire range of combined regulation and since one might expect these parameters to fluctuate over time the likelihood of these fixed outcomes ever impacting the population in each sustained way they are represented is unlikely, but importantly the results allow for visualisation and quantification of a surface of vulnerability, against which mean, least and worst case scenarios or some gradient across these may be modelled. Whilst currently arbitrary environmental stochasticity, density-dependence or density-independent models are favoured in practice, realistic regulation derived and represented in the context of population trend and the life-history of species as per the evidence provided in this paper, should motivate practitioners towards including methods like these in their toolbox of assessment.

5.2 Environmental regulation of seabirds, causes and responses to additional mortality

A challenge in both retrospective and prospective investigations of the drivers of population growth is quantifying and identifying the stochasticity that affects population growth. By its very nature stochasticity may be difficult to predict in terms of cause, but one can infer consequences of stochasticity through modelling of perturbation and demography (Frederiksen *et al*. 2008). In my first model (Chapter two), environmental perturbation was not only quantified, but was highlighted as being influential both in the presence and absence of additional mortality. Given the red-listed vulnerable status of the kittiwake and the in-combination results of additional mortality under environmental stochasticity (leading to multiple declines and extinctions across the space, Figure 2.3), I was motivated to investigate environmental stochasticity in a follow-up, three-pronged approach. Firstly, the original model presumed the impact from environment may be synchronous to both breeding success and survival- this however may not entirely be the case. For example, carry-over effects may operate on a lagged time-scale to affect individual breeding success in seasons within the same year or years after an environmental perturbation (Daunt *et al*. 2014, Szostek and Becker 2015, Fayet *et al*. 2016), migration areas of breeding adults may vary in quality (Norris and Marra 2007, Phillips *et al*. 2017) and so if adults from one colony are differentially exposed to perturbation they may exhibit mixed fitness impacting upon breeding success, although this is difficult to identify and quantify. Individuals may also be more experienced breeders or more successful foragers (Daunt *et al*. 2007, Lescroël *et al*. 2009), buffering against environmental stochasticity or be buffered from physical perturbations of environment by their place in the colony (Coulson 2011, Bonter *et al*. 2014). Whilst my inclusion of demographic stochasticity in the models moves towards addressing some of this individual variation in quality, it made intuitive sense to explore environmental regulation further with separate environmental terms to be estimated for productivity and survival. Secondly, both conservationists and policy managers seek to derive evidence of tangible drivers of regulation to deploy mitigation against catastrophic declines. This was a particular motivation in seeking to identify broad or local covariates as influential in regulating survival or productivity. The resulting outcomes did indeed show varying influences of environmental covariates to productivity (such as sandeel total stock biomass, Figure 3.2) but with factors influencing survival being much more difficult to identify. This lack of reduced variation in the survival environmental error upon addition of co-variates highlights the difficulties of identifiable influences particularly when using a crude index, the NAO to attempt to capture prevalent conditions during their non-breeding stages. Other authors have suggested potential non-breeding areas and drivers of survival (Reiertsen *et al*. 2014). As further empirical evidence of the distribution of non-breeding ages and stages emerges from tracking studies, it would be a valuable exercise to continue trying to identify potential conditions that impact survival.

Thirdly, whilst there is a lack of knowledge as to the distribution and survival of non-breeding stages, there is the aforementioned evidence of a trade-off between the probability of survival with experience, habitat quality and condition. Therefore, it seemed pertinent to explore the possibility of a potential magnitude effect from environment to survival at different ages, because we may assume they are differentially experienced and distributed (at least during adult breeding season) (Coulson 2011). Here, I find evidence for different mean impacts of environment to survival at different ages (Figure 3.3). Whilst these estimates do not significantly vary between age-classes, there is continuity across models for the mean magnitude each age-class experienced This continuity is an important finding worthy of further exploration, because if we have a slow-maturing, low-producing species with multiple immature age-classes, in general not only might these immature classes make up the bulk of a population (Saether and Bakke 2000), the interplay between survival, distribution, experience and breeding attempts may highlight existing vulnerabilities of stages in a population before any further investigation into additional impact from offshore wind.

5.3 Density-dependence: an argument for inclusion in impact assessments.

As set out in the general introduction, density-dependence is not considered precautionary in environmental impact assessments because it is assumed in its most-frequently applied state, compensation, that the liberation from penalties to productivity from additional mortality compensate population effects and therefore are not as precautionary as to exclude this mechanism (Green *et al*. 2016). But density-dependence does not function as a regulatory process exclusively in its own right. The strength or form of density-dependence in any given year may vary depending on of course the density of animals but also on the environmental conditions that support the population. In this way, density-dependence and environmental stochasticity work to create a dynamic carrying capacity (Goyert *et al*. 2017). My results in chapter 2 (Figures 2.1-2.4) show that capturing the interaction between these two regulatory processes serves to highlight the potential effect one has on the other and the then likely consequences to population growth if we add mortality. We see this most obviously in the impact to the Bass Rock gannets, that, further to high density-dependence and high environmental stochasticity, the compensatory effect on productivity is not enough to offset decline in the face of additional mortality. Other studies have also highlighted the effect of positive density-dependence, depensation, (where in low densities, below a critical threshold, populations may have a reduced growth rate) operating in small populations of gull spp. and terns (Horswill *et al*. 2017). During the kittiwake modelling in chapter three, there was an initial attempt to capture any estimate for depensation in the Isle of May population by inclusion of a quadratic term, however the time-series used in fitting did not

include data low enough to robustly estimate this process. If depensation is operating in pockets of the breeding colony at the Isle of May (the spatial structure of the colony does allow for some areas of the island to be pocketed and thus potentially operate with depensation via predation risk) one potential solution for addressing the magnitude of this effect both in isolation as applied to a smaller sub-section of the population and in combination with the rest of the breeding population on the Isle of May, could be to do bespoke monitoring of a smaller subset of the data in abundance and productivity across a gradient of sites of different layouts and sizes on the island.

Further to chapter two results, density of seabirds is influential as an attraction mechanism for recruits (Crespin *et al*. 2006), a predation limiting strategy (Oro 1996) and a competitive disadvantage for resources (Lewis *et al*. 2001a). Each of these competing density trade-offs operates, one assumes, across unknown thresholds. By estimating density-dependence for my regional metapopulation model, I capture a signal of the effect of competition as a compensation mechanism on productivity (in the presence of environmental stochasticity). It may be useful or negligible to estimate the parameters of density-dependence in the region independently as a closed model and compare the results found, if any, to understand further the equivalence (or lack of) in describing an open system as a closed one. As we have seen across chapter two and chapter three the domination of environmental stochasticity in regulating the kittiwake population of the Isle of May kittiwake, may also be the predominant feature regulating the Shetland colonies also, as in general there has been a similar decline. If we are to understand the shape and magnitude of density-dependence in metapopulations, the model in chapter four provides a framework with which to assess, the influence of philopatry, thresholds of density-attraction, the influence of environmental stochasticity and density-dependence to productivity and the occurrence of extinction-recolonisation dynamics.

In general, in light of my results and by offering a method with which to derive empirical estimates of density-dependence, it appears pertinent that precaution involves density-dependence in tandem with environmental stochasticity being evaluated alongside density-independent scenarios of impact from additional mortality.

5.4 Connectivity: Moving towards more informative models

From chapter two and chapter four we see the influence that a simple rescue-effect and metapopulation transfer may have on population persistence under regulation and in the presence or absence of additional mortality. It is accepted that in kittiwake there is transfer between colonies of individuals, but the degree of transfer, the spatial distribution and the effect this transfer has to population dynamics is little known. If we observe the token addition of one individual re-seeded into the population annually in chapter 2, we observe the ability for extinctions to be followed by re-colonisations, as we might

expect (Hanski and Gilpin 1997). The results of model fitting in chapter four indicate further insights, here we observe ripple effects throughout the colonies as individuals recruit into colonies based on their productivity (which is influenced by both density-dependence and environmental stochasticity) and the distance between colonies. In this way we observe net gain of individuals driving colony growth in some colonies, notably Fetlar SPA, while we see a net loss via emigrants from other colonies- e.g. Fair Isle SPA. Whilst both the very basic rescue-effect model and the much more informative metapopulation model vary in their complexity, both offer us novel insight into the robustness or vulnerability of populations to additional mortality. The chapter two rescue-effect simulations indicate that we observe radically different outcomes in persistence when we consider impacted population as closed or open. The results of chapter four observe a redistribution of individuals across a landscape that would not be considered if impacts were modelled to closed populations. Here, we may misidentify a decline in a particular sub-population and misdirect action towards mitigating a perceived threat, such as by moving a development to an area with a presumed lower impact. For example, the results suggest that Fair Isle is a net donor of individuals to the mainland. If it is then impacted by additional mortality we see a knock-on effect to other colonies throughout the network, in size and growth rate. Conversely, we observe other SPA colonies that appear to have very different behaviour whether modelled as closed or open such as Saxavord, Hermaness and Valla Field, which may mean that additional mortality to that SPA may be unlikely to cause ripple effects to other colonies. Here, I highlight the variation in outcomes when we include more realistic demographic processes in our models and provide an argument for further steps to be made to establish the patterns of demography that contribute to seabird population dynamic and allow us to predict scenarios of impact.

5.5 The missing: How do we manage when we have both incomplete knowledge of demography and incomplete datasets?

One of the most challenging aspects of modelling a population of any species is missing information. With seabirds we have both missing knowledge surrounding aspects of their demography and missing information from inconsistent effort on aspects that we can observe. The degree to which we can reliably utilise incomplete datasets depends on the framework used to model, the life-history of the species, the outcomes we expect to estimate and the underlying trend of the species, that whilst we may not have a complete empirical dataset for, we have a general understanding of the complexity or linearity of the population trend. For example, in the gannet model of chapter two, this model was fit to a time-series from across 29 years that included only five survey points. I argue that this approach is entirely suitable, using state-space Bayesian frameworks for this population of this species. Of course, increased observations would likely reduce the credible intervals around parameter estimates, increase fitting time and in general I advocate for as consistent and thorough a monitoring programme as resources allow.

But in the case of the gannets at the Bass Rock they have been following a growth trajectory that the sampling effort, although low will capture effectively. The same could not be said to expectations of robustness of our estimates if we had a survey effort that failed to capture the predominant trend, either capturing a decline or growth in a fluctuating species or indeed capturing a period of growth in a species that overall has been suffering a decline. So, whilst the Bayesian integrated state-space approach is a powerful tool, the limitations with which we approach demographic models need to come from a wider understanding of the representativeness of the datasets and additionally the study colonies we choose to investigate. Indeed, as mentioned the gannet population at the Bass Rock may well see a curtailment in growth and also potentially a decline, depending on intrinsic and extrinsic conditions, would current sampling efforts predict a decline? I propose as a future exercise, to test parameter estimation of these models under varied sampling scenarios. Not only could this highlight the limitations of inference for less well monitored populations, but it may also allow for practical direction towards the best timeline for survey efforts in allowing detection and fit to trends in general and for estimation of parameters regulating populations and vital rates of demography.

Furthermore, the data I fit the models to (nest abundance and productivity) is publicly available and whilst subject to standardised methodologies (Walsh *et al*. 1995) it may be subject to often unmeasured (or unreported) error associated with each colony and each metric. Thus, as a precaution, I applied arbitrary terms of variance around observation processes in the models for abundance and an informed, (but maybe out of date in kittiwake) error around productivity. From chapter three I fit time-series of adult survival, estimated form capture-mark-recapture studies and models for the long-term monitoring at the Isle of May. An interesting outcome of the model fitting was the effect of including the adult survival data from the Isle of May. If we recall from the general introduction that we would expect emergent properties of the population dynamic to best be described by that which we observe at the individual we see that inclusion of this data does not improve model fit. Is this because of an overtly conservative observation error in adult abundance (thought to be a less robust indicator of demography)? Does inclusion of adult survival highlight increased variation in estimates of other vital rates? Whilst, I did not have the time to further explore these and other questions surrounding this dichotomy, the subsequent fit to the population data when I include survival data suggests an elevated productivity estimate and a fluctuating fit to the abundance data comparative to excluding the survival data (Figure 3.7). Further investigations of this might include providing a greater degree of observation error to the abundance data, updating the productivity error and including a more complete analysis on the impact to other vital rate estimates when we include or exclude adult survival. This is important as many colonies do not have estimates of survival, so assessment of the limitations or lack of in modelling demographic processes with the two commonly available datasets: productivity and abundance, against that which additionally include adult survival may allow further insight into the magnitude of estimates and predictions under differently informed models.

In terms of missing processes of demography, each chapter here provides methodology that allows for an approach that consolidates both incomplete data (integrated state-space modelling) with parameterisation of models that captures and estimates demographic processes with which we have missing direct empirical evidence of, such as density-dependence, environmental stochasticity, immigration, emigration and age-class variation in the magnitude of impacts. These methods also provide a measure of uncertainty by their provision of the posterior density distributions, allowing for additional subsequent enquiries, such as in sensitivity analyses in PVA.

5.6 Impact assessment: are current methods robust?

We should regard precaution as a mechanism for maintaining persistence of populations under the absolute worst-case scenario comparative to un-impacted baselines. However with competing outlets for conservation resources, economic growth and green energy targets, precaution is not afforded the luxury of error in misidentifying threats to wildlife or limiting industry and there are real consequences both in the short term and in the long term for either population decline due directly to collision impact or from carbon offsetting (a major contributor to environmental perturbations that are negatively affecting biodiversity) being delayed by investment into greener energies. For example, we establish from chapter 2, that a previously favoured technique, PBR is wholly unsuitable for providing a precautionary threshold of mortality to a population modelled under empirical combinations of density-dependence and environmental stochasticity. This is in-keeping with other studies, detailing similar concerns and results (Green et al. 2016, O'Brien *et al*. 2017) however it is still a preferred method outside of the UK. To my knowledge, no other modelling approach has considered, directly, estimating or evaluating the impact of the same environmental pressure to survival at each stage. Are we asking the right questions in offshore wind assessment (or other industries- by-catch) for some life stages. For example, how frequently may a second-year bird encounter a turbine and die and is mortality at this life-stage a pivotal stage in the population structure, sensitivity and therefore predicted vulnerability. Using the state-space modelling approach we are able to derive full posterior estimates of demographic processes and relationships of vital rates to regulation and combine all of this information in a spatially structured network. Clearly this is a computationally advanced approach, however the foundations of which are rigorous in both ecological and mathematical theory. Whilst the principle of parsimony stands for many experimental scientific advances, population assessment models may over-simplify natural complexity in the system they aim to describe. There is a stark contrast between undue complexity and omission of complex but fundamental drivers of growth in predicting unknown consequences under unknown conditions. I provide here methods and evidence towards using updated techniques to assess impacts against populations under more realistic conditions.

5.7 Future directions and improvements

Throughout this work I have built upon methodologies and results to present methods and evidence for estimating multiple demographic processes using empirical data and using PVA, subsequent examples of sensitivity to additional mortality. After fitting the first model I was interested in exploring the assumption made when I applied the same environmental effect to both productivity and survival. This led me to adding separate terms for survival and productivity and then focussing on establishing if there was any pattern of magnitude in environmental effects to age-class survival. Further to this investigation, another key avenue I did not have time for, would have been to look across the relative contribution of important co-variates for environment and each vital rate. It would be of interest to update the original model with the productivity and survival rates having different terms for environmental perturbation and then re-assess the patterns of regulation across age-class. As mentioned in section 5.1 there is the opportunity here to test how sampling effort changes the results for different life histories- increasing gannets, do we still see same estimates of demography with reduced sampling, as they head towards K do we need increased sampling? What happens if I remove some of the years of the guillemot and kittiwake? How does this affect estimates of demographic processes and can I use this information to inform sampling census timelines? Identifying proximate causes of variability in environmental drivers of survival in seabirds still remains elusive and it would be of interest to update the model in chapter 3 using chlorophyll indicators and or sea-surface temperatures from identifiable latitudes/areas of non-breeding importance (Reiertsen et al 2014) do we see a reduction in the variation of the environmental survival term? With hindsight, it would be beneficial to explore the effect of error sensitivity around abundance estimates and evaluate how my models respond to increased uncertainty around counts? Does this improve the fit of survival estimates, is there a trade-off in assumed precision of abundance data and the effect of quantified survival data? In the metapopulation model it would be interesting to fit this model to other regional networks and assess the patterns as they emerge, it would be useful also to tease apart the relative contribution of productivity as a function of distance, further to the distance influence reported in the results (there was no productivity matrix saved whereby I could represent this faithfully from the model). Further experiments regarding the influence on the non-SPA colonies in the metapopulation structure would also be useful in establishing the nature of the structure and function of this metapopulation. Finally, applying adapted forms of these models to other species, in the context of their life history, could help us understand not just sensitivity to impacts but biological function of seabird populations and so too their relative resilience or vulnerability to the many threats that face them.

Conclusions

Seabird population dynamics are complex and are therefore a challenge to describe and evaluate vital rates and regulatory processes. Technological progression is allowing insight into the particular life-strategies of individuals within a colony/species and growing datasets from collaborations crossing our (not the birds') geographical boundaries are offering new information on connectivity. The degree to which we attribute the measure of infallibility in models should be reflected in both the capture of reality and the relative application of precaution in the methods. To which end, current approaches may be misdirecting resources and conservation strategies, by describing what we know to be a network as a closed system or by oversimplifying impact from mortality by not capturing uncertainty in regulation, both of which have the potential for missing an anthropogenic additional mortality induced decline or extinction.

Bayes theory is not a modern concept, but instead modern technology allows us to computationally capture and estimate unobserved states and parameters in a system combining theory with technology. In a world of competing demands, limited funding and existing datasets (of various quality) these approaches allow for commonly available data to be harnessed in free computational software to estimate processes and then simulate populations for assessment. Key to this is the capture of uncertainty throughout in parameter and latent state posteriors. This is a thesis about population dynamics and evaluating anthropogenic threat. Whilst my model organisms are seabirds there is no reason the fundamental methods here could not be adapted to other species. For example, barrier effects to migrating animals or harvesting of a given species.

Finally, in investigating either the mechanism or consequences of population dynamics, data is key. It is a result of the combined effort of many people that I was able to apply modern techniques to model dynamics. Looking ahead to challenging times for industry, governments and biodiversity the need to continue monitoring colonies with which we can attempt to predict and then mitigate anthropogenic impacts to has never been greater. Responsibility of maximising the efficacy of these hard-won data into real informative approaches lies with science, industry and policy.

Appendix 1: Supplementary information for Chapter 2: The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality

A.1.1 Scalar Derivation

Under the assumption that environmental stochasticity affects productivity to a different (probably greater) degree than survival (Weimerskirch 2001, Oro 2004) it was necessary to derive a scaling parameter describing the relative strength of effects on those different demographic processes.

We consider the intrinsic rates for productivity and the mean for survival, respectively B_I, S_I . In the logit scale of our population models, these values are the intercepts (b and s) of our linear predictors:

$$\text{logit}(B_I) = b, \qquad \text{logit}(S_I) = s \tag{6.1}$$

We define the proportional deviations of annual productivity and survival from these values as

$$\delta B = 1 - \frac{B}{B_I}, \qquad \delta S = 1 - \frac{S}{S_I} \tag{6.2}$$

We then define the ratio of proportional deviations as a measure of the relative strength of environmental impacts on survival relative to productivity.

$$p = \frac{\delta B}{\delta S} \tag{6.3}$$

Using the logit formulations of productivity and fecundity contained in the population model, we consider a specific value B_u which corresponds to a unitary environmental perturbation from the intrinsic rate of reproduction

$$\text{logit}(B_u) = b - 1 \tag{6.4}$$

The corresponding environmental impact on survival is an unknown so, in the scale of the linear predictor, we will denote it by C giving:

$$\text{logit}(S_u) = s - C \tag{6.5}$$

These represent proportional deviations of:

$$\delta B_u = 1 - \frac{B_u}{B_I}, \quad \delta S_u = 1 - \frac{S_u}{S_I} \tag{6.6}$$

and

$$p = \frac{\delta B_u}{\delta S_u} \tag{6.7}$$

A value of p may be derived from available data. As a crude approximation $\hat{p}$, we used aggregated minima and maxima (intrinsic) estimates of productivity and age-specific survival obtained over comparable time periods (Horswill and Robinson 2015, CEH, SMP). We calculated both proportional productivity change and proportional survival change using the minimum and maximum observations. In general, the following relationship applies

$$\hat{p} \cong \frac{S_I \delta B}{S_I - \exp(s - C)/(1 + \exp(s - C))} \tag{6.8}$$

Which allows us to solve for C

$$C = s - \text{logit}\left(S_I \left(1 - \frac{\delta B_u}{\hat{p}} \right) \right) \tag{6.9}$$

Table A1.1: Calculated scalars for each age class of each species

	1	**2**	**3**	**4**	**5**	**6**
Gannet	0.752	0.665	0.6182	0.6017	0.6143	NA
Guillemot	0.977	0.741	0.547	0.556	0.584	0.584
Kittiwake	1.49	0.83	0.83	1.08	NA	NA

Our assumption of synchronicity was made to reflect the paucity of empirical estimates on the relationship between vital rates and environment. We assume there is some correlation between survival and fecundity as an individual accumulates condition throughout the year affecting both their survival and their ability to breed. The magnitude of our environmental stochasticity estimated through our population dynamic is subject to our assumption, derived from and reflected in our data and therefore directing our model to capture some correlation. We accept there may be other ways to assume and apply this derivation.

A.1.2 Fixed Parameters in model fitting

Vital rates for each species at each life stage (productivity adjusted for female only post breeding census in bold). All data acquiesced from colony specific citation from Horswill and Robinson 2015 (e.g. Harris, Frederiksen & Wanless 1997) and/or Newell *et al.* 2016.

Table A.1.2. Gannet Vital Rates

S1	S2	S3	S4	S5
				0.47
0.542				
	0.779			
		0.859		
			0.869	0.916

Table A.1.3. Kittiwake Vital Rates

S1	S2	S3	S4
			0.68
0.76			
	0.85		
		0.87	0.882

Table A.1.4. Guillemot vital rates

S1	S2	S3	S4	S5	S6
					0.45
0.56					
	0.792				
		0.917			
			0.939		
				0.939	0.939

Table A.1.5. Fixed Parameters

Variable	**Description**	**Parameter**	**Value**
Productivity	Number female chicks fledged per nest	bmax	See tables A2-A4
Survival	Probability of survival at each life stage	S	See tables A2-A4

Variable	Description	Parameter	Value
Observation error	Observational error in nest counts	obsR	0.01
Observation Variance	The variance around a nest count	ObsV	0.01*adult population
Observation precision	Precision in the observed nest distribution	ObsTau	$1/ObsV^2$
Scalar for each life stage	Coefficient for environmental impact at each life stage	Scalar(x)	See section: A.1.1Scalar Derivation
Initial population size	Population starting size	Popstart	First data point multiplied by last age class dominant eigenvalue

N.B

A typo in equation 2.2 on page 29 should be corrected in future applications to:

$$B = \frac{f}{2} S_a$$

Where B is intrinsic productivity, f is highest reported chicks fledged and S_a is adult survival. Under correct calculation the productivity parameters should be: Gannet:0.41, Guillemot:0.40 and kittiwake: 0.50

Whilst this is likely to have minimal effect to guillemot and gannet modelling and simulation, kittiwake models and simulation results may have wider credible intervals in density-dependent and environmental stochasticity estimates or slightly enhanced population persistence in PVA with the increased intrinsic productivity rate provided. However, given the allowance of demographic stochasticity and the simultaneous estimation of parameters of interest, it is very likely the results from all species reflect similar theoretical patterns of response to regulation and anthropogenic mortality and the effect of the productivity supplied is negligible.

A.1.3 Stochastic parameters in model fitting

Table A.1.6. Stochastic Parameters

Variable	Parameter	JAGS code	Distribution	Prior	Mean/Variance
Density-dependence	ϕ	a1	Gamma	See Table A7	
Environmental Stochasticity	Eps1	Eps1	Normal	(0,prec)	$(0, 1/\sigma^2)$

Variable	Parameter	JAGS code	Distribution	Prior	Mean/Variance
Environmental perturbation magnitude	σ	sigma	Gamma	See Table A7	
Initial population size each age class	n[6,1] etc.	N[6,1]etc.	Poisson	(Dominant eigen value*popstart)	(Resulting value)
Demographic stochasiticty in process model	N[1,t+1] etc.	N[1,t+1] etc.	Binomial	(dbin(b[t],n[6,t]) etc.	Probability of survival/productivity, population size of dependent life stage)

A.1.4 Priors

Table A.1.7. Prior probability density functions (PDFs) for density-dependence and environmental stochasticity parameters in all models (~dgamma (shape,rate))

Parameter	Form of the prior		
	Gannet	Kittiwake	Guillemot
Density-dependence	~Gamma(1e-12,1e-4)	~Gamma (1,1e-6)	~Gamma (1e-6,10)
Environmental stochasticity	~Gamma (100,100)	~Gamma (100,100)	~Gamma (16,8)

Priors were chosen as a distribution appropriate for the biological theory of the process we wished to describe, where possible (e.g. compensatory DD was constrained to a gamma distribution and its effect was a-priori assumed to be negative on population growth). Priors were then designated a sensible but arbitrary mean and variance in a minimally informative approach.

Different species are fundamentally different in terms of how they experience their environment and density-dependence. All species were initially modelled on the same priors. However, modelling runs clearly indicated the priors were limiting on some parameters, for some species, as the models failed to run or converge, with errors indicating computational difficulties.

Prior adjustment was only made if the model would not run.

Each species follows differing trends, had different lengths of time-series and had different periods and volumes of omission in data. As such, the time periods the models ran for varied with the complexity, length and structure of each dataset and species.

Models were ran for kittiwake: burn-in $3E^6$, sample $5E^5$, thin=10; Guillemot: burn-in $2E^6$,sample $8E^5$, thin=10 , Gannet: burn-in $2E^{6,}$, sample $18E^5$,thin=10

Model length reflected convergence diagnostics. Burn-in reflects the discretion of the modeller. Models were intermittently checked for convergence diagnostics before being accepted or extended.

The results of the model fitting for each species are presented below in Figure A1 with the estimates for density dependence and environmental stochasticity for each species presented in Table A8.

A.1.5 Results from model fitting

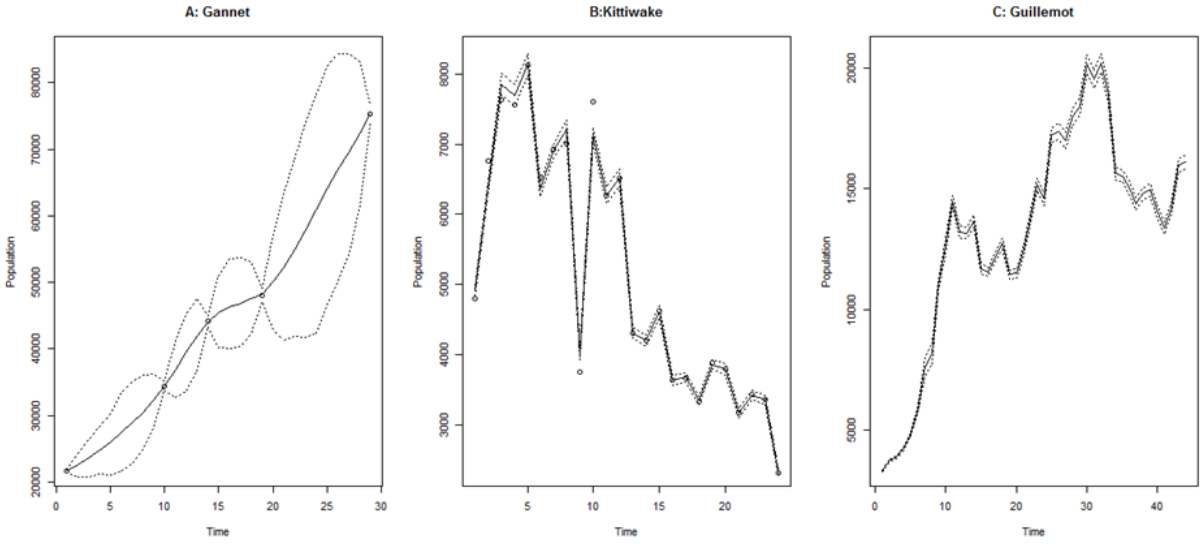

Figure A.1.1. Results of the model fit for A: Gannet, B: Kittiwake and C: Guillemot. The true datasets are the points, with the solid line being the mean estimate, dashed line indicates credible intervals of estimates.

Table A.1.8. Results of parameter estimates for each species. Mean in bold with lower and upper credible intervals in parentheses.

	Species		
Parameter	Gannet	Kittiwake	Guillemot
Density-dependence	(1.00E-11) 3.21E-07 (1.57e-06)	(3.6E-05) 5.13E-05 (6.48E-05)	(1.00E-11) 1.55E-07 (9.27e-07)
Environmental stochasticity	(0.77) 0.96 (1.16)	(1.08) 1.26 (1.44)	(1.85) 2.42 (3.04)

A.1.6 Read in files for population data:

Kittiwake and Guillemot from Newell *et al*. 2016, Gannet from JNCC 2017.

```
Kittiwake<-c(4801,6765,7638,7564,8129,6535,6916,7009,3751,
    7603,6269,6518,4306,4196,4618,3639,3666,3335,3876,3790,3167,3424,3354,2316,NA)
Gannet<-c(21591,NA,NA,NA,NA,NA,NA,NA,NA,34397,NA,
```

```
NA,NA,44110,NA,NA,NA,NA,48065,NA,NA,NA,NA,NA,NA,NA,NA,NA,75259,NA)

Guillemot<-c(3360,3920,3880,3790,NA,NA,NA,NA,11250,NA,14750,13000,
13000,13700,11680,11223,12736,12632,11440,11511,12418,13843,15326,
14500,17340,17384,16933,17979,18442,20185,19519,20332,18858,15578,
15536,15036,14143,15029,14955,14100,13349,14248,15945,16132, NA)
```

A.1.7 JAGS code: example model, guillemots.

```
IOMGUpopmodel<-"model{

bmax<-0.45 #female only post breeding census productivity
s1<- 0.56 #vital rate for each age class
s2<-0.792
s3<-0.917
s4<-0.939
s5<-0.939
s6<-0.939

a0<-log(bmax/(1-bmax)) #natural log transformation
s1a0<-log(s1/(1-s1))
s2a0<-log(s2/(1-s2))
s3a0<-log(s3/(1-s3))
s4a0<-log(s4/(1-s4))
s5a0<-log(s5/(1-s5))
s6a0<-log(s6/(1-s6))

# fixed species specific values for scalar
scalar1<-0.977
scalar2<-0.741
scalar3<-0.547
scalar4<-0.556
scalar5<-0.584
scalar6<-0.584

obsR<-0.01#observation error

#_____________time loop_____________
for (t in 1:(tmax-1))
{

  ntot[t]<-sum(n[,t]) # Total density

  eps1[t]~dnorm(0, prec) #full impact of environmental stochasticity
  eps2[t]<-scalar1*eps1[t] #relative impact as scaled by each age class relationship to productivity
  eps3[t]<-scalar2*eps1[t]
  eps4[t]<-scalar3*eps1[t]
  eps5[t]<-scalar4*eps1[t]
  eps6[t]<-scalar5*eps1[t]
  eps7[t]<-scalar6*eps1[t]

  lt[t]<-a0-a1*ntot[t]+eps1[t] # Linear predictor for productivity, with density-dependence and
environmental stochasticity
```

```
  logit(b[t])<-lt[t] # logit of Lt, representing proportion of maximum vital rate that is actually realised
  lts1[t]<-s1a0+eps2[t] #probability of survival at each age class on logit scale with environment
  logit(s1E[t])<-lts1[t]
  lts2[t]<-s2a0+eps3[t]
  logit(s2E[t])<-lts2[t]
  lts3[t]<-s3a0+eps4[t]
  logit(s3E[t])<-lts3[t]
  lts4[t]<-s4a0+eps5[t]
  logit(s4E[t])<-lts4[t]
  lts5[t]<-s5a0+eps6[t]
  logit(s5E[t])<-lts5[t]
  lts6[t]<-s6a0+eps7[t]
  logit(s6E[t])<-lts6[t]


#update rules for process model, with demographic stochasticity included as binomial distribution

  n[1,t+1]~dbin(b[t],n[6,t])
  n[2,t+1]~dbin(s1E[t],n[1,t])
  n[3,t+1]~dbin(s2E[t],n[2,t])
  n[4,t+1]~dbin(s3E[t],n[3,t])
  n[5,t+1]~dbin(s4E[t],n[4,t])
  nnew[t]~dbin(s5E[t],n[5,t])
  nold[t]~dbin(s6E[t],n[6,t])
  n[6,t+1]<-nnew[t]+nold[t]

#observation error
  obsR<-0.01
  ObsV[t]<-obsR*n[6,t]
  ObsTau[t]<-1/ObsV[t]^2
  nDat[t]~dnorm(n[6,t], ObsTau[t])
#eigenvector for initialisation
  EV<-(c( 0.20, 0.10, 0.08, 0.07, 0.07, 0.48))
#data points to monitor
  expectNests[t]<-n[6,t]

}
# PRIORS ------

prec<-1/sigma^2

# Prior for density-dependence
mu1<-0.0000001
sd<-0.0001
s<-mu1^2/sd^2
r<-mu1/sd^2
a1~dgamma(s,r) T(0.00000000001,0.001)  # Truncation as searching incomputable lower values

#Prior for environmental stochasticity
prec<-1/sigma^2
mu<-2
sdi<-0.5
p<-mu^2/sdi^2
q<-mu/sdi^2
```

```
sigma~dgamma(p,q)

popstart<-7024 #initial starting population size scaled to each stage
n[6,1]~dpois(EV[6]*popstart)
n[1,1]~dpois(EV[1]*popstart)
n[2,1]~dpois(EV[2]*popstart)
n[3,1]~dpois(EV[3]*popstart)
n[4,1]~dpois(EV[4]*popstart)
n[5,1]~dpois(EV[5]*popstart)

#data# tmax, nDat
#monitor# expectNests,a1, sigma,
}"



##DATA
#Length of time series
tmax<-45
#Nest observations
nDat<-c(3360,3920,3880,3790,NA,NA,NA,NA,11250,NA,14750,13000,
      13000,13700,11680,11223,12736,12632,11440,11511,12418,13843,15326,
      14500,17340,17384,16933,17979,18442,20185,19519,20332,18858,15578,
      15536,15036,14143,15029,14955,14100,13349,14248,15945,16132,NA)
```

A.1.8 JAGS code: PVA/PBR simulation, example guillemots

```
#COMMON GUILLEMOT

#Model data based on Isle of May
IOMGUpopmodel<-function (a1, sigma, tmax, tinit,tmed, FRi){

 bmax<-  0.45   s1<- 0.56 #Harris et al. 2007
  s2<-0.792 #Harris et al.2007
  s3<-0.917 #Harries et al. 2007
  s4<-0.939 #Harris et al. 2007
  s5<-0.939 #Harris et al.2007
  s6<-0.939 #Harris et al. 2007
  a0<-log(bmax/(1-bmax)) # Intercept representing fecundity when there is no DD and eps is zero
  s1a0<-log(s1/(1-s1))
  s2a0<-log(s2/(1-s2))
  s3a0<-log(s3/(1-s3))
  s4a0<-log(s4/(1-s4))
  s5a0<-log(s5/(1-s5))
  s6a0<-log(s6/(1-s6))


  n<-array(0,dim=c(6,tmax)) # Population data
  L<-matrix(0, 6,6)         # The Leslie matrix


  EV<-(c(0.20, 0.10, 0.08, 0.07, 0.07 ,0.48))
  popUpper<-10^9 #ceiling to allow for computation when density-dependence values very low and
environmental favourable
  popstart<-42502.34
  n[6,1]<-round(EV[6]*popstart)
  n[1,1]<-round(EV[1]*popstart)
```

```
n[2,1]<-round(EV[2]*popstart)
n[3,1]<-round(EV[3]*popstart)
n[4,1]<-round(EV[4]*popstart)
n[5,1]<-round(EV[5]*popstart)

# Main time loop/ PVA
for (t in 2:tmax)
{
 ntot<-sum(n[,t-1]) # Total density
 scalar1<-0.977
 scalar2<-0.741
 scalar3<-0.547
 scalar4<-0.556
 scalar5<-0.584
 scalar6<-0.584

 eps1<-rnorm(1,0,sigma)
 eps2<-scalar1*eps1
 eps3<-scalar2*eps1
 eps4<-scalar3*eps1
 eps5<-scalar4*eps1
 eps6<-scalar5*eps1
 eps7<-scalar6*eps1

 lt<-a0-a1*ntot+eps1 # Linear predictor
 b<-inv.logit(lt) # logit of L, representing proportion of maximum vital rate that is actually realised
 lts1<-s1a0+eps2
 s1E<-inv.logit(lts1)
 lts2<-s2a0+eps3
 s2E<-inv.logit(lts2)
 lts3<-s3a0+eps4
 s3E<-inv.logit(lts3)
 lts4<-s4a0+eps5
 s4E<-inv.logit(lts4)
 lts5<-s5a0+eps6
 s5E<-inv.logit(lts5)
 lts6<-s6a0+eps7
 s6E<-inv.logit(lts6)



 n[1,t]<-min(popUpper,rbinom(1,n[6,t-1],b))
 n[2,t]<-min(popUpper,rbinom(1,n[1,t-1],s1E))
 n[3,t]<-min(popUpper,rbinom(1,n[2,t-1],s2E))
 n[4,t]<-min(popUpper,rbinom(1,n[3,t-1],s3E))
 n[5,t]<-min(popUpper,rbinom(1,n[4,t-1],s4E))
 n[6,t]<-min(popUpper,rbinom(1,n[5,t-1],s5E))+min(popUpper,rbinom(1,n[6,t-1],s6E))

 if(t==tmed){
  Nhat<-sum((n[6,t]*2))
  harvest<-PBRGU(Nhat,FRi)
 }
 if(t>tmed) {
  har<-min(harvest, sum(n[,t]))
  n[,t]<-round(n[,t]-har*n[,t]/sum(n[,t]))
```

```
    }
    if(is.na(sum(n[,t])==0)) break()

  }

  return(n)
}

####GUILLEMOT



PBRGU<-function (Nhat, FR){
  #Nmin: the minimum population estimate
  Zp<-qnorm(0.2,0,1) #The pth standard normal variate. Wade 1998 suggest lower 60th percentile
0.2 on sensitivity
  CVnhat<-0.1 #estimate of coefficient of variation for Nhat : Dillingham and Fletcher 2008
  Nmin<-Nhat*exp(Zp*CVnhat)
  ## Rmax: the maximum net recruitment rate formula from Neil & Lebreton 2005
  # parameters
  s<-0.939 #adult survival
  a<-6 #age at first breeding
  Rmax <- (((s*a - s + a +1) + (((s-s*a-a-1)^2) - (4 *s * a^2))^0.5) / (2 * a))-1

  PBR<-Nmin*(Rmax/2)*FR
  return(PBR)
}



#############################################################################################
PVA and PBR Model
#################################################################
### PVA model coding for comparison of the effect of stochasticity, both environmental and
### demographic, with varying strengths of density dependence to a named population without and
### then with a mortality regime. Regulation is manipulated via the a1 and sigma terms.
### The mortality regime is called from a function where
### all values are set save for the FR (recovery factor). This allows for varied levels of
### precaution to be assessed.
maxa1<-0.000000607929#highest/lowest value of a1
mina1<-0.0000000000100023
incra1<-(maxa1-mina1)/50 #increments by which we reach a1
maxsigma<-3.01154 #highest value of sigma
minsigma<-1.80446#1.83669
incrsigma<-(maxsigma-minsigma)/50 #increments by which we reach highest sigma
tmax<-300 #maximum number of years
tinit<-100 # Settling time
tmed<-200 # Allows for no influence of initial conditions and allows for the system to reach a steadier
state in the face of stochasticity. Allowing for baseline comparisons of populations under regulation
that can still persist against the impact of additional mortality
a1Range<-seq(mina1,maxa1,incra1)
sigmaRange<-seq(minsigma, maxsigma, incrsigma)
FR<-c(0,0.1,0.3,0.5,1.0) #adjusted recovery factor for amount of mortality applied
maxreps<-50 #number of times to repeat loop for values
data<-array(0, dim=c(c(length(a1Range)*length(sigmaRange)),6,5))#data store
```

```
##_____simulate_____
for(i in 1:length(FR))
{
 j<-0
 for (a1 in a1Range)
 {
  print(a1) #sense check working through
  for(sigma in sigmaRange)
  {
   estT<-SDT<-DropT<-rep(0,maxreps)
   for(rep in 1:maxreps)

   {
    pops<-IOMGUpopmodel(a1, sigma, tmax, tinit, tmed, FR[i])
    pop<-colSums(pops) #total population size
    estT[rep]<-mean(pop[(tmax-100):(tmax-75)])#years 200-225 (mortality applied)
    SDT[rep]<-sd(pop[(tmax-100):(tmax-75)])#years 200-225 (mortality applied)
    DropT[rep]<-(mean(pop[(tmed-25):tmed])-mean(pop[(tmax-100):(tmax-75)]))/mean(pop[(tmed-
25):tmed]) # population change years 175-200 and years 200-225
   }
   j<-j+1 #counter for data storage
   data[j,1,i]<-a1
   data[j,2,i]<-sigma
   data[j,3,i]<-mean(estT)
   data[j,4,i]<-mean(SDT)
   data[j,5,i]<-mean(DropT) #comparison of mean pop size, pre/post treatment
   data[j,6,i]<-sd(DropT)

  }
 }
}
```

Appendix 2: Journal of Applied Ecology published article and supplementary materials

The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality

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Abstract

1. The balance between economic growth and wildlife conservation is a priority for many governments. Enhancing realism in assessment of population-level impacts of anthropogenic mortality can help achieve this balance. Population Viability Analysis (PVA) is commonly applied to

investigate population vulnerability, but outcomes of PVA are sensitive to formulations of density-dependence, environmental stochasticity and life-history. Current practice in marine assessments is to use precautionary models that assume no compensation from density-dependence or rescue-effects via "re-seeding" from other colonies. However, if we could empirically quantify regulatory population processes, the responses of populations to additional anthropogenic mortality may be assessed with more realism in PVA.

2. Using Bayesian state-space models fitted to population time-series from three sympatric seabird populations, selected for varied life histories, we inferred the extent to which their dynamics are driven by environmental stochasticity and density-dependence.

3. Based on these inferences, we conducted an exhaustive PVA across credible parameterisations for intrinsic and extrinsic population regulation, simulated as a closed and re-seeded system. Scenarios of anthropogenic mortality, along a sliding scale of precaution, were applied both proportionally and as a fixed quota using Potential Biological Removal (PBR).

4. Baseline results from fitting revealed clear environmental regulation in two of our three species. Crucially, we found that for our empirically derived, realistic model parameterisations there are risks of decline to real populations even under very precautionary mortality scenarios. We find that PBR is dubious in application as a sustainable tool for population assessment when we account for regulation. Closed versus re-seeded models showed a large divergence in outcomes, with sharper declines in closed simulations. Fixed-quota mortality typically induced greater population declines comparative to proportional mortality, subject to regulation and re-seeding.

5. *Synthesis and applications*: Practitioners using arbitrary formulations of population regulation risk over-precaution (economic constraint) or under-precaution (endangering populations). The demands of increased economic development and preservation of wildlife require that methodologies apply techniques that confer reality and rigour to assessment. The current practice of employing models lacking density-dependence and empirical environmental information imposes limitations in the

efficacy of estimating impacts. Here, we provide a method to quantify the conditions that predominantly regulate a population and exacerbate the risk of decline from anthropogenic mortality. It is in the interests of both developers and conservationists to apply methods in population impact assessments that capture realism in the processes driving population dynamics.

Keywords: density-dependence, environmental stochasticity, marine renewables, population dynamics, rescue-effect

1. Introduction

Globally, many species are facing decline and potential extinction from anthropogenic activities (Murphy & Romanuk 2014; Ripple *et al*. 2016). Seabird populations are at risk from additional anthropogenic mortality from by-catch, oiling, harvesting and marine renewables (Croxall *et al*. 2012). The UK coastline hosts internationally significant numbers of seabirds, especially during the breeding season, and several of these species have been assessed as potentially at risk from offshore wind installations (Furness, Wade & Masden 2013). The marine renewables industry (Platteeuw *et al*. 2017) is seeking expansion, incentivised, in part, by internationally agreed sustainable-energy targets (Marques, Fuinhas & Manso 2010). Poorly planned developments may cause impacts such as additional mortality from collision strikes (Johnston *et al*. 2014). Industry, especially in countries bearing a legal requirement for environmental assessment (European Commission 2011), has a responsibility to minimize its impact on wildlife. Assessment approaches vary, but generally contain an appraisal of risk to populations from impacts of additional mortality (Buckland, Goudie & Borchers 2000), following the precautionary principle (Sands & Peel 2012), supported by EU directives (European Commission 2009).

Determining the consequences of additional mortality to a population requires an estimate of population size, an understanding of life history, estimates of demographic rates and how these are affected by regulating influences such as density-dependence and environmental stochasticity (Lande, Engen & Saether 2003). At the point of assessment and more generally in population ecology, there are inherent uncertainties associated with these parameters (Clark 2003). Assessments of inadequately studied populations may use proxy values from populations of the same or similar species for productivity or survival rates (Kindsvater *et al*. 2018). In addition, a lack of empirical estimation of connectivity (immigration or emigration) often leads practitioners to use closed system models (Hanski 1998). Empirical estimates of population regulation across spatio-temporal scales are also deficient. The shape and magnitude of density-dependence is difficult to quantify in wild populations despite its recognized importance for population dynamics (Bonenfant *et al*. 2009; Knape

and deValpine 2012). It is also challenging to derive quantitative estimates for extrinsic regulation from environmental stochasticity, especially since it may be confounded with intrinsic regulation in short time series (Engen, Bakke & Islam 1998). Understanding how population persistence is affected by variable combinations of density-dependence and environmental regulation is unknown (Saether *et al*. 2002). To increase the credibility of predicted outcomes from population assessments it is essential to represent biological reality whilst capturing uncertainty in estimates of understudied processes (Saunders, Cuthbert & Zipkin 2018). Failure to faithfully reflect accuracy and precision in predictions leads to one of two detrimental outcomes for human-wildlife conflict; over-precaution due to an inflated estimate of risk may curtail economically important activities, whilst undetected risks to population viability, could set sensitive populations on a path to extinction.

Reflecting knowledge gaps in connectivity and the ability to capture population regulation, UK seabird populations are modeled in an environmental impact assessment (EIA) assuming no immigration and, often, no density-dependence. The risk of additional mortality to a seabird population from collision is estimated typically across a period of 25 years, the operational life span of a wind farm, and evaluated as to how this estimate will affect the population. Population viability analysis (PVA) (Boyce 1992) and Potential Biological Removal (PBR) (Wade 1998), are among the methods used to evaluate anthropogenic additional mortality on seabird populations under assessment. PVA is an application of projection matrix modelling. PBR, designed initially for marine mammal assessment, is a simple harvest assessment calculating the maximum number of animals that may be sustainably removed from a given population. In EIA, PVA usually contains some estimate of demographic rates, with more recent assessments attempting to include environmental stochasticity by implementing the demographic rates as stochastic processes. Although some models may include a form of density-dependence, there is ongoing debate about the practical justification for its inclusion (Green *et al.* 2016; Horswill, O'Brien & Robinson 2016). In general, PVA has been shown to be sensitive to estimates of parameters, affecting predicted outcomes (Reed *et al*. 2002; Cook & Robinson 2016). PBR requires minimal demographic input, save for an adult survival estimate and the age at first breeding. There is

an assumption of compensatory density-dependence included in the model background (Niel & Lebreton 2005). The PBR calculation returns a threshold value of additional mortality to a population above which a decline is expected, it contains no stochastic component and no population projection. PBR has been criticised as a tool for EIA as it fails to quantify potentially serious population consequences which can occur below this threshold (Green et al. 2016; O'Brien, Cook & Robinson 2017).

Environmental signals affecting population dynamics can be explored using time-series data (Leirs *et al*. 1997; Frederiksen, Mavor & Wanless 2007), and density-dependence signals may also be extracted from population time-series (Lande *et al*. 2002; Brook & Bradshaw 2006). For realistic assessment, we should aim to derive empirical values for the strength of density-dependence and the magnitude of environmental stochasticity from such data. Exploring these values in a PVA would provide multiple intrinsic and extrinsic regulatory scenarios against which additional mortality may be assessed. Furthermore, modelling the populations with a rescue-effect (where immigration prevents extinction (Brown & Kodric-Brown 1977)) could help us assess the sensitivity of outcomes to the assumption of closed populations. We therefore aimed to assess how several levels of anthropogenic mortality can impact real seabird populations (both closed and open to a rescue-effect), operating under empirically derived estimates of environmental stochasticity and density-dependence.

We used Bayesian methods to fit a state-space population model to historical data from sympatric populations of three well-studied UK seabird species with divergent life histories: Northern gannet *Morus bassanus* L., black-legged kittiwake *Rissa tridactyla* L. and common guillemot *Uria aalge* Pontoppidan. This provided posterior credible intervals for density-dependence and environmental stochasticity for each population. These intervals defined parameter ranges for the strength of density-dependence and environmental regulation, which we explored systematically using our population model, generating predictions of population viability across the entire space of plausible combinations of intrinsic versus extrinsic regulation. To assess risk from additional mortality we

utilised PBR as a tool providing a range of values across a precautionary gradient, allowing a general approach to visualising 25-year mortality impact. Populations were modelled both under assumed closedness and under the possibility of annual rescue-effects from immigration.

2. Materials and Methods

2.1 Demographic Model

High-quality demographic rate and population abundance data were obtained for the sympatric island populations of Bass Rock (gannet) and the Isle of May (kittiwake and guillemot), Scotland (Appendix: S1(A1)).

All modelling and analysis was undertaken in R (R Core Team 2016). A stochastic stage-structured matrix model was developed for each species. The dimensions of the annual transition matrix were based on each species' age-at-maturity. For example, the deterministic version of our model, using rates, for a species with one juvenile and three sub-adult classes would take the form:

$$\begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \\ n_{4,t+1} \\ n_{5,t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & B_t \\ S_{j,t} & 0 & 0 & 0 & 0 \\ 0 & S_{1,t} & 0 & 0 & 0 \\ 0 & 0 & S_{2,t} & 0 & 0 \\ 0 & 0 & 0 & S_{3,t} & S_{a,t} \end{pmatrix} \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \end{pmatrix} \quad (6.10)$$

Where B and S represent the vital rates of productivity and survival, and the subscripts $j, 1, 2, 3$ and a on the vital rates denote juvenile, sub adult and adult age classes respectively.

As a female-only model, productivity was adjusted (Appendix: S1(A2)) under the assumption of a 1:1 sex-ratio. In the stochastic model, the number of chicks fledged and number of animals of each age class surviving were modelled as binomial processes, for all species, including kittiwake (Appendix: S1A3).

Generally, seabirds are characterised as long-lived animals that exhibit delayed reproduction, low fecundity linked to ecological constraints of resource patchiness and there is evidence of compensatory density-dependence in several studies (Horswill, O'Brien & Robinson 2016; Bried & Jouventin 2002) (Appendix: S1(A4)). There is evidence across all species that adults forego breeding when extrinsic and intrinsic conditions are sub-optimal to maintain condition (Weimerskirch 2001; Oro & Martinez-Abrain 2004). The model therefore estimates the strength of compensatory density-dependence in productivity alone, under the assumption that this would be the demographic rate most likely to be affected

We do not attempt in this model to account for a potential 'floater' population of adults that have the potential to breed but have not.

The probability of fledging female chicks at each time step B_t was modelled as a logit function of a linear predictor b_t. The logit transformation was used to ensure that B_t remained bounded within the 0-to-1 range. The linear predictor took the form,

$$b_t = b_0 - \phi n_{t-1} + \varepsilon_t \quad (6.11)$$

The terms on the right-hand side of equation (2) correspond to an intercept b_0, the effect of density (n_{t-1}) on productivity, measured as a penalty to the intercept by a coefficient (ϕ), and the effect of an environmental perturbation term (ε_t) comprising a time series of identically distributed Gaussian terms $\varepsilon_t \sim N(0,\sigma)$. The standard deviation (σ) of this term, was used as our metric for the magnitude of environmental stochasticity acting on the populations. The intercept represented intrinsic productivity, in the absence of density-dependence and environmental perturbations and

was derived from female-only reported maximal values of B (Supplementary Information) as the inverse logit transformation:

$$b_0 = \log \frac{B}{1-B} \tag{6.12}$$

Environmental variation can affect survival at all life stages (Weimerskirch 2001; Jenouvrier *et al*. 2005; Frederiksen *et al*. 2008; Lewis *et al*. 2009) and we assume that its impact is synchronous to the impact on productivity. In the model, the same fluctuations in environmental stochasticity are therefore also applied to survival, using a scaling term (p) (expressing the relative importance of environmental stochasticity for breeding and the survival rates of different life stages). This scalar was calculated from available time-series of demographic data, specific to each of our study populations (Appendix: S1(A5)). Survival for each age class $(S_{*,t})$ was modelled as a logit of baseline survival (S_{*0}) and environmental stochasticity ($p_* \varepsilon_t$). For example, in the case of juveniles, the linear predictor took the form:

$$s_{j,t} = s_{j0} + p_j \varepsilon_{,t} \tag{6.13}$$

The population's initial age and sex structure was unknown, so as a plausible start (assuming equal sex-ratio), we used the population's stable age distribution, derived from the dominant eigenvector (Caswell 2001) of the density-independent projection matrix. This distribution was then scaled using the population starting size to derive numbers for each age class (Appendix: S1(A6)).

2.2 State space model fitting to derive regulation

The above population model was fitted to the observations of historical population trend data for each species at each colony using the program JAGS (Plummer 2003) interfaced with R via the runjags package (Denwood 2016). There were missing data from years between counts in all the colonies

except kittiwake. The datasets for each species were: kittiwake: years=24; estimates across years=24; gannet: years=29; estimates across years=5; guillemot: years=44; estimates across years=39. Observation error was included in the model by allowing for a 1% sampling error in colony counts.

To estimate the regulatory parameters of interest: strength of density-dependence (ϕ) and strength of environmental stochasticity (σ), minimally informative priors were used for the models (Appendix: S1(A7)).

The density-dependence parameter ϕ (Equation 3) was assigned a gamma distribution, restricting density-dependence to a compensatory form. During model fitting, the MCMC chains explored extremely low values for density-dependence in some species. To facilitate computation in these cases we imposed a floor-truncation to this prior at the value 10^{-11}. Our model estimated the strength of environmental stochasticity as the precision ($\tau = \sigma^{-2}$) of the stochastic process ε_t. This was assigned a gamma prior (constraining σ^2 to positive values). Models were run until satisfactory convergence, based on the Gelman-Rubin diagnostic, PSRF (Brooks & Gelman 1997), effective sample sizes for all model parameters and visual inspection of traceplots (Kass *et al*. 1998). The ranges of values for the strength of density-dependence and environmental stochasticity were given by the upper and lower 95% credible intervals of the posteriors for ϕ, σ.

2.3 Mortality sensitivity: Population viability analysis

Populations were projected in a PVA analysis using the demographic matrix model outlined in 2.1 with ranges of values for density-dependence and environmental stochasticity taken from the posterior credible intervals (2.2) obtained from model-fitting. We divided each interval into 51 increments, producing 2601 pairwise combinations of values for density-dependence and environmental stochasticity. For each species, every combination was examined via population projections from our PVA model. Firstly, to gain a broader overview of the dynamics of these models and to allow comparisons between species, the estimated posterior values for density-dependence and environmental stochasticity were extended beyond their credible values and projected in PVA with no

additional mortality. To assess what impact mortality had on populations under different regulation, populations were again projected under each pair-wise combination. After a settling-in period of 200 years (Appendix: S1(A8)), mortality treatment was applied with the PBR derived from the starting population size at the 200-year mark. Severity of mortality was manipulated by the recovery factor term (FR) in the equation (Appendix: S1(A9)). The PBR was applied annually as a fixed number, and as a proportion removed annually based on the starting population size at 200 years. In all cases mortality was applied across all age classes in proportion to their annual size. Mortality was applied over a 25-year period, a typical windfarm lifespan. The mean population size μ_1 across this period, was then calculated and compared to the 25-year population mean μ_0 directly prior to the introduction of anthropogenic mortality. Impact (I) was calculated as a proportional change in population thus:

$$I = \frac{\mu_0 - \mu_1}{\mu_0} \tag{6.14}$$

To further explore the effects of mortality in this system we simulated the PVA analysis under a traditional 'closed' system, where we first assumed no connectivity in the populations and then allowed an annual rescue-effect by the introduction of a female, re-seeding the population and preventing extinction, but not avoiding declines.

3. Results

3.1 Baseline population change beyond boundaries of empirically derived density-dependence and environmental stochasticity

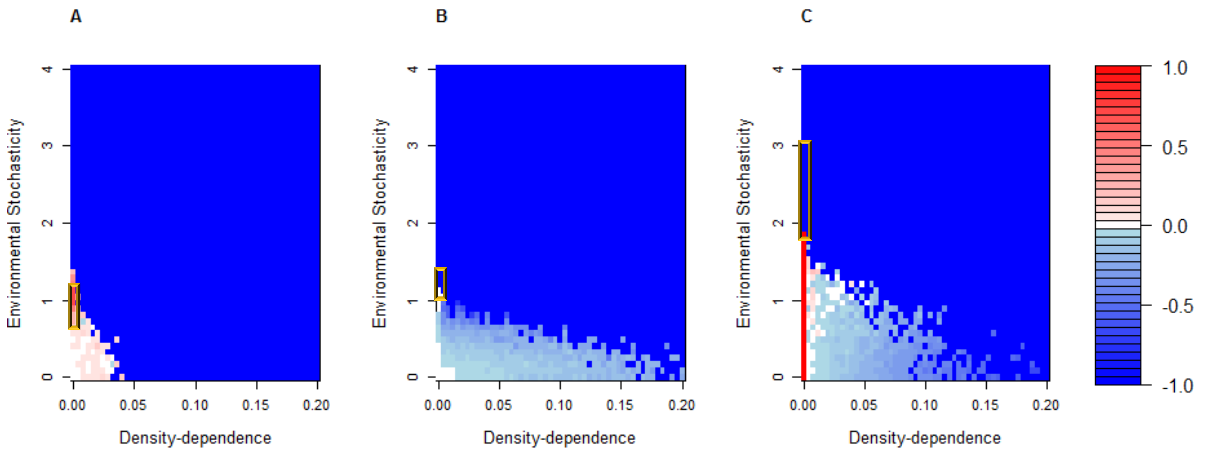

Figure 1: Baseline population change when density-dependence (DD) varies between 1e-11 and 0.2 and environmental stochasticity (ES) varies between 0 and 4. Panels A, B and C represent gannet, kittiwake and guillemot respectively, with boxes indicating the posterior boundaries of DD and ES derived from fitting and used in subsequent mortality projections. Pale colours are near-zero changes, pink through to red indicate proportional increases. Light blue indicates small declines through to darker blues indicating greater decline.

With no additional mortality, each species displayed declines and eventual extinctions under higher strengths of density-dependence and higher environmental stochasticity (Figure 1). All species produced similar qualitative patterns to increased regulation but varied in their response and sensitivity to regulation at lower values. The boxes overlaying plots in Figure 1 indicate the fit-derived estimates for density-dependence and environmental stochasticity (Appendix: S1(A11)). The boxes vary in their shape and limits across each of the species, but all are estimated near the lower limits of the full range of density-dependence explored, where colony persistence is unaffected by density regulation.

3.2 Mortality treatment results: Gannet

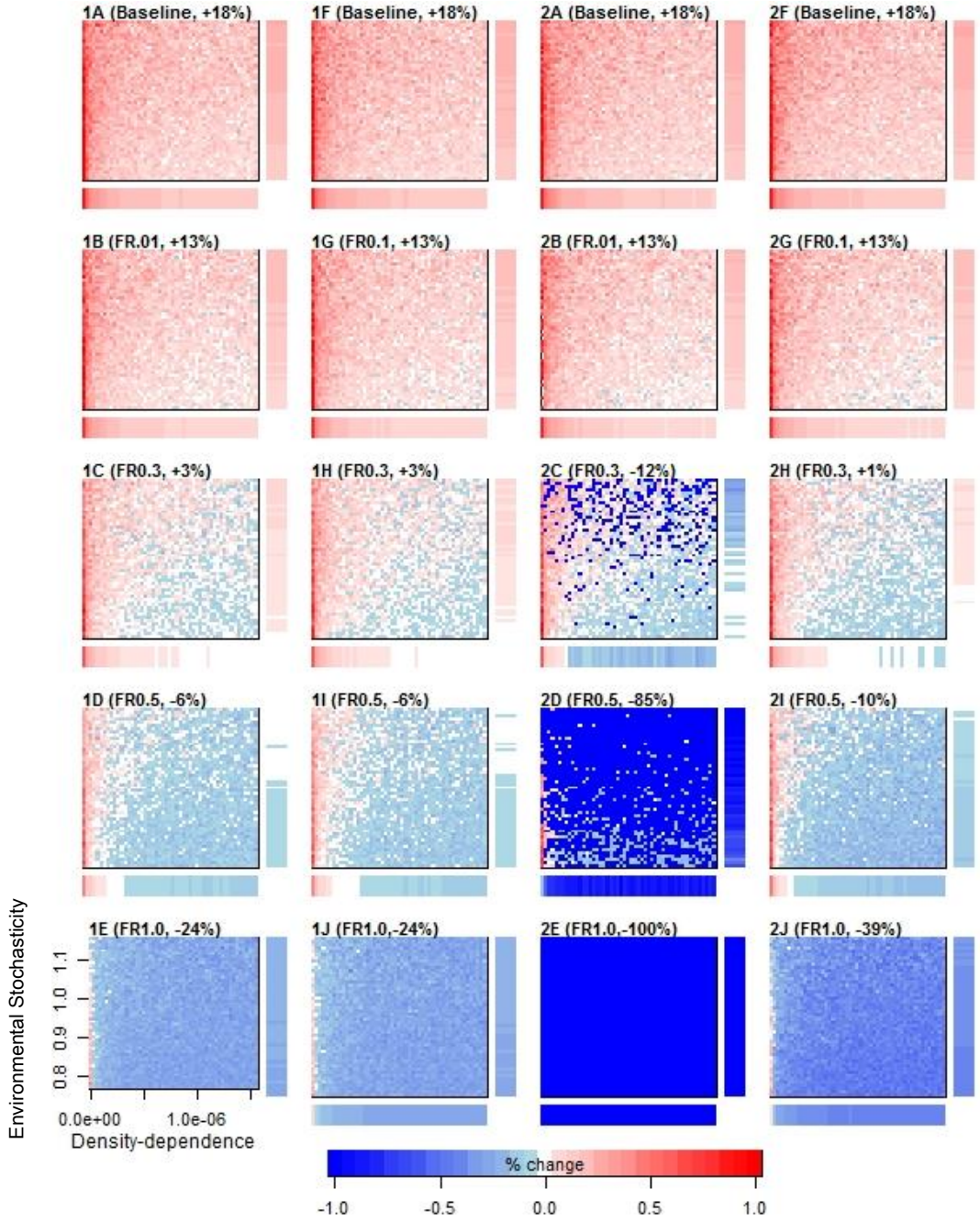

Figure 2: Gannet population projections under estimates of strength of density-dependence (x-axis) and environmental stochasticity (y-axis). Closed proportional removal (1A-1E) and re-seeded (1F-1J). Closed fixed removal (2A-2E) and re-seeded (2F-2J). A-J represent different mortality treatments, reporting the corresponding impact (mean population change (%) pre and post mortality) across each plot. The bands to the right and below each plot represent mean % change across rows and columns.
A & F- no additional mortality (baseline); B &G- additional mortality with PBR FR of 0.1; C & H-additional mortality with PBR FR of 0.3; D & I- additional mortality with PBR FR of 0.5, E & J- additional mortality with PBR FR of 1.0. Coloration indicates impact. Blues indicate population decline, white indicate zero change and pinks through to red indicate population increases, with darkest reds being any proportional increase of 1.0 or greater.

The gannet baseline, with no mortality treatment, showed no clear pattern of population change regulated by environmental stochasticity, strength of density-dependence or any combination of these. Both closed and re-seeded baseline projections were found to have increased across the 25-year period on average (Figure 2, panels 1A, 2A & 1F, 2F). Under a proportional mortality there was no difference in impact between the closed and re-seeded projections. Density-dependence contributed to decline under increased proportional mortality in both (declines seen from RHS to LHS along x-axis), with the full proportional impact causing loss across much of the projected populations (mean -24%) (Figure 2, panels 1A-1J). In the fixed mortality analyses results varied between the closed and re-seeded simulations. Increasing mortality resulted in higher vulnerability predominantly under higher environmental stochasticity in the closed analyses (decline seen in populations nearer the upper limit of the y-axis (Figure 2 panels 2A-2E)) with decline more prominent under higher density-dependence in the re-seeded versions (Figure 2, panels 2F-2J). Closed, fixed take simulations with the highest mortality experienced extinction across density-dependence and environmental stochasticity combinations. In contrast re-seeded simulations under the same conditions averaged -39% change (Figure 2, panels 2E & 2J).

3.3 Mortality treatment results Kittiwake

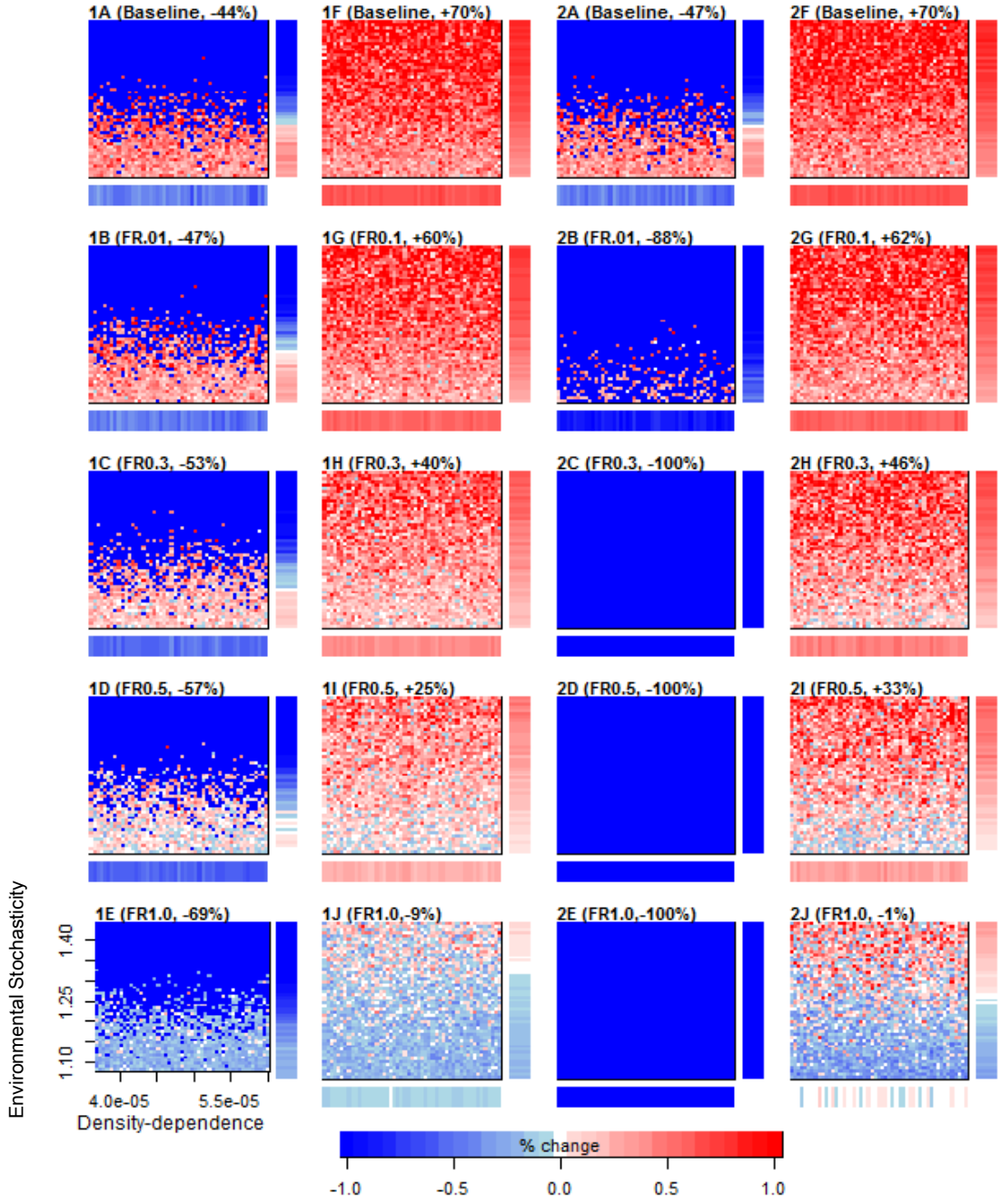

Figure 3: Kittiwake population projections under estimates of strength of density-dependence (x-axis) and environmental stochasticity (y-axis). Closed proportional removal (1A-1E) and re-seeded (1F-1J). Closed fixed removal (2A-2E) and re-seeded (2F-2J). A-J represent different mortality treatments reporting the corresponding impact (mean population change (%) pre and post mortality) across each plot. The bands to the right and below each plot represent mean % change across rows and columns. A & F- no additional mortality (baseline); B &G- additional mortality with PBR FR of 0.1; C & H-additional mortality with PBR FR of 0.3; D & I- additional mortality with PBR FR of 0.5, E & J- additional mortality with PBR FR of 1.0. Coloration indicates impact. Blues indicate population decline, white indicate zero change and pinks through to red indicate population increases, with darkest reds being any proportional increase of 1.0 or greater.

The kittiwake closed baseline simulations indicated extinction and therefore regulation by environmental stochasticity to all projections above a clear threshold (Figure 3, panels 1A and 2A). Projections below this level showed increases but no pattern was seen from density-dependence. The re-seeded baseline (Figure 3, panels 1F and 2F) showed increases in the areas previously declining or extinct in the closed scenarios. Closed baseline scenarios showed a mean population drop across the simulated space, whilst the re-seeded baseline found a mean increase in population change across projections (Figure 3, panels 1A, 2A & 1F, 2F). In the closed simulations, as mortality treatment was applied, both proportional (Figure 3 panels 1A- 1E) and fixed (Figure 3, panels 2A-2E) declined, with the fixed declining to a greater extent than the proportional projections. The re-seeded simulations were found to also decline as mortality treatment was increased, the decline was more gradual than their closed counterparts (Figure 3, panels A-J). Different magnitudes of decline were seen between the proportional and fixed re-seeded simulations (Figure 3, panels G-J). As mortality increased, those populations facing a proportional mortality reduced more than those under a fixed mortality. Overwhelmingly, re-seeded simulations maintained positive growth (dark red pixels) under high environmental stochasticity, whilst those simulations under increased mortality and lower environmental stochasticity were found to decline (blue pixels) (Figure 3, panels F-J).

3.4 Mortality treatment results Guillemot

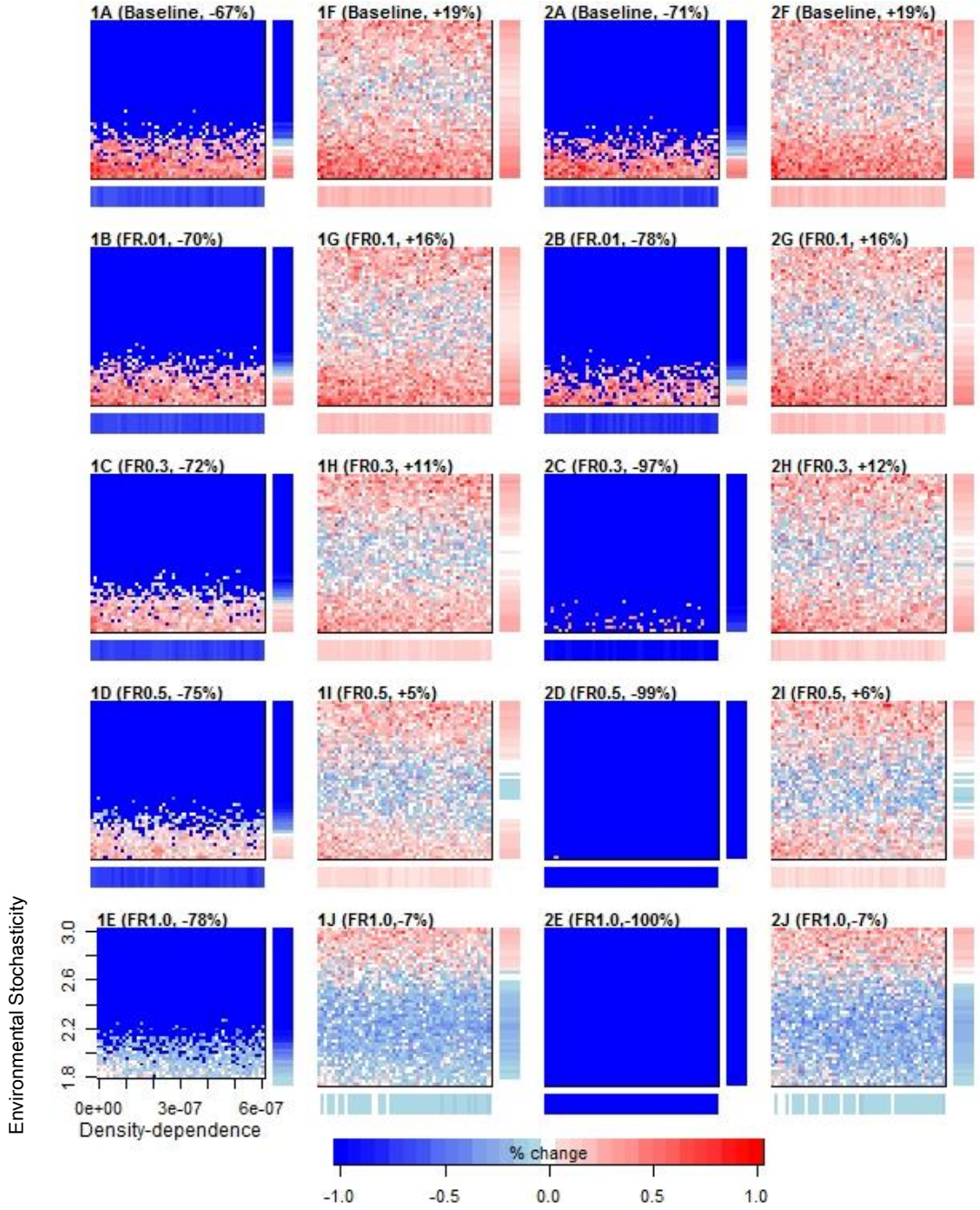

Figure 4: Guillemot population projections under estimates of strength of density-dependence (x-axis) and environmental stochasticity (y-axis). Closed proportional removal (1A-1E) and re-seeded (1F-1J). Closed fixed removal (2A-2E) and re-seeded (2F-2J). A-J represent different mortality treatments reporting the corresponding impact (mean population change (%) pre and post mortality) across each plot. The bands to the right and below each plot represent mean % change across rows and columns.
A & F- no additional mortality (baseline); B &G- additional mortality with PBR FR of 0.1; C & H-additional mortality with PBR FR of 0.3; D & I- additional mortality with PBR FR of 0.5, E & J- additional mortality with PBR FR of 1.0. Coloration indicates impact. Blues indicate population decline, white indicate zero change and pinks through to red indicate population increases, with darkest reds being any proportional increase of 1.0 or greater.

The guillemot closed baseline projections indicated clear extinction and therefore regulation by environmental stochasticity to all projections above ~ '2.2' strength. The re-seeded populations however reversed this effect, with increases shown (Figure 4, panels 1A, 2A, 1F & 2F). In the closed simulations all mortality treatments reported extinctions, with mean values higher than the baseline. However, the risk of decline as mortality increased was reduced in the proportional harvests comparative to the fixed harvest rate (Figure 4, panels 1B-1E, 2B- 2E). The re-seeded simulations were found to also decline as mortality treatment was increased (Figure 4, panels G-J), the decline was more gradual than their closed counterparts. In the re-seeded simulations a very different pattern was observed than in the closed. Here, under lower mortality those populations experiencing neither intermediate environmental conditions experienced decline (Figure 4, panels F-I). As mortality increased, this pattern enhanced, capturing more of the middle band of environmental stochasticity as vulnerable to decline and eventually at the highest proportional mortality causing decline even in those projections with lower environmental stochasticity (Figure 4, panels 1G- 1J). There is also a very slight hint at density-dependent risk to decline from the bottom right-hand side of the highest mortality (Fig.4 plot 1J &2J) comparative to those projections with lower density-dependence on the bottom left-hand side of the same plots.

Discussion

Population persistence is a function of quantifiable effects (e.g. mortality from collisions at wind farms), population dynamics (life history, strength of density-dependence, connectivity), and random effects (variable environmental conditions) and these may conspire to cause declines in seemingly stable populations. Quantifying internal and external processes and associated population change are still fundamental problems in population biology and conservation (Elton 1924; Turchin 1995; Matthiopoulos *et al*. 2015).

In our study, exploring extended ranges for the strength of density-dependence and environmental stochasticity allowed a visual comparison of vulnerability between our study species. All three-study species presented extinctions under higher strength of density-dependence (penalized fecundity) and high environmental stochasticity (high unpredictability), but the shape of these effects varied depending on each species' demography. The gannet and guillemot time series we used for model fitting were intermittent. These lower sample sizes and the necessary data-imputation carried out by our model, extended the time necessary for convergence and generated broader credible intervals than we might expect with more data-rich populations (Appendix: S1(A11)). Hence, our broader ranges of scenarios examined along the environmental stochasticity axis, for these populations, are also the result of greater observational uncertainty.

Under the explicit assumptions of population structure in these simulations, i.e. closedness, and in the absence of additional mortality, the baseline windows derived from the model fitting show kittiwake and guillemot straddle a well-defined threshold separating proliferation and extinction- mediated by environmental stochasticity. Notably, the gannets are not operating close to this threshold, possibly reflecting the fact that although current population growth is slowing down, the Bass Rock population has been increasing and gannets are arguably more robust to environmental perturbations due their life-history (Wanless, Murray & Harris 2005; Montevecchi *et al.* 2009; Garthe, Montevecchi and Davoren 2011). When we allowed rescue-effects, the picture changed for kittiwakes and guillemots. There is a clear indication, particularly for kittiwake, that population re-seeding can offset detrimental

environmental stochasticity. The results are similar albeit more stochastic for guillemot where re-seeded simulations also offset the magnitude of decline under certain mortality treatments.

This work highlights several findings of interest to conservation strategists and population assessments. Firstly, the PBR calculation, is questionable in its theoretical sustainability of the population. Results here show clearly that for all species there were some stark reductions from the baseline mean population size under mortality estimated using PBR, exacerbated by regulatory processes. This was seen in both the closed and re-seeded simulations of each mortality type (fixed or proportional), where population baselines were not maintained. Whilst perhaps some lower levels of PBR applied mortality may be considered 'sustainable', a switch in regulation may further reduce a population, potentially affecting sustainability. PBR has come under criticism from conservationists and industry advisors as to its appropriateness in assessment and is now broadly considered unsuitable for seabird assessment in the U.K EIA process. The results here agree with recent work suggesting it should not be utilised in seabird population management (Green et al. 2016; O'Brien, Cook & Robinson 2017).

Secondly, there is no permissible value of decline to a population under assessment from industry impact. In renewable energy impact assessment, mortality is usually applied as a proportion thereby treating the impact as a per capita effect. Intuitively, we expect a fixed mortality to have a stronger effect on a declining population and a weaker effect on an increasing population. In most of our treatments the proportional application of mortality conveyed a reduction in mean decline comparable to the fixed mortality. However, our results also indicated different patterns in regulation and risk when the same population baseline was subjected to a proportional or fixed mortality. For example, in the kittiwake re-seeded models, risk of decline from mortality was greater to those projections under lower environmental stochasticity compared to the closed projections; the decline from baseline was marginally greater under a proportional mortality than a fixed when re-seeded. This suggests that regulation from environmental stochasticity can mediate between mortality estimate

and population size to either enhance the buffering effects of the re-seeding to decline or effectively absorb the buffering re-seed. In such cases the fixed calculation may be more conservative in application than a proportional, dependent on starting population size, period of mortality and subsequent environmental stochasticity. The closed simulations showed that environmental conditions and a fixed mortality will result in extinctions. This suggests that the population dynamics, starting population size, time-series trend and regulation is crucial to consider when applying a mortality treatment. For example, the gannets at Bass Rock, an increasing population thought to slowly be reaching their carrying capacity (k) (Murray, Harris & Wanless 2015) reflected no difference in results between the closed and re-seeded simulations and a proportional take. Given the inherent positive growth of this population, re-seeding the population has very little influence on the risk of extinction. Density-dependent regulation was clear in patterns from multiple mortality treatments applied to the gannets; this does suggest that, particularly in the case of the gannets that they are likely to be sensitive to regulation from their conspecifics, such that mortality and higher strengths of density-dependence (penalized maximal fecundity) work together to confer decline. Our re-seeded models for guillemot and kittiwake returned a band of decline at intermediate and lower environmental stochasticity respectively. This suggests that the guillemot, in intermediate levels of environmental stochasticity are either being simulated with successive 'bad years', lowering k and exacerbating density-dependence penalties to fecundity (reflected as a decline in % change between the means we are comparing across timescales) or hit by successive 'good years' mediated by density-dependence and show no change. For the kittiwake example of more decline in lower fluctuations of environmental stochasticity, two scenarios may be unfolding. In higher fluctuations of successive 'good years' of environmental stochasticity, density-dependence becomes irrelevant and is over-ridden by radical growth or in higher levels of negative environmental perturbations, re-seeding forces a recovery, biasing our proxy for impact (this % change).

With a paucity of reliable connectivity estimates between populations of the same species, closed system modelling is the preferred precautionary approach to population assessment. There is clear

evidence of connectivity through immigration and emigration in many seabird populations (Horswill & Robinson 2015) and low rates of either may impact on colony population growth. Our basic theoretical re-seeded models followed classic metapopulation theory where local extinctions have the potential for local increases in the face of connectivity for our kittiwake and guillemot (Hanski & Gilpin 1997). Our results show a clear reduction in sensitivity to decline for many projections under this basic rescue-effect, but what it does not reveal is the true spatial population dynamics of connectivity between colonies of each species. For example, the risk of decline and extinction of a colony, we can hypothesize, will be different for those acting as sinks rather than sources within a metapopulation structure (Sanz-Aguilar *et al*. 2016). It would be of benefit to industry and conservation objectives alike to encourage research empirically and theoretically exploring connectivity estimates to examine this dynamic further in the context of regulation and risk.

Thirdly, the ongoing debate around the inclusion or exclusion of density-dependence in population assessment modelling derives from the stance that density-independent models are a more precautionary approach. Our results indicate that risk of decline was enhanced by the penalty effect on fecundity at higher strengths of density-dependence under certain conditions upon application of even our lowest mortality. Density-dependence was included as a compensatory mechanism in the models. However, there is a growing literature suggesting other forms of density-dependence may be appropriate to explore in future adaptations of these models, particularly in the case of species such as kittiwake, where severely reduced population sizes can experience enhanced predation, accelerating declines (Horswill & Robinson 2015). Here we explore the effect of direct mortality, but guillemot may suffer displacement (Furness, Wade & Masden 2013). This may manifest a different pattern in impact under regulation, the ecological mechanisms of which are not captured here, but we provide a baseline method against which such effects may also be assessed.

Conclusions

Seabird populations are dynamic systems, regulated by extrinsic and intrinsic influences. Insights from this work unveil vulnerability in different seabird populations from these influences even in the absence of additional anthropogenic mortality. Assessment in wildlife systems is rarely able to derive estimates for the strength of intrinsic and extrinsic regulation reducing our confidence in PVA predictions. Clearly, as our results show, unpredictability in the environment is key to population viability and subsequent carrying capacity (Lande 1993) affecting density-dependent responses on fecundity. We understand that extreme weather events may be more frequent and that climate change is affecting processes like the synchronicity of breeding attempts with prey availability and changing the accessibility of prey spatially. Our approach captures information contained in demography to allow us to theorise about the risk of decline in future, reflecting how our populations may respond to unknown conditions and highlighting how regulation is affected by mortality and the sensitivity of projections to mortality treatment. We show that this method can be applicable to data-limited populations, a benefit of a Bayesian approach. Populations lacking time-series for example would produce larger credible intervals, capturing more uncertainty. Care must be taken in these instances to describe the data-limitation, rather than assume a potential greater effect signal from the process estimated. Complementing current literature, this work determines that PBR is not a rigorous tool for seabird assessment and furthermore we recommend it not be used to facilitate EIA for seabirds. Here we demonstrate that population decline, together with regulation may confer opposing outcomes of risk depending on the population dynamics and the type of mortality applied. Our results suggest that populations experiencing higher environmental perturbations, such as unpredictable foraging sources, require enhanced protection from additional mortality. The responses to the rescue-effect in our analyses were interesting to note between our study species and their underlying dynamics. Further exploration of the connectivity in these systems would be beneficial. For example, our assumption that colonies experiencing more environmental dynamism might be more vulnerable is confounded by the knowledge gaps in the mechanisms of connectivity i.e. to what extent is connectivity driven by extrinsic or intrinsic factors and what is the availability of immigrants for

species, such as the kittiwake, where multiple colonies are in decline? We should stress that, in the absence of empirical rates of connectivity, precaution remains with the assumption of a closed-system. Resolution of human-wildlife conflict happens at the space between over-precaution and recklessness. This can only be found and navigated with sound quantitative knowledge of the certainties and uncertainties in the systems involved. Adding realism in impact assessment can only improve upon mediating positive outcomes in both conservation, environmental and economic goals.

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Author contributions

RWF and MT formulated the original idea, with JM and JAOM developing the idea and approach. JAOM analysed the data and drafted the original manuscript with all authors providing further editorial advice.

Data accessibility

Seabird data was taken from JNCC (2017). Seabird Monitoring Programme http://jncc.defra.gov.uk/smp/default.aspx and https://doi.org/10.5285/02c98a4f-8e20-4c48-8167-1cd5044c4afe (Newell et al. 2016). Supplemented with vital rates from http://jncc.defra.gov.uk/pdf/JNCC_Report_552_March_2015.web.pdf (Horswill and Robinson 2015). The full model is available in Appendix S2.

References

Bonenfant,C.,Gaillard,J.M.,Coulson,T.,Festa-Bianchet,M.,Loison,A.,Garel,M.,Loe,L.E.,Blanchard,P., Pettorelli,N.,Owen-Smith,N. and DuToit,J., (2009). *Empirical evidence of density-dependence in populations of large herbivores*. Advances in ecological research,41, pp.313-357.

Boyce, M.S. (1992). *Population viability analysis*. Annual review of Ecology and Systematics, 23(1), 481-497.

Bried,J., &Jouventin,P. (2002). *Site and mate choice in seabirds: an evolutionary approach*. Biology of marine birds, *435*,263-305.

Brook,B.W. and Bradshaw,C.J., (2006). *Strength of evidence for density dependence in abundance time series of 1198 species*. Ecology,87(6), pp.1445-1451.

Brooks,S.P., and Gelman,A. (1997). *General Methods for Monitoring Convergence of Iterative Simulations*. Journal of Computational and Graphical Statistics 7: 434–455.

Brown,J.H., and A.Kodric-Brown. (1977) *Turnover rates in insular biogeography: effect of immigration on extinction*. Ecology 58:445-449.

Buckland,S.T.,Goudie,I.B.J., & Borchers,D.L. (2000). *Wildlife population assessment: past developments and future directions*. Biometrics, *56*(1), 1-12.

Caswell,H., (2001). *Matrix Population Models*, *Sinauer Assoc. Inc., Sunderland, MA.*

Clark,J.S., (2003). *Uncertainty and variability in demography and population growth: a hierarchical approach*. Ecology, *84*(6), pp.1370-1381.

Cook, AonghaisS.C.P. & Robinson,Robert A. (2016), *Testing sensitivity of metrics of seabird population response to offshore wind farm effects*, JNCC Report 553, ISSN 0963-8901

Croxall,J.P.,Butchart,S.H.,Lascelles,B.E.N.,Stattersfield,A.J.,Sullivan,B.E.N.,Symes,A.,&Taylor,P. (2012). *Seabird conservation status, threats and priority actions: a global assessment*. Bird Conservation International, *22*(1), 1-34.

Denwood,Matthew,J (2016). *runjags: An R Package Providing Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS*. Journal of Statistical Software, 71(9), 1-25.<doi:10.18637/jss.v071.i09>

Elton,C.S. (1924). *Periodic fluctuations in the numbers of animals: their causes and effects*. British Journal of Experimental Biology. 2: 119-63.

Engen,S.,Bakke,Ø. and Islam,A., (1998). *Demographic and environmental stochasticity-concepts and definitions*. Biometrics, pp.840-846.

European Commission Directive 2009/147/EC of the European Parliament and the Council of 30 November 2009 Off. J. Eur. Union L, 20 (7)

European Commission(2011) *EU Guidance on Wind Energy Development in Accordance With the EU Nature Legislation*. Publications Office of the European Union, Luxembourg.

Furness,R.W.,Wade,H.M., & Masden,E.A. (2013). *Assessing vulnerability of marine bird populations to offshore wind farms*. Journal of environmental management, *119*, 56-66.

Frederiksen,M., Mavor,R.A., & Wanless,S. (2007). *Seabirds as environmental indicators: the advantages of combining data sets*. Marine Ecology Progress Series, 352, 205-211.

Frederiksen,M.,Daunt,F.,Harris,M.P., & Wanless,S. (2008). *The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird*. Journal of Animal Ecology, *77*(5), 1020-1029.

Garthe,S,Montevecchi,WA,Davoren,GK (2011) *Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator*. Limnol Oceanogr 56:802–812

Green,R.E., Langston,R.H., McCluskie,A., Sutherland,R. and Wilson,J.D., (2016). *Lack of sound science in assessing wind farm impacts on seabirds*. Journal of Applied Ecology, *53*(6), pp.1635-1641.

Hanski,I & Gilpin,M.E (1997). *Metapopulation Biology. Ecology, Genetics, and Evolution*. Academic Press Limited.

Hanski,I., (1998). *Metapopulation dynamics*. Nature, *396*(6706), p.41.

Horswill,C., & Robinson,R.A. (2015). *Review of Seabird Demographic Rates and Density Dependence*. JNCC Report no. 552.

Horswill,C.,O'Brien,S.H., & Robinson,R.A. (2016). *Density dependence and marine bird populations: are wind farm assessments precautionary?* Journal of Applied Ecology. 54(5), pp.1406-1414.

Jenouvrier,S.,Barbraud,C.,Cazelles,B., & Weimerskirch,H. (2005). *Modelling population dynamics of seabirds: importance of the effects of climate fluctuations on breeding proportions*. Oikos, 108(3), 511-522.

Johnston,A.,Cook,A.S.,Wright,L.J.,Humphreys,E.M., & Burton,N.H. (2014). *Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines*. Journal of Applied Ecology, 51(1), 31-41.

Kass,R.E.,Carlin,B.P.,Gelman,A.and Neal,R.M., (1998). *Markov chain Monte Carlo in practice: a roundtable discussion*. The American Statistician, 52(2), pp.93-100.

Kindsvater,H.K.,Dulvy,N.K.,Horswill,C.,Juan-Jordá,M.J.,Mangel,M. and Matthiopoulos,J.,(2018). *Overcoming the data crisis in biodiversity conservation*. Trends in ecology & evolution.

Knape,J. and deValpine,P., (2012). *Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance?* Ecology letters, 15(1), pp.17-23.

Lande,R. (1993). *Risks of population extinction from demographic and environmental stochasticity and random catastrophes*. The American Naturalist, 142(6), 911-927.

Lande,R.,Engen,S. and Saether,B.E., (2003). *Stochastic population dynamics in ecology and conservation*. Oxford University Press on Demand.

Lande,R.,Engen,S.,Sæther,B.E.,Filli,F., Matthysen,E. and Weimerskirch,H., 2002. *Estimating density dependence from population time series using demographic theory and life-history data*. The American Naturalist, 159(4), pp.321-337.

Leirs,H., Stenseth,N.C., Nichols,J.D., Hines,J.E., Verhagen,R. & Verheyen,W. (1997) *Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent.* Nature, 389, 176–180.

Lewis,S.,Elston,D.A.,Daunt,F.,Cheney,B., &Thompson,P. M. (2009). *Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird*. Oikos, 118(4), 521-528.

Marques,A.C.,Fuinhas,J.A., &Manso,J.P. (2010). *Motivations driving renewable energy in European countries: A panel data approach*. Energy policy, 38(11), 6877-6885.

Matthiopoulos,J.,Fieberg,J.,Aarts,G., Beyer,H.L., Morales,J.M., &Haydon,D.T. (2015). *Establishing the link between habitat selection and animal population dynamics. Ecological Monographs, 85(3), 413-436.*

Montevecchi,W.A.,Benvenuti,S.,Garthe,S.,Davoren,G.K.,&Fifield,D. (2009). *Flexible foraging tactics by a large opportunistic seabird preying on forage-and large pelagic fishes*. Marine Ecology Progress Series, 385, 295-306.

Murphy,G.E., & Romanuk,T.N. (2014). *A meta-analysis of declines in local species richness from human disturbances*. Ecology and evolution, 4(1), 91-103. http://doi.org/10.1002/ece3.909

Murray,S., Harris,M.P. and Wanless, S., (2015). *The status of the gannet in Scotland in 2013-14*. Scottish Birds, *35*(1), pp.3-18.

Newell,M.; Harris,M.P.; Wanless,S.; Burthe,S.; Bogdanova,M.; Gunn,C.M.; Daunt,F. (2016). *The Isle of May long-term study seabird annual breeding success 1982-2016*. NERC Environmental Information Data Centre. https://doi.org/10.5285/02c98a4f-8e20-4c48-8167-1cd5044c4afe

Niel,C.,&Lebreton,J.D. (2005). *Using demographic invariants to detect overharvested bird populations from incomplete data*. Conservation Biology, 19(3), 826-835.

O'Brien,S.H.,Cook,A.S.andRobinson,R.A., (2017). *Implicit assumptions underlying simple harvest models of marine bird populations can mislead environmental management decisions*. Journal of environmental management, 201, pp.163-171.

Oro,D,&Martinez-Abrain,A (2004). *Ecology and behaviour of seabirds*. Duarte,CM, editor. The Encyclopedia of Life Support Systems (EOLSS). Oxford, UK: Eolss PublishersUNESCO.

Platteeuw,M.,Bakker,J.,van den Bosch, I., Erkman,A.,Graafland,M.,Lubbe,S., & Warnas, M. (2017). *A Framework for Assessing Ecological and Cumulative Effects (FAECE) of Offshore Wind Farms on Birds, Bats and Marine Mammals in the Southern North Sea*. In Wind Energy and Wildlife Interactions (pp. 219-237). Springer International Publishing.

Plummer M. (2003)*JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Proceedings of the 3rd International Workshop on Distributed Statistical Computing.

R Core Team (2016). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*, Vienna, Austria. URL https://www.R-project.org/.

Reed,J.M.,Mills,L.S.,Dunning,J.B.,Menges,E.S., McKelvey,K.S.,Frye,R.,Beissinger,S.R.,Anstett,M.C. and Miller,P.,(2002). *Emerging issues in population viability analysis*. Conservation biology, 16(1), pp.7-19.

Ripple,W.J.,Chapron,G.,López-Bao,J.V.,Durant,S.M.,Macdonald,D.W.,Lindsey,P.A., … Zhang,L. (2016). *Saving the World's Terrestrial Megafauna*. Bioscience, 66(10), 807–812. http://doi.org/10.1093/biosci/biw092

Saether,B.-E.,Engen,S.,Lande,R.,Both,C.andVisser,M.E. (2002), *Density dependence and stochastic variation in a newly established population of a small songbird*. Oikos, 99: 331–337.

Sands,P., & Peel,J. (2012). *Principles of international environmental law*. Cambridge University Press.

Sanz-Aguilar,A.,Igual,J.M.,Tavecchia,G.,Genovart,M. and Oro,D., (2016). *When immigration mask threats: The rescue effect of a Scopoli's shearwater colony in the Western Mediterranean as a case study*. Biological Conservation, 198, pp.33-36

Saunders,S.P,Cuthbert,F.J and Zipkin,E.F (2018). *Evaluating population viability and efficacy of conservation management using integrated population models*. Journal of Applied Ecology 00:1-13

Turchin,P. (1995). *Population regulation: old arguments and a new synthesis*. Population dynamics: new approaches and synthesis, 19-40.

Wade,P.R. (1998). *Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds*. Marine Mammal Science, 14(1), 1-37. https://doi.org/10.1016/j.biocon.2011.04.014

2005

Wanless,S., Murray,S. & Harris,M.P.(2005) *The status of northern gannet in Britain & Ireland in 2003/04*. British Birds 98, 280–294.

Weimerskirch,H. (2001). *Seabird demography and its relationship with the marine environment*. Biology of Marine Birds (EA Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, FL, 115-136.

Appendix 3: Supplementary information for Chapter 3: Partitioning population variability reveals hidden relationship between environment and age.

A.3.1 Literature review for kittiwake environmental co-variates

Table A.3.1. Literature review of environmental variables and kittiwake

Metric	Period	Lag	Parameter measured against	Relationship?
SST	February - March	1 year	Adult survival, Breeding success	Negative in east Scotland and Orkney (Frederiksen *et al*. 2007a paper) varied elsewhere
SST	Jan-Feb-march	1 and 2	breeding	Only found with other predictors (Carroll *et al*. 2017)
SST	April, May and June	1 and 2	breeding	None found Carroll *et al* 2017)

SST	Jan Feb March then April, may June	1 year lagged produced higher AIC- so **unlagged**	breeding	Negative (Carroll *et al*. 2015) with spring sst
SST	August - Oct	0	Adult survival	None found (Sandvik *et al*. 2005)
SST	November - March	0	Adult survival	None found(Sandvik et a.l 2005)
SST	April- August	0	Adult survival	Slight finding(Sandvik *et al*. 2005)
NAO	Winter index	5 different lags (0-4)	Adult survival	Slight finding – zero lag (Sandvik *et al*. 2005)
NAO	Winter index	1 year lag	Breeding success	Explained more variation than zero lag (Frederiksen *et al*. 2004b)

A.3.2 Productivity time-series

The typo in productivity has been carried over from chapter 2 into the kittiwake data used in this chapter, resulting in adjustment of the productivity time-series. Here I present the plots of the time-series calculated as per the original equation (in black) and the adjusted time-series productivity with the correct equation (in red). Again, there is an increased estimation in productivity using the original, with further examination of the plot revealing that the highest disparity in original versus correct estimations of productivity is 0.15 whilst the lowest values is 0.002.

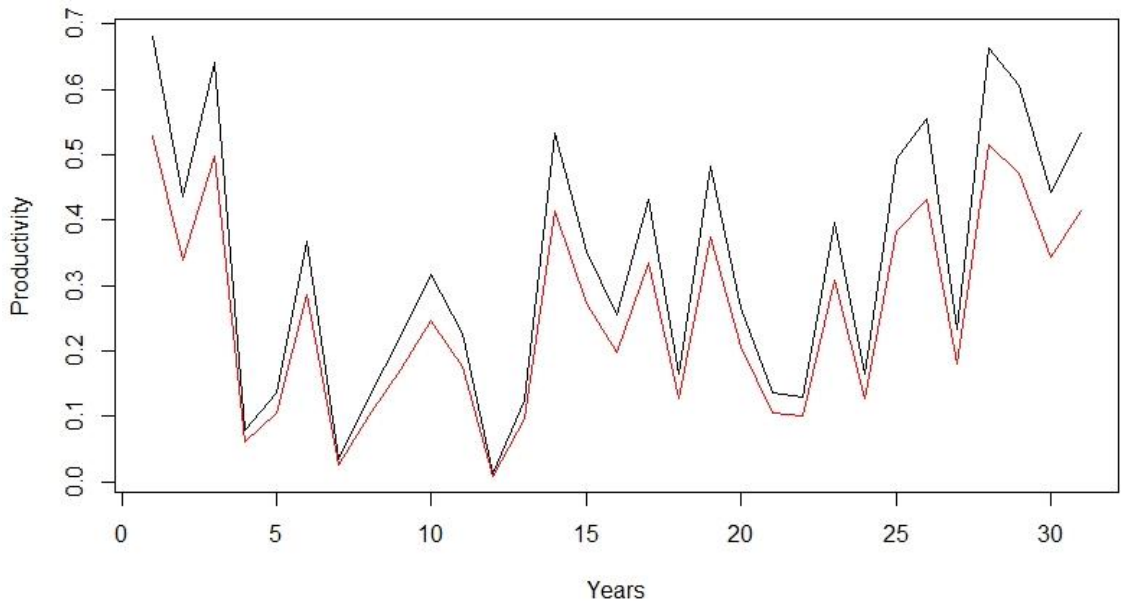

Figure A.3.1: Values of productivity supplied as time-series to chapter 3 model baseline. Black line is the data provided under the original equation; red is the 'correct' equation.

Regardless of this disparity, there are potentially more influential outcomes from the miscalculation of productivity in this chapter than chapter 2 because:

1/The intrinsic vital rate is being estimated and is not fixed.
2/The models are estimating annual productivity time-series and intrinsic values for all vital rates (as well as other terms-e.g. density-dependence)
3/The model is directly fitting to this productivity time-series (and others) to facilitate estimation of these and other terms in the model.

Points 1-3 indicate some of the processes the higher values of productivity provided to the model (comparative to the correct equation values) may influence the estimation of. Potential effects of this are wider credible limits for estimates of vital rates, density-dependence, environmental stochasticity-which *may* have subtle effects on the influence of model fit and selection as environmental time-series are added to the baseline model. Future iterations of this work should seek to use the corrected equation.

A.3.3 JAGS code: Baseline scalar model

```
IMKIpopmodel<-"model{


bmax<-0.5+0.4*Sbmax  #mean of 0.7,with +/- 0.2
s1<-0.5+0.4*Ss1   #mean of 0.7, with +/- 0.2
s2<-0.7+0.2*Ss2  #mean of 0.8,with +/- 0.1
s3<-0.75+0.24*Ss3 #mean of 0.87 with +/- 0.12
s4<-0.8+0.1*Ss4   #mean of 0.9 with +/- 0.1

###convert to log scale#########
#################################
a0<-log(bmax/(1-bmax))
s1a0<-log(s1/(1-s1))
s2a0<-log(s2/(1-s2))
s3a0<-log(s3/(1-s3))
s4a0<-log(s4/(1-s4))

###Initialiser for start matrix, using EV. Ev based on fecundity and population size of empirical data.
#################################
EV<-(c(0.25,0.18,0.13,0.44))


#the observation error
#################################
ObsR<-0.05

####fit loop######
```

```
################################

for (t in 1:(tmax-1))
{
 #Total density

 ntot[t]<-sum(n[,t])

 ###error terms for environmental stochasticity influencing our linear predictors
 ###different for fecundity/survival, drawn from the same prior distributions/sigma
 ################################


 eps1[t]~dnorm(0, prec) #environmental stochasticty affecting fecundity
 eps2[t]~dnorm(0, prec1) #environmental stochasticity affecting survival1


 ###put a tracer on density dependence at each time step

 ##############################################

 D[t]<-a1*ntot[t]

 ####linear predictor for fecundity###################

 ######################################

 lt[t]<-a0-a1*ntot[t]+eps1[t]

 #log and logit of fecundity and survival  predictors, representing proportion of maximum vital rate
that is actually realised

 ################################

 logit(b[t])<-lt[t]

 #Survival predictors perturbed by environmental stochasticity
 ################################
 lts1[t]<-s1a0+(eps2[t])
 logit(s1E[t])<-lts1[t]
 lts2[t]<-s2a0+ES3*(eps2[t])
 logit(s2E[t])<-lts2[t]
 lts3[t]<-s3a0+ES4*(eps2[t])
 logit(s3E[t])<-lts3[t]
 lts4[t]<-s4a0+ES5*(eps2[t])
 logit(s4E[t])<-lts4[t]


# Remember that this 'survival' is also used to capture floaters and immigrants.
```

```
  ##matrix multiplication for population growth, based on population size at stage and predictors
  ##binomial distribution to account for individual stochasticity within a population
  ###################################


  n[1,t+1]~dbin(b[t],n[4,t])
  n[2,t+1]~dbin(s1E[t],n[1,t])
  n[3,t+1]~dbin(s2E[t],n[2,t])
  nnew[t]~dbin(s3E[t],n[3,t])
  nold[t]~dpois(s4E[t]*n[4,t])
  n[4,t+1]<-nnew[t]+nold[t]


  nDat[t]~dnorm(n[4,t], ObsTau[t])

  #the STDev around the counts
  ObsV[t]<-ObsR*n[4,t]
  #the tau for distrbuiton as derived above
  ObsTau[t]<-1/ObsV[t]^2

  bDat[t]~dnorm(lt[t], btau) # Define prior for btau based on precision of experimental data.
  #Logit transform bDat


  ###Estimate the size of final stage of population for comparison of fit

  ##########################################

  expectNests[t]<-n[4,t]


}




# PRIORS ------
### Priors for stochasticity and DDependence
#environmental stochasticity prior
########################################
mu1<-1
sd1<-0.5
#shape and rate for mean 1, variance 0.25 (SD^2)
s<-mu1^2/sd1^2
r<-mu1/sd1^2
sigma~dgamma(s,r)
sigma1~dgamma(s,r)


#precision for environmental stochasticity, set by the sigma estimate

prec<-1/sigma^2
prec1<-1/sigma1^2
```

```
mu2<-1
sd2<-0.5
ss<-mu2^2/sd2^2
rr<-mu2/sd2^2


#precision for environmental stochasticity, set by the sigma estimate

#SCALARS
ES3~dgamma(ss,rr)T(0.00000001,5)
ES4~dgamma(ss,rr)T(0.00000001,5)
ES5~dgamma(ss,rr)T(0.00000001,5)


########################################

###Density dependence prior


mu<-0.000001
variance<-1e-12  #small (0.00001) to make highly constrained variance around mu or large (1)

# NOTE THE TRUNCATION TERMS.
##gamma(1e-9,0.001)
##shape and rate for mean 1e-6, variance 1e-3
p1<-mu^2/variance
p2<-mu/variance
a1~dgamma(p1,p2)T(0.000000000001,0.1)


#####priors for vital rates##############
#####infl, how many draws from distribution, 1-100 etc.
infl<-10
Sbmax~dbeta(infl,infl)
Ss1~dbeta(infl,infl)
Ss2~dbeta(infl,infl)
Ss3~dbeta(infl,infl)
Ss4~dbeta(infl,infl)


####initialise model. Popstart based on first nDat/EV value to scale up to whole population.
####EV defined above and based on first bDat and vital rates as per chapter 2
popstart<-15375

n[4,1]~dpois(EV[4]*popstart)
n[1,1]~dpois(EV[1]*popstart)
n[2,1]~dpois(EV[2]*popstart)
n[3,1]~dpois(EV[3]*popstart)



####btau hard wired for small obs error around fec data###
```

```
###ERROR IN REPORTS FOR EXAMPLE IS AROUND = OR - 0.1 FROM MEAN### CODE AS 0.05
###sd-0.05, var=0.0025######
################################
btau<-400


#data# tmax, nDat,bDat

#monitor#
ES3,ES4,ES5,D,s4E,s3E,s2E,s1E,b,eps1,expectNests,bmax,s1,s2,s3,s4,a1,sigma,sigma1,deviance,DIC,p
ed

}"

########Julie Miller 2016 ############
###Bayesian Model fitting of population data####
################################################
library(runjags)


##JNCC population trends and AON counts (starting population sizes)###

####POPULATION COUNTS RAW 1987-2017###
tmax<-31 #Length of time series
nDat<-
c(6765,7638,7564,8129,6535,6916,7009,3751,7603,6269,6518,4306,4196,4618,3639,3666,3335,387
6,3790,3167,3424,3354,2316,3422,2685,2465,1712,2464,3433,2922,3507,NA)

##BREEDING SUCCESS RAW 1987-2017#####
fec<-c(1.2,0.77,1.13,0.14,0.24,0.65,0.06,0.23,0.39,0.56,0.4,0.02,0.22,0.94,0.62,0.45,0.76,
    0.29,0.85,0.47,0.24,0.23,0.7,0.29,0.87,0.98,0.41,1.17,1.07,0.78,0.94,NA)
###### function to make productivity into female only for model
postbreedfemale<-function(fec){
 s<-0.882
 female<-fec/(2*s)
 scaled<-log(female/(1-female))
 return(scaled)
}


###scaled fecundity to be same as model-female only, log etc.####
bDat<-postbreedfemale(fec)
```

Appendix 4: Supplementary information for Chapter 4: Estimating connectivity and vulnerability in a metapopulation: a case study of Shetland Black-legged kittiwakes (*Rissa tridactyla*).

A.4.1 Data summary for metapopulation model

Table A.4.1. Colony information, Shetland Region from JNCC Seabird Monitoring Programme (JNCC 2018)

Site	Site Name	Parent SPA	Nest Data (Years)	Chick Data (Years)	Count Data (Years)
1	Bannaminn to Whale Wick		0	0	1
2	BO01		0	0	0
3	Brei Wick to Virdick	Saxavord,Hermaness and Valla Field	0	0	7
4	Broad Stack to Stack of Barons Geo		0	0	2
5	Broch of Culswick to Seli Stack		0	0	1
6	Burga Stacks to Caves		0	0	15
7	Burki Waters		0	0	8
8	Burn of Garth to Broad Stack		0	0	1
9	Calders Geo		0	0	9
10	Clett Head		3	3	11
11	Compass Head	Sumburgh Head	8	8	16
12	Dale to Huxter		0	0	4
13	Dore Holm		0	0	8
14	East Yell		0	0	6
15	Fair Isle	Fair Isle	32	32	13
16	Fitful Head		0	0	11
17	Fladda		0	0	3
18	Foula	Foula	29	29	20
19	Funzie Bay to Wick of Aith	Fetlar	0	0	1
20	Galti Stack		0	0	1
21	Gilsa Ayre to Quilt Ness		0	0	3
22	Gloup Holm		0	0	4
23	Gluibuil to Stack of Cuillan		0	0	1
24	Griskerry to Taing of Maywick		0	0	1
25	Gruna Stack		0	0	10
26	Gruney		0	0	8
27	Hermaness	Saxavord,Hermaness and Valla Field	28	28	9
28	Hich Holm		3	3	12
29	Hinda Stack - The Nev		0	0	7
30	Horse Island (HU30)		0	0	16
31	Housay		0	0	6
32	HU 3165		0	0	1
33	HU5139		0	0	1

Site	Site Name	Parent SPA	Nest Data (Years)	Chick Data (Years)	Count Data (Years)
34	HU660880	Fetlar	0	0	1
35	Kettlaness		10	10	13
36	Klifts to Big Holm	Fetlar	0	0	1
37	Lamb Hoga	Fetlar	0	0	1
38	Landvillas to Scarfi Taing		0	0	1
39	Lang Holm		0	0	5
40	Lanyar Taing to Lotaki Kame		0	0	7
41	Meo Ness to the Haa		0	0	3
42	Mousa RSPB		0	0	16
43	Muckle Flugga	Saxavord,Hermaness and Valla Field	0	0	8
44	Muckle Roe		0	0	6
45	Ness of Ireland		0	0	12
46	Noness		20	20	19
47	North Benelip		0	0	1
48	Norwick Hevda to Hols Hellier	Saxavord,Hermaness and Valla Field	0	0	1
49	Noss	Noss	32	32	10
50	Ofoora		0	0	1
51	Outer Brough	Fetlar	0	0	11
52	Outer Stack		0	0	2
53	Papa Stour Whole Island		0	0	8
54	Point of Hus to Hevdigarth		0	0	4
55	Reawick Ness		0	0	14
56	Saxavord	Saxavord,Hermaness and Valla Field	0	0	8
57	Scordar		0	0	1
58	SE Yell (inc. Burravoe)		12	12	14
59	Selie Ness to Grobs Ness		0	0	1
60	Siggar Ness		0	0	11
61	Skeld, Westerwick and Culswick		17	17	12
62	Snarra Voe to The Keen		0	0	1
63	South Havra		0	0	15
64	South Holms		0	0	5
65	South West Unst		0	0	5
66	St. Ninian's Isle		0	0	12
67	Staraster to Shaabers Head		0	0	2
68	Stenness		14	14	7
69	Strandburgh Ness	Fetlar	4	4	1
70	Sumburgh Head	Sumburgh Head	30	30	15
71	The Nev to The Kame		0	0	1
72	The Poil		0	0	12
73	The Taing - Hinda Stack		0	0	6

Site	Site Name	Parent SPA	Nest Data (Years)	Chick Data (Years)	Count Data (Years)
74	Tingon Cliffs		0	0	7
75	Troswick Beach to Boddam		0	0	20
76	Troswick Ness		10	10	20
77	Turla		0	0	3
78	Uyea		0	0	10
79	Vaila		0	0	14
80	Vementry		0	0	1
81	West Burra		0	0	13
82	West Of The Nev - Stead Of Culswick		0	0	1
83	West Sandwick to Horns of the Roe		0	0	1
84	Whale Wick to Sandwick		23	23	1

A.4.2 Evidence of connectivity from literature

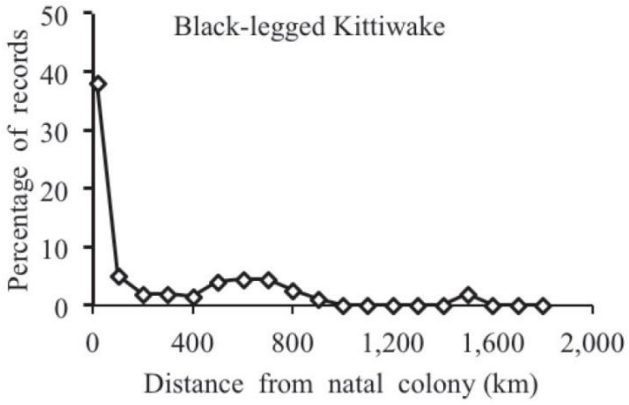

Figure A.4.1. Figure taken from Coulson 2016, with caption, 'The distance Black-legged Kittiwakes (Rissa tridactyla) nested from their natal colonies. Based on Coulson and Neve de Mevergnies (1992) with additions. Note the bimodality of the distribution.' See references, for further information.

A.4.3 Productivity

Unlike the previous chapters, this model sought only to do a minimal transformation of productivity values supplied to the model, representing a female only cohort with an assumed 1:1 ratio. This is because as a metapopulation model, we lack data on survival for many of the colonies with which we might use to transform productivity into a pre or post breeding census. Given the focus of the model is to attempt to estimate connectivity, this simple adjustment is deemed appropriate for productivity in this first prototype of the method. Further productivity modifications may be appropriate depending on the application of this general method to other regions or species and the information available.

A.4.3 JAGS code for metapopulation fit

```
######the model#######
IMKIpopmodel<-"model{

bmax<-0+0.6*Sbmax  #mean of 0.3,with +/- 0.3 (mean female only for shetland is 0.2, max is 0.6 )
s1<-0.49+0.44*Ss1   #mean of 0.71, with +/- 0.22
s2<-0.65+0.3*Ss2  #mean of 0.8,with +/- 0.15
s3<-0.67+0.33*Ss3 #mean of 0.83.5 with +/- 0.16.5
s4<-0.6+0.4*Ss4   #mean of 0.8 with +/- 0.2

###convert to log scale#########
################################
a0<-log(bmax/(1-bmax))
s1a0<-log(s1/(1-s1))
s2a0<-log(s2/(1-s2))
s3a0<-log(s3/(1-s3))
s4a0<-log(s4/(1-s4))

###Initialiser for start matrix, using EV. Ev based on fecundity and population size of empirical data.
################################
EV<-(c(0.24,0.17,0.13,0.46))

#the observation error
################################
ObsR<-0.05

####fit loop######
################################

for(i in 1:p)
{

datastart[i]~dgamma(0.01,0.01)
popstart[i]<-datastart[i]/0.46
 n[i,4,1]~dpois(EV[4]*popstart[i])
 n[i,1,1]~dpois(EV[1]*popstart[i])
 n[i,2,1]~dpois(EV[2]*popstart[i])
 n[i,3,1]~dpois(EV[3]*popstart[i])
}


for (t in 1:(tmax-1)){


###make density colony specific###
#Total density
ntot[t]<-sum(n[1:p,4,t])


###error terms for environmental stochasticity influencing our linear predictors
###different for fecundity/survival, drawn from the same prior distributions/sigma
################################
```

```
eps1[t]~dnorm(0, prec) #environmental stochasticty affecting fecundity
eps2[t]~dnorm(0, prec1) #environmental stochasticity affecting survival

#### r is the distance matrix

for (i in 1:p)
{
 lt[i,t]<-a0-a1*n[i,4,t]+eps1[t]
 logit(b[i,t])<-lt[i,t]
 bchicks[i,t]~dpois(b[i,t]*bnest[i,t]*0.9)
 for (j in 1:p)
 {
  transfer[i,j,t] <-exp(c1*(b[i,t]-b[j,t])-c2*r[i,j])
  P[i,j,t]<- transfer[i,j,t]/(sum(transfer[i,1:p,t]))
 }
}



##put a tracer on density at time
#log and logit of fecundity and survival  predictors, representing proportion of maximum vital rate that is actually realised
###################################
sc1[t]~dgamma(1.2,2)
sc2[t]~dgamma(2.916,2.7)
sc3[t]~dgamma(4.2632,2.92)



lts1[t]<-s1a0+eps2[t]
logit(s1E[t])<-lts1[t]
lts2[t]<-s2a0+sc1[t]*(eps2[t])
logit(s2E[t])<-lts2[t]
lts3[t]<-s3a0+sc2[t]*(eps2[t])
logit(s3E[t])<-lts3[t]
lts4[t]<-s4a0+sc3[t]*(eps2[t])
logit(s4E[t])<-lts4[t]


for(i in 1:p){
ObsTau[i,t]<-1/(1+n[i,4,t]*0.05)^2
nDat[i,t]~dnorm(n[i,4,t], ObsTau[i,t])

##matrix multiplication for population growth, based on population size at stage and predictors
##binomial distribution to account for individual stochasticity within a population
###################################

n[i,1,t+1]~dbin(b[i,t],n[i,4,t])
n[i,2,t+1]~dbin(s1E[t],n[i,1,t])
n[i,3,t+1]~dbin(s2E[t],n[i,2,t])
nnew[i,t]~dbin(s3E[t],n[i,3,t])

nnewM[i,1:p,t]<-P[i,1:p,t]*nnew[i,t] # Relocating animals
nnewR[i,t]~dpois(sum(nnewM[1:p,i,t]))
```

```
nold[i,t]~dpois(s4E[t]*n[i,4,t])
n[i,4,t+1]<-nnewR[i,t]+nold[i,t]


expectNests[i,t]<-(n[i,4,t])
}
}

# PRIORS ------

### Priors for transfer matrix, density dependence, environmental term
mean<-0.5
varian<-0.25
shape<-mean^2/varian
rate<-mean/varian
c1~dgamma(shape,rate)

meanc<-0.01
varianc<-1e-04
shapec<-meanc^2/varianc
ratec<-meanc/varianc
c2~dgamma(shapec,ratec)


mu1<-1
sd1<-0.5
s<-mu1^2/sd1^2
r1<-mu1/sd1^2


sigma~dgamma(s,r1)
sigma1~dgamma(s,r1)

#precision for environmental stochasticity, set by the sigma estimate

prec<-1/sigma^2
prec1<-1/sigma1^2


########################################


mu<-0.000001
variance<-1e-12


p1<-mu^2/variance
p2<-mu/variance
a1~dgamma(p1,p2)T(0.00000000001,0.01)



#####priors for vital rate##############
infl<-10
Sbmax~dbeta(infl,infl)
```

```
Ss1~dbeta(infl,infl)
Ss2~dbeta(infl,infl)
Ss3~dbeta(infl,infl)
Ss4~dbeta(infl,infl)


}"
```

References

Aebischer, N.J. and Coulson, J.C., (1990). Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *The Journal of Animal Ecology*, pp.1063-1071.

Ainley, D. G., Spear, L. B., Allen, S. G., & Ribic, C. A. (1996). Temporal and spatial patterns in the diet of the common murre in California waters. *Condor*, 98: 691-705.

Ainley, D.G., Ford, R.G., Brown, E.D., Suryan, R.M. and Irons, D.B., (2003). Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology*, *84*, pp.709-723.

Allee, W. C. (1931). Animal aggregations, a study in general sociology. - Univ. of Chicago Press, Chicago.

Alvarez-Fernandez, S., Licandro, P., van Damme, C. J. G., & Hufnagl, M. (2015). Effect of zooplankton on fish larval abundance and distribution: a long-term study on North Sea herring (*Clupea harengus*). *ICES Journal of Marine Science*, 72: 2569-2577.

Anderson, H. B., Evans, P. G., Potts, J. M., Harris, M. P., & Wanless, S. (2014). The diet of Common Guillemot (*Uria aalge*) chicks provides evidence of changing prey communities in the North Sea. *Ibis*, *156*, 23-34.

Anderson, O., Cleo, J. , Croxall, J. , Dunn, E.K. , Sullivan, B.J., Yates, O. , Black, A. (2011) "Global seabird bycatch in longline fisheries. "*Endangered Species Research* 14:91-106.

Arnott, S.A. and Ruxton, G.D., (2002). Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. *Marine Ecology Progress Series*, *238*, pp.199-210.

Ashbrook, K., Wanless, S., Harris, M. P., & Hamer, K. C. (2008). Hitting the buffers: conspecific aggression undermines benefits of colonial breeding under adverse conditions. *Biology Letters*, *4*: 630-633.

Ashmole, N.P. (1963). The regulation of numbers of tropical ocean birds. *Ibis* 103b: 458–473.

Aubry, L.M., Cam, E. and Monnat, J.Y., (2009). Habitat selection, age-specific recruitment and reproductive success in a long-lived seabird. In *Modeling demographic processes in marked populations* (pp. 365-392). Springer, Boston, MA.

Ballance, L.T., Ainley, D.G., Ballard, G. and Barton, K., (2009). An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin Pygoscelis adeliae. *Journal of Avian Biology*, *40*(3), pp.279-288.

Band, W. (2012). *Using a Collision Risk Model to Assess Bird Collision Risks for Offshore Windfarms*. Final Report to SOSS. Available at: http://www.bto.org/sites/default/files/u28/downloads/Projects/Final_Report_SOSS02_Band1ModelGuidance.pdf

Beaugrand, G. (2004). The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245–262.

Bicknell, A. W. J., Oro, D., Camphuysen, K. C. J., and Votier, S. C. (2013). Potential consequences of discard reform for seabird communities. *Journal of Applied Ecology*, 50: 649–658.

Bicknell, A.W., Knight, M.E., Bilton, D.T., Campbell, M., Reid, J.B., Newton, J. and Votier, S.C., (2014). Intercolony movement of pre-breeding seabirds over oceanic scales: implications of cryptic age-classes for conservation and metapopulation dynamics. *Diversity and Distributions*, *20*(2), pp.160-168.

BirdLife International (2018). *Rissa tridactyla*. *The IUCN Red List of Threatened Species* 2018: e.T22694497A132556442. http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694497A132556442.en. Downloaded on 18 November 2019.

Birkhead, T.R. & Furness, R.W. (1985). Regulation of seabird populations. In: Sibley, R.M. & Smith, R.H. (Eds). Behavioural Ecology. Oxford: Blackwell Scientific Publishing. pp. 145–167.

Birkhead, T.R., 1977. The effect of habitat and density on breeding success in the common guillemot (Uria aalge). *The Journal of Animal Ecology*, pp.751-764.

Bogdanova, M.I., Daunt, F., Newell, M., Phillips, R.A., Harris, M.P. and Wanless, S., (2011). Seasonal interactions in the black-legged kittiwake, Rissa tridactyla: links between breeding performance and winter distribution. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1717), pp.2412-2418.

Bonenfant,C.,Gaillard,J.M.,Coulson,T.,Festa-Bianchet,M.,Loison,A.,Garel,M.,Loe,L.E.,Blanchard,P., Pettorelli,N.,Owen-Smith,N. and DuToit,J., (2009). Empirical evidence of density-dependence in populations of large herbivores. *Advances in ecological research*,41, pp.313-357.

Bonter, D.N., MacLean, S.A., Shah, S.S. and Moglia, M.C., (2014). Storm-induced shifts in optimal nesting sites: a potential effect of climate change. *Journal of Ornithology*, *155*(3), pp.631-638.

Boulinier, T., Danchin, E., Monnat, J.Y., Doutrelant, C. and Cadiou, B., (1996). Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology*, pp.252-256.

Boulinier, T., McCoy, K.D., Yoccoz, N.G., Gasparini, J. & Tveraa, T. (2008) Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters*, 4, 538–540.

Bouwhuis, S., Oscar, V., and Peter H. Becker. "Sex-specific pathways of parental age effects on offspring lifetime reproductive success in a long-lived seabird." *Evolution* 69.7 (2015): 1760-1771.

Boyce, M.S. (1992). Population viability analysis. *Annual review of Ecology and Systematics*, 23(1), 481-497.

Boyd, C., Punt, A.E., Weimerskirch, H. and Bertrand, S., (2014). Movement models provide insights into variation in the foraging effort of central place foragers. *Ecological modelling*, *286*, pp.13-25.

Boyd, I, Wanless, S, and Camphuysen, C.J (2006). Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge.

Bradbury, G., Trinder, M., Furness, B., Banks, A.N., Caldow, R.W. and Hume, D., (2014). Mapping seabird sensitivity to offshore wind farms. *PloS one*, *9*, p.e106366.

Breton, A.R., Diamond, A.W. & Kress, S.W. (2006). Encounter, survival, and movement probabilities from an Atlantic Puffin (Fratercula arctica) metapopulation. *Ecological Monographs* 76: 133–149

Bried, J., and Jouventin, P.(2002). Site and mate choice in seabirds: an evolutionary approach. Biology of marine birds CRC Press, pp. 263-305.

Brook, C.E., Herrera, J.P., Borgerson, C., Fuller, E.C., Andriamahazoarivosoa, P., Rasolofoniaina, B.R., Randrianasolo, J.R.R., Rakotondrafarasata, Z.E., Randriamady, H.J., Dobson, A.P. and Golden, C.D., (2019). Population viability and harvest sustainability for Madagascar lemurs. *Conservation biology*, *33*(1), pp.99-111.

Brook,B.W. and Bradshaw,C.J., (2006). Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*,87(6), pp.1445-1451.

Brooks,S.P., and Gelman,A. (1997). General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics* 7: 434–455.

Brown,J.H., and A.Kodric-Brown. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.

Buckland,S.T.,Goudie,I.B.J., & Borchers,D.L. (2000). Wildlife population assessment: past developments and future directions. *Biometrics*, *56*(1), 1-12.

Burke, C. M., & Montevecchi, W. A. (2009). The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology*, *278*(4), 354-361

Burthe, S., Daunt, F., Butler, A., Elston, D. A., Frederiksen, M., Johns, D., ... & Wanless, S. (2012). Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series*, *454*, 119-133.

Busch, M., Kannen, A., Garthe, S. and Jessopp, M., (2013). Consequences of a cumulative perspective on marine environmental impacts: offshore wind farming and seabirds at North Sea scale in context of the EU Marine Strategy Framework Directive. *Ocean & Coastal Management*, *71*, pp.213-224.

Cabrelli, A., Harwood, J., Matthiopoulos, J., New, L. F., & Thomas, L. (2009). A critical review of the literature on population modelling. Available online from: https://research-repository.st-andrews.ac.uk/bitstream/handle/10023/2241/Cabrelli_et_al_JIP22_07_20_Final_report.pdf?sequence=1

Cadiou, B., Monnat, J. Y., & Danchin, E. (1994). Prospecting in the kittiwake, Rissa tridactyla: different behavioural patterns and the role of squatting in recruitment. *Animal Behaviour*, *47*(4), 847-856.

Cairns, D. K. (1987). Seabirds as indicators of marine food supplies. *Biological Oceanography* 5:261– 271.

Cam, E. (2009) Contribution of capture-mark-recapture modeling to studies of evolution by natural selection. *Modeling demographic processes in marked populations*.pp83-129. Springer US,

Cam, E., Oro, D., Pradel, R. and Jimenez, J., (2004). Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture–recapture models. *Journal of Animal Ecology*, *73*(4), pp.723-736.

Campbell, B., E. Lack. 1985. A Dictionary of Birds. Vermillion: Buteo Books. Published by T & A D Poyser

Camphuysen, K., Scott, B. and Wanless, S. (2011). Distribution and foraging interactions of seabirds and marine mammals in the North Sea: a metapopulation analysis. Available online from: http://www.abdn.ac.uk/staffpages/uploads/nhi635/ZSLpaper-kees.pdf

Campioni, L., Granadeiro, J.P. and Catry, P., (2015). Niche segregation between immature and adult seabirds: does progressive maturation play a role?. *Behavioral Ecology*, *27*(2), pp.426-433.

Carrete, M., Sánchez-Zapata, J. A., Benítez, J. R., Lobón, M., & Donázar, J. A. (2009). Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biological Conservation*,*142*(12), 2954-2961.

Carroll, M.J., Bolton, M., Owen, E., Anderson, G.Q., Mackley, E.K., Dunn, E.K. and Furness, R.W., (2017). Kittiwake breeding success in the southern North Sea correlates with prior sandeel fishing mortality. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(6), pp.1164-1175.

Carroll, M.J., Butler, A., Owen, E., Ewing, S.R., Cole, T., Green, J.A., Soanes, L.M., Arnould, J.P.Y., Newton, S.F., Baer, J. and Daunt, F., (2015). Effects of sea temperature and stratification changes on seabird breeding success. *Climate Research*, *66*(1), pp.75-89.

Caswell, H. (2001). Matrix population models: construction, analysis and interpretation, 2nd edition. Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers

Chamberlain, D. E., Rehfisch, M. R., Fox, A. D., Desholm, M., & Anthony, S. J. (2006). The effect of avoidance rates on bird mortality predictions made by wind turbine collision risk models. *Ibis*, *148*(s1), 198-202.

Cherel, Y., Phillips, R. A., Hobson, K. A., & McGill, R. (2006). Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters*, *2*, 301-303.

Christensen-Dalsgaard, S., May, R.F., Barrett, R.T., Langset, M., Sandercock, B.K. and Lorentsen, S.H., (2018). Prevailing weather conditions and diet composition affect chick growth and survival in the black-legged kittiwake. *Marine Ecology Progress Series*, *604*, pp.237-249.

Clark,J.S., (2003). Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology*, *84*(6), pp.1370-1381.

Clobert, J., Lebreton, J. D., Clobert-Gillet, M., & Coquillart, H. (1985). The estimation of survival in bird populations by recaptures or sightings of marked individuals. In *Statistics in ornithology* (pp. 197-213). Springer, New York, NY.

Cook, A.S.C.P., Johnston, A., Wright, L.J., Burton, N.H.K., (2012). A Review of Flight Heights and Avoidance Rates of Birds in Relation to Offshore Wind Farms. Crown Estate Strategic Ornithological Support Services. Project SOSS-02. http:// www.bto.org/science/wetland-and-marine/soss/projects.

Cook, AonghaisS.C.P. & Robinson,Robert A. (2016), Testing sensitivity of metrics of seabird population response to offshore wind farm effects, JNCC Report 553, ISSN 0963-8901

Cooke, J., Leaper, R., Wade, P., Lavigne, D. and Taylor, B. (2012). Management rules for marine mammal populations: a response to Longeran. *Marine Policy* 36: 389-392.

Coulson (2011). The kittiwake Poyser Monographs

Coulson, J. C. (2017). Productivity of the Black-legged Kittiwake Rissa tridactyla required to maintain numbers. *Bird Study*, *64*(1), 84-89.

Coulson, J. C. and G. Neve de Mevergnies. (1992). Where do young Kittiwakes *Rissa tridactyla* breed, philopatry or dispersal? *Ardea* 80: 187–197

Coulson, J.C. and Coulson, B.A., (2008). Measuring immigration and philopatry in seabirds; recruitment to Black-legged Kittiwake colonies. *Ibis*, 150(2), pp.288-299.

Coulson, J.C., (2016). A review of philopatry in seabirds and comparisons with other waterbird species. *Waterbirds*, *39*(3), pp.229-241.

Cox, S. L., Scott, B. E., & Camphuysen, C. (2013). Combined spatial and tidal processes identify links between pelagic prey species and seabirds. *Marine Ecology Progress Series*, *479*, 203-221.

Cramp S. Bourne W.R.P. & Saunders D.R. (1974). The seabirds of Britain and Ireland. Collins, London.

Crespin, L., Harris, M.P., Lebreton, J.D., Frederiksen, M. and Wanless, S.,(2006). Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology*, *75*(1), pp.228-238.

Croxall, J.P., Butchart, S.H., Lascelles, B, Stattersfield, A.J., Sullivan, B., Symes, A. and Taylor, P., (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, *22*(1), pp.1-34.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M. and Piatt, J.F., (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science*, *334*, pp.1703-1706.

Danchin, E. & Monnat, J.Y. (1992). Population dynamics modeling of two neighboring kittiwake Rissa tridactyla colonies. *Ardea* 80: 171–180.

Danchin, E., B.Cadiou, J. Y. Monnat, & R.Rodriguez Estrella. (1991). Recruitment in long-lived birds: conceptual framework and behavioural mechanisms. *Proceedings of the International Ornithological Congress* 20:1641–1656.

Danchin, E., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004) Public Information: from Nosy Neighbors to Cultural Evolution. *Science*, 305, 487–491.

Danchin, E.,Boulinier, T. & Massot T, M.(1998).Conspecific reproductive success and breeding habitatselection: implications for the study of coloniality. *Ecology* 79: 2415–2428.

Daunt F, Afanasyev V, Adam A, Croxall JP, Wanless S. (2007) From cradle to early grave: juvenile mortality in European shags Phalacrocorax aristotelis results from inadequate development of foraging proficiency. *Biology. Letters*. 3, 371–374. (doi:10.1098/rsbl.2007.0157)

Daunt, F., Reed, T.E., Newell, M., Burthe, S., Phillips, R.A., Lewis, S. and Wanless, S.,(2014). Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. *Ecology*, *95*(8), pp.2077-2083.

Daunt, F., Wanless, S., Greenstreet, S.P., Jensen, H., Hamer, K.C. and Harris, M.P., (2008). The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian journal of fisheries and aquatic sciences*, *65*(3), pp.362-381.

Daunt, F., Wanless, S., Harris, M.P., Money, L. and Monaghan, P., (2007). Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, *21*(3), pp.561-567.

Davoren, G. K. and Montevecchi, W. A. (2003), Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalgae*. *Journal of Avian Biology*, 34: 44–53.

Denwood,Matthew,J (2016). runjags: An R Package Providing Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS. *Journal of Statistical Software*, 71(9), 1-25.<doi:10.18637/jss.v071.i09>

Desholm, M. & Kahlert, J. (2005) Avian collision risk at an offshore wind farm. *Biology Letters*, 1, 296–298.

Dillingham,P.W. and Fletcher,D., (2008). Estimating the ability of birds to sustain additional human-caused mortalities using a simple decision rule and allometric relationships. *Biological Conservation*, *141*(7), pp.1783-1792.

Dillingham,P.W. and Fletcher,D.,(2011). Potential biological removal of albatrosses and petrels with minimal demographic information. *Biological Conservation*, 144(6), pp.1885-1894.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, 66, 973–988.

Drewitt, A. L., & Langston, R. H. (2006). Assessing the impacts of wind farms on birds. *Ibis*, *148*(s1), 29-42.

Elton,C.S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *British Journal of Experimental Biology*. 2: 119-63.

Engelhard, G.H., Peck, M.A., Rindorf, A., Smout, S.C., van Deurs, M., Raab, K., Andersen, K.H., Garthe, S., Lauerburg, R.A., Scott, F. and Brunel, T., (2014). Forage fish, their fisheries, and their predators: who drives whom?.*ICES Journal of Marine Science: 71*, pp.90-104.

Engen,S.,Bakke,Ø. and Islam,A., (1998). Demographic and environmental stochasticity-concepts and definitions. *Biometrics*, pp.840-846.

European Commission (2009). DIRECTIVE 2009/28/EC OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL of 23 April 2009on the promotion of the use of energy from renewable. http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=uriserv:OJ.L_.2009.140.01.0016.01.ENG. Last accessed: 08/03/2016. Last Updated: Unnknown

European Commission Directive 2009/147/EC of the European Parliament and the Council of 30 November 2009 on the conservation of wild birds Off. J. Eur. Union L, 20 (7)

European Commission(2011) EU Guidance on Wind Energy Development in Accordance With the EU Nature Legislation. Publications Office of the European Union, Luxembourg.

Fayet, A.L., Freeman, R., Shoji, A., Kirk, H.L., Padget, O., Perrins, C.M. and Guilford, T., (2016). Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology*, *85*(6), pp.1516-1527.

Fayet, A.L., Freeman, R., Shoji, A., Padget, O., Perrins, C.M. and Guilford, T., (2015). Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. *Animal behaviour*, *110*, pp.79-89.

Fernández-Chacón, A., Genovart, M., Pradel, R., Tavecchia, G., Bertolero, A., Piccardo, J., Forero, M.G., Afán, I., Muntaner, J. and Oro, D., (2013). When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population. *Ecography*, *36*(10), pp.1117-1126.

Finney, S.K., Wanless, S. and Harris, M.P., (1999). The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot Uria aalge. *Journal of Avian Biology*, pp.23-30.

Fleischer, T., Gampe, J., Scheuerlein, A. and Kerth, G., (2017). Rare catastrophic events drive population dynamics in a bat species with negligible senescence. *Scientific reports*, *7*(1), p.7370.

Foley, P., (1997). Extinction models for local populations. In *Metapopulation biology* (pp. 215-246). Academic Press

Forbes, L.S. & Kaiser, G.W. (1994). Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos* 70: 377–384.

Fox, A. D., Desholm, M., Kahlert, J., Christensen, T. K., & Krag Petersen, I. B. (2006). Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. *Ibis*, *148*(s1), 129-144.

Frederiksen, M., Anker-Nilssen, T., Beaugrand, G. and Wanless, S., (2013). Climate, copepods and seabirds in the boreal Northeast Atlantic–current state and future outlook. *Global change biology*, *19*, pp.364-372.

Frederiksen, M., Daunt, F., Harris, M.P. and Wanless, S., (2008). The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, *77*(5), pp.1020-1029.

Frederiksen, M., Edwards, M., Mavor, R.A. and Wanless, S., (2007a). Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series*, *350*, pp.137-143.

Frederiksen, M., Elston, D.A., Edwards, M., Mann, A.D. and Wanless, S., (2011). Mechanisms of long-term decline in size of lesser sandeels in the North Sea explored using a growth and phenology model. *Marine Ecology Progress Series*, *432*, pp.137-147.

Frederiksen, M., Harris, M. P., & Wanless, S. (2005a). Inter-population variation in demographic parameters: a neglected subject?. *Oikos*, *111*(2), 209-214.

Frederiksen, M., Moe, B., Daunt, F., Phillips, R.A., Barrett, R.T., Bogdanova, M.I., Boulinier, T., Chardine, J.W., Chastel, O., Chivers, L.S. and Christensen-Dalsgaard, S., (2012.) Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions*, *18*(6), pp.530-542

Frederiksen, M., Wanless, S. and Harris, M.P., (2004a). Estimating true age–dependence in survival when only adults can be observed: an example with Black–legged Kittiwakes. *Animal Biodiversity and Conservation*, *27*(1), pp.541-548.

Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. and Wilson, L.J., (2004b). The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, *41*(6), pp.1129-1139.

Frederiksen, M., Wright, P. J., Harris, M. P., Mavor, R. A., Heubeck, M., & Wanless, S. (2005b). Regional patterns of kittiwake Rissa tridactyla breeding success are related to variability in sandeel recruitment. *Marine Ecology Progress Series*, *300*, 201-211

Frederiksen,M., Mavor,R.A., & Wanless,S. (2007b). Seabirds as environmental indicators: the advantages of combining data sets. *Marine Ecology Progress Series*, 352, 205-211.

Freeman, S., Searle, K., Bogdanova, M., Wanless, S., Daunt F (2014) Population dynamics of Forth & Tay breeding seabirds: Review of available models and modeling of breeding populations. Centre for Hydrology and Ecology. Available at: http://www.gov.scot/resource/0044/00449072.pdf

Fretwell, S.D. (1972). Populations in a seasonal environment. Princeton: Princeton University Press.

Furness, R. W., Wade, H. M., & Masden, E. A. (2013). Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of environmental management*, *119*, 56-66.

Furness, R.W. & Monaghan, P. (1987). Seabird Ecology. New York: Blackie.

Furness, R.W. (2015). Non-breeding season populations of seabirds in UK waters: Population sizes for Biologically Defined Minimum Population Scales (BDMPS). Natural England Commissioned Reports, Number 164.

Furness, R.W. and Birkhead, T.R. (1984). Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature*, 311, 655-656.

Furness,R.W and Trinder,M (2014). PBR for Flamborough Head and Filey Coast pSPA populations of Kittiwake and Gannet. Habitats Regulations Assessment Report. Appendix E: Potential Biological Removals.*https://infrastructure.planninginspectorate.gov.uk/wpcontent/ipc/uploads/projects/EN010051/EN010051-000356-5.2.5%20Habitats%20Regulations%20Assessment%20Appendix%20E.pdf*

Furness,R.W.,Wade,H.M., & Masden,E.A. (2013). Assessing vulnerability of marine bird populations to offshore wind farms. Journal of environmental management, *119*, 56-66.

Garthe, S. and Hüppop, O., (2004). Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of applied Ecology*, *41*(4), pp.724-734.

Garthe, S., Montevecchi, W.A. and Davoren, G.K., (2011). Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnology and Oceanography*, *56*(3), pp.802-812.

Gauthier, G., Milot, E. and Weimerskirch, H.,(2012). Estimating dispersal, recruitment and survival in a biennially breeding species, the Wandering Albatross. *Journal of Ornithology*, *152*(2), pp.457-467.

Gerber, L. & González-Suárez, M. (2010) Population Viability Analysis: Origins and Contributions. *Nature Education Knowledge* 3(10):15

Goldsmith, M. E.(1954) "The Seafarer and the birds." *Review of English Studies* V19: 225-235.

Golet GH, Irons DB, Estes JA (1998) Survival costs of chick rearing in black-legged kittiwakes. *Journal of Animal Ecology* 67: 827−841

Gotelli,N. 2001. A Primer of Ecology, Third Edition. Sinauer Associates, Sunderland, MA.

Goyert, H.F., Garton, E.O., Drummond, B.A. and Renner, H.M., (2017). Density dependence and changes in the carrying capacity of Alaskan seabird populations. *Biological Conservation*, *209*, pp.178-187.

Grecian, W. J., Inger, R., Attrill, M. J., Bearhop, S., Godley, B. J., Witt, M. J., & Votier, S. C. (2010). Potential impacts of wave-powered marine renewable energy installations on marine birds. *Ibis*, *152*(4), 683-697.

Green,R.E., Langston,R.H., McCluskie,A., Sutherland,R. and Wilson,J.D., (2016). Lack of sound science in assessing wind farm impacts on seabirds. *Journal of Applied Ecology*, *53*(6), pp.1635-1641.

Greenstreet, S.P., Armstrong, E., Mosegaard, H., Jensen, H., Gibb, I.M., Fraser, H.M., Scott, B.E., Holland, G.J. and Sharples, J., 2006. Variation in the abundance of sandeels Ammodytes marinus off southeast Scotland: an evaluation of area-closure fisheries management and stock abundance assessment methods. *ICES Journal of Marine Science*, *63*(8), pp.1530-1550

Gurney, J. H, (1913). The gannet: a bird with a history. Witherby, London.

Hamer, K. C., Schreiber E.A, and Burger, J. (2002) "Breeding biology, life histories, and life history–environment interactions in seabirds." Biology of marine birds. CRC Press, pp: 217-261.

Hanski, I. (1999). Metapopulation ecology. – Oxford University Press.

Hanski,I & Gilpin,M.E (1997). *Metapopulation Biology. Ecology, Genetics, and Evolution*. Academic Press Limited.

Hanski,I., (1998). *Metapopulation dynamics*. Nature, *396*(6706), p.41.

Harris, M. P., Daunt, F., Newell, M., Phillips, R. A., & Wanless, S. (2010). Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Marine biology*, *157*, 827-836.

Harris, M.P, Wanless, S, (1998), Isle of May seabird studies in 1998, JNCC Report 282, ISSN 0963-8091

Harris.M.P, Frederiksen,M. & Wanless,S. (2007). Within- and between-year variation in the juvenile survival of common guillemots Uria aalge. *Ibis*, 149, 472–481.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80: 4−18

Hatch, S.A., (2013). Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Marine Ecology Progress Series*, *477*, pp.271-284.

Hatchwell, B.J. and Birkhead, T.R., (1991). Population dynamics of common guillemots Uria aalge on Skomer Island, Wales. *Ornis Scandinavica*, pp.55-59.

Heubeck, M., Mellor, R.M., Harvey, P.V., Mainwood, A.R. and Riddington, R., (1999). Estimating the population size and rate of decline of kittiwakes Rissa tridactyla breeding in Shetland, 1981–97. *Bird Study*, *46*(1), pp.48-61.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, *97*, 5-60.

Holt, R.D., (1997). On the evolutionary stability of sink populations. *Evolutionary Ecology*, *11*(6), pp.723-731.

Holt, R.D.,(1985). Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical population biology*, *28*(2), pp.181-208.

Horswill, C., Kindsvater, H.K., Juan-Jordá, M.J., Dulvy, N.K., Mangel, M., Matthiopoulos, J. (2019). Global reconstruction of life-history strategies: a case study using tunas. *Journal of Applied Ecology*, 56, 855-865. doi: 10.1111/1365-2664.13327

Horswill,C., & Robinson,R.A. (2015). Review of Seabird Demographic Rates and Density Dependence. JNCC Report no. 552.

Horswill,C.,O'Brien,S.H., & Robinson,R.A. (2017). Density dependence and marine bird populations: are wind farm assessments precautionary? *Journal of Applied Ecology*. 54(5), pp.1406-1414.

Howells, R.J., Burthe, S.J., Green, J.A., Harris, M.P., Newell, M.A., Butler, A., Johns, D.G., Carnell, E.J., Wanless, S. and Daunt, F., (2017). From days to decades: short-and long-term variation in environmental conditions affect offspring diet composition of a marine top predator. *Marine Ecology Progress Series*, *583*, pp.227-242.

Hurrell, J., (1995). NAO index data provided by the climate analysis section, NCAR, Boulder, USA. *Online: http://www. cgd. ucar. edu/cas/jhurrell/indices. html*.

Hurrell, J.W., Kushnir, Y., Ottersen, G. and Visbeck, M., (2003). An overview of the North Atlantic oscillation. *The North Atlantic Oscillation: climatic significance and environmental impact*, *134*, pp.1-35.

ICES. (2018). Sandeel in Division 3.a and Subarea 4. Section 9 in Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG), 29–31 January and 12–20 March 2018, ICES HQ, Denmark. ICES CM 2018/ACOM:07.

Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., James Grecian, W., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J. and Godley, B.J., (2009). Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*, *46*(6), pp.1145-1153.

IUCN 2019. The IUCN Red List of Threatened Species. Version 2019-1. http://www.iucnredlist.org. Downloaded on 21 March 2019.

Jenouvrier,S.,Barbraud,C.,Cazelles,B., & Weimerskirch,H. (2005). Modelling population dynamics of seabirds: importance of the effects of climate fluctuations on breeding proportions. *Oikos*, 108(3), 511-522.

JNCC, (2008), http://jncc.defra.gov.uk/page-2773. Last Updated 19/10/2015. Last accessed: 19/02/2016

JNCC, (2009), UK Seabirds in 2008, ISBN 978 1 86107 611 3

JNCC (2015a) Northern gannet *Morus bassanus*, http://jncc.defra.gov.uk/page-2875. Last Updated 19/10/2015. Last accessed: 19/02/2016.

JNCC (2015b) Guillemot *Uria aalge*, https://jncc.gov.uk/our-work/guillemot-uria-aalge/. Last updated: 19/10/2015. Last accessed 19/02/2016

JNCC (2015c) Black legged kittiwake *Rissa tridactyla*, http://jncc.defra.gov.uk/page-2889Last Updated 19/10/2015. Last accessed: 19/02/2016

JNCC. 2016. Seabird Population Trends and Causes of Change: 1986-2015 Report (http://jncc.defra.gov.uk/page-3201). Joint Nature Conservation Committee. Updated September 2016.

JNCC (2017). Seabird Monitoring Programme http://jncc.defra.gov.uk/smp/default.aspx. Last accessed:03/04/2018.

JNCC (2018). Seabird Monitoring Programme http://jncc.defra.gov.uk/smp/default.aspx Last accessed:26/05/2019.

Johnston, A., Cook, A. S. C. P., Wright, L. J., Humphreys, E. M., Burton, N. H. K. (2014), Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *Journal of Applied Ecology*, 51: 31–41.

Kadin, M., Olsson, O., Hentati-Sundberg, J., Ehrning, E. W., Blenckner, T. (2016), Common Guillemot *Uria aalge* parents adjust provisioning rates to compensate for low food quality. *Ibis*, 158: 167–178.

Kass,R.E.,Carlin,B.P.,Gelman,A.and Neal,R.M., (1998). Markov chain Monte Carlo in practice: a roundtable discussion. *The American Statistician*, 52(2), pp.93-100.

Kildaw, D., Irons, D.B. and Buck, C.L., (2008). Habitat quality and metapopulation dynamics of Black-legged Kittiwakes Rissa tridactyla. *Marine Ornithology*, *36*, pp.35-45.

Kildaw, S.D., Irons, D.B., Nysewander, D.R. and Buck, C.L., (2005). Formation and growth of new seabird colonies: the significance of habitat quality. *Marine Ornithology*, *33*, pp.49-58.

Kindsvater, H.K., Dulvy, N.K., Horswill, C., Juan-Jordá, M.J., Mangel, M. and Matthiopoulos, J., (2018). Overcoming the data crisis in biodiversity conservation. *Trends in ecology & evolution*, *33*(9), pp.676-688.

Kitaysky, A.S., Piatt, J.F., Hatch, S.A., Kitaiskaia, E.V., Benowitz-Fredericks, Z.M., Shultz, M.T. and Wingfield, J.C., (2010). Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology*, *24*(3), pp.625-637.

Klomp, N.I.& Furness, R.W., (1992). The dispersal and philopatry of Great Skuas from Foula, Shetland. *Ringing & Migration*, *13*(2), pp.73-82.

Knape,J. and deValpine,P., (2012). Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance? *Ecology letters*, 15(1), pp.17-23.

Kress, S. W. (1983). The use of decoys, sound recordings, and gull control for re-establishing a tern colony in Maine. *Colonial Waterbirds* 6:185–196.

Kress, S. W. (1997). Using animal behavior for conservation: case studies in seabird restoration from the Maine coast, USA. Journal of the Yamashina Institute of Ornithology 29:1–26.

Lande,R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, 142(6), 911-927.

Lande,R.,Engen,S. and Saether,B.E., (2003). Stochastic population dynamics in ecology and conservation. Oxford University Press on Demand.

Lande,R.,Engen,S. and Saether,B.E., (2003). Stochastic population dynamics in ecology and conservation. Oxford University Press on Demand.

Lande,R.,Engen,S.,Sæther,B.E.,Filli,F., Matthysen,E. and Weimerskirch,H., (2002). Estimating density dependence from population time series using demographic theory and life-history data. *The American Naturalist*, 159(4), pp.321-337.

Lebreton, J.D., Hines, J.E., Pradel, R., Nichols, J.D. & Spendelow, J.A. (2003). Estimation by capture–recapture of recruitment and dispersal over several sites. *Oikos* 101: 255–264

Leirs,H., Stenseth,N.C., Nichols,J.D., Hines,J.E., Verhagen,R. & Verheyen,W. (1997) Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature*, 389, 176–180.

Lescroël, A., Dugger, K.M., Ballard, G. and Ainley, D.G.,(2009). Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology*, *78*(4), pp.798-806.

Levins, R., (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *American Entomologist*, *15*(3), pp.237-240.

Lewis, S., Sheratt, T.N., Hamer, K.C. & Wanless, S. (2001a). Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412: 816–819.

Lewis, S., Wanless, S., Wright, P.J., Harris, M.P., Bull, J. and Elston, D.A., (2001b). Diet and breeding performance of black-legged kittiwakes Rissa tridactyla at a North Sea colony. *Marine Ecology Progress Series*, *221*, pp.277-284.

Lewis,S.,Elston,D.A.,Daunt,F.,Cheney,B., &Thompson,P. M. (2009). Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. *Oikos*, 118(4), 521-528.

Lewison, R., Oro, D., Godley, B.J., Underhill, L., Bearhop, S., Wilson, R.P., Ainley, D., Arcos, J.M., Boersma, P.D., Borboroglu, P.G. and Boulinier, T., (2012). Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research*, *17*(2), pp.93-121.

Lindeboom, H.J., Kouwenhoven, H.J., Bergman, M.J.N., Bouma, S., Brasseur, S.M.J.M., Daan, R., Fijn, R.C., De Haan, D., Dirksen, S., Van Hal, R. and Lambers, R.H.R., (2011). Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environmental Research Letters*, *6*(3), p.035101.

Link, W.A. (1999) Modeling pattern in collections of parameters. *Journal of Wildlife Management*, **63**, 1017–1027.

Lloyd, Clare, Mark L. Tasker, and Ken Partridge.(2010) The status of seabirds in Britain and Ireland. A&C Black.

Lotka, A. J. (1922): The stability of the normal age distribution. *Proceedings of the National Academy of Sciences*, VIII, 339-345.

MacArthur Green (2014) PBR for Flamborough Head and Filey Coast pSPA populations of Kittiwake and Gannet. Available at: http://www.forewind.co.uk/uploads/files/TeessideAB/Application_Documents/5.Reports/5.2.5_Habitats_Regulations_Assessment_Appendix_E.pdf

MacArthur Green (2015). Flamborough and Filey Coast pSPA Seabird PVA Report. Available at: http://infrastructure.planningportal.gov.uk/wpcontent/ipc/uploads/projects/EN010053/Events/Deadline%202a%20Responses%20to%20Rule%2017%20letter%20issued%20by%20the%20ExA%20on%204%20August%202015.%20-%2025082015/Appendix%20M_MacArthur%20Green%20Seabird%20PVA%20Report%20-%20August%202015.pdf

MacDonald, A., Heath, M.R., Edwards, M., Furness, R.W., Pinnegar, J.K., Wanless, S., Spiers, D.C. and Greenstreet, S.P., (2015). Climate-driven trophic cascades affecting seabirds around the British Isles. *Oceanography and Marine Biology: An Annual Review*, *53*, pp.55-79.

MacDonald, A., Speirs, D.C., Greenstreet, S. and Heath, M., (2018). Exploring the influence of food and temperature on North Sea sandeels using a new dynamic energy budget model. *Frontiers in Marine Science*, *5*, p.339.

Maclean, I. M., Frederiksen, M., & Rehfisch, M. M. (2007). Potential use of population viability analysis to assess the impact of offshore wind farms on bird populations. BTO Research Report No. 480 to COWRIE. BTO, Thetford.

Major, H.L. and Jones, I.L., (2011). An experimental study of the use of social information by prospecting nocturnal burrow-nesting seabirds. *The Condor*, *113*(3), pp.572-580.

Maravelias, C. D. (1997). Trends in abundance and geographic distribution of North Sea herring in relation to environmental factors. *Marine Ecology Progress Series*, *159*, 151-164.

Margalida, A., Colomer, M.À., Oro, D., Arlettaz, R. and Donázar, J.A., (2015). Assessing the impact of removal scenarios on population viability of a threatened, long-lived avian scavenger. *Scientific reports*, *5*, p.16962.

Marques,A.C.,Fuinhas,J.A., &Manso,J.P. (2010). Motivations driving renewable energy in European countries: A panel data approach. *Energy policy*, 38(11), 6877-6885.

Plummer,M., Best, N, Cowles, K and Vines,K (2006). CODA: Convergence Diagnosis and Output Analysis for MCMC, R News, vol 6, 7-11

Masden, E. A., Haydon, D. T., Fox, A. D., & Furness, R. W. (2010). Barriers to movement: modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. *Marine Pollution Bulletin*, *60*, 1085-1091.

Masden, E.A., Haydon, D.T., Fox, A.D., Furness, R.W., Bullman, R. and Desholm, M., (2009). Barriers to movement: impacts of wind farms on migrating birds. *ICES Journal of marine Science*, *66*(4), pp.746-753.

Matthiopoulos, J. (2003). The use of space by animals as a function of accessibility and preference. *Ecological Modelling*, *159*, 239-268.

Matthiopoulos,J.,Fieberg,J.,Aarts,G., Beyer,H.L., Morales,J.M., &Haydon,D.T. (2015). Establishing the link between habitat selection and animal population dynamics. *Ecological Monographs, 85(3), 413-436.*

Miles,W and Mellor,M (2018). SOTEAG Ornithological Monitoring Report. https://www.soteag.org.uk/files/2019/04/2018-SOTEAG-Bird-Report.pdf

Miller, J.A., Furness, R.W., Trinder, M. and Matthiopoulos, J., (2019). The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality. *Journal of Applied Ecology*, *56*(9), pp.2118-2130.

Miller, P.S., Lacy, R.C., Medina-Miranda, R., López-Ortiz, R. and Díaz-Soltero, H., (2016). Confronting the invasive species crisis with metamodel analysis: An explicit, two-species demographic assessment of an endangered bird and its brood parasite in Puerto Rico. *Biological Conservation*, *196*, pp.124-132.

Miller. L. (2014). (https://lukemiller.org/index.php/2014/11/extracting-noaa-sea-surface-temperatures-with-ncdf4/).

Mitchell, P.I., Newton, S.F., Ratcliffe, N. and Dunn, T.E., (2004). Seabird populations of Britain and Ireland. T & AD Poyser, London.

Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine, and J. Blackwood. (1989). The relationship between food supply, reproductive effort and breeding success in Arctic terns Sterna paradisaea. *Journal of Animal Ecology* 58:261–274

Montevecchi,W.A.,Benvenuti,S.,Garthe,S.,Davoren,G.K.,&Fifield,D. (2009). Flexible foraging tactics by a large opportunistic seabird preying on forage-and large pelagic fishes. *Marine Ecology Progress Series*, 385, 295-306.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., ... & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*, 2289-2301.

Murphy,G.E., & Romanuk,T.N. (2014). A meta-analysis of declines in local species richness from human disturbances. *Ecology and evolution*, 4(1), 91-103. http://doi.org/10.1002/ece3.909

Murray,S., Harris,M.P. and Wanless, S., (2015). The status of the gannet in Scotland in 2013-14. *Scottish Birds*, *35*(1), pp.3-18.

Nelson, B.F., Daunt, F., Monaghan, P., Wanless, S., Butler, A., Heidinger, B.J., Newell, M. and Dawson, A., (2015). Protracted treatment with corticosterone reduces breeding success in a long-lived bird. *General and comparative endocrinology*, *210*, pp.38-45.

Newell, M.; Harris, M.P.; Wanless, S.; Burthe, S.; Bogdanova, M.; Gunn, C.M.; Daunt, F. (2016). The Isle of May long-term study (IMLOTS) seabird annual breeding success 1982-2016. NERC Environmental Information Data Centre. https://doi.org/10.5285/02c98a4f-8e20-4c48-8167-1cd5044c4afe

Niel,C.,&Lebreton,J.D. (2005). Using demographic invariants to detect overharvested bird populations from incomplete data. *Conservation Biology*, *19*(3), 826-835.

NOAA High Resolution SST data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/

O'Brien,S.H.,Cook,A.S.andRobinson,R.A., (2017). Implicit assumptions underlying simple harvest models of marine bird populations can mislead environmental management decisions. *Journal of environmental management*, 201, pp.163-171.

Orians GH, Pearson NE. (1979). On the theory of central place foraging. In: Horn DJ, Staris GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH

Oro D, Torres R, Rodríguez C, Drummond H. (2010). Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology* 91: 1205−1214

Oro, D. & Ruxton, G.D. (2001) The formation and growth of seabird colonies: Audouin's gull as a case study. *Journal of Animal Ecology*, 70, 527–535.

Oro, D. and Furness, R.W., (2002). Influences of food availability and predation on survival of kittiwakes. *Ecology*, *83*(9), pp.2516-2528.

Oro, D., (1996). Colonial seabird nesting in dense and small sub-colonies: an advantage against aerial predation. *The Condor*, *98*(4), pp.848-850.

Oro, D., (2014). Seabirds and climate: knowledge, pitfalls, and opportunities.*Frontiers in Ecology and Evolution*, *2*, p.79.

Oro, D., Cam, E. & Martınez-Abraın, A. (2004) Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society B*, 271, 387–396.

Oro,D,&Martinez-Abrain,A (2004). *Ecology and behaviour of seabirds*. Duarte,CM, editor. The Encyclopedia of Life Support Systems (EOLSS). Oxford, UK: Eolss PublishersUNESCO.

Parker, M. W., S. W. Kress, R. T. Golightly, H. R. Carter, E. B. Parsons, S. E. Schubel, J. A. Boyce, G. J. Mc Chesney, AND S. M. Wisely. (2007). Assessment of social attraction techniques used to restore a Common Murre colony in central California. *Waterbirds* 30:17–28.

Patrick, S.C., Bearhop, S., Bodey, T.W., Grecian, W.J., Hamer, K.C., Lee, J. and Votier, S.C., (2015). Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. *Journal of Avian Biology*, *46*, pp.431-440.

Péron, C. and Grémillet, D., (2013). Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. *PLoS One*, *8*(8), p.e72713.

Pettex, E., Lambert, C., Fort, J., Dorémus, G. and Ridoux, V. (2019). Spatial segregation between immatures and adults in a pelagic seabird suggests age-related competition. *Journal of Avian Biology* doi 10.1111/jav.01935.

Phillips, R. A., Bearhop, S., Mcgill, R. A., & Dawson, D. A. (2009). Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia,160*, 795-806.

Phillips, R.A., Lewis, S., González-Solís, J. and Daunt, F., (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series*, *578*, pp.117-150.

Platteeuw,M.,Bakker,J.,van den Bosch, I., Erkman,A.,Graafland,M.,Lubbe,S., & Warnas, M. (2017). A Framework for Assessing Ecological and Cumulative Effects (FAECE) of Offshore Wind Farms on Birds, Bats and Marine Mammals in the Southern North Sea. In Wind Energy and Wildlife Interactions (pp. 219-237). Springer International Publishing.

Plummer M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing.

Plummer,M., Best, N, Cowles, K and Vines,K (2006). CODA: Convergence Diagnosis and Output Analysis for MCMC, R News, vol 6, 7-11

Ponchon, A., Garnier, R., Grémillet, D. and Boulinier, T., (2015). Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. *Diversity and Distributions*, *21*(1), pp.88-100.

Porter, J.M. & Coulson, J.C. (1987). Long-term changes in recruitment to the breeding group and the quality of recruits at a kittiwake Rissa tridactyla colony. *Journal of Animal Ecology* 56: 675–689.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* 132:652–661.

Puyravaud, J.P., Davidar, P., Srivastava, R.K. and Wright, B., (2017). Modelling harvest of Asian elephants Elephas maximus on the basis of faulty assumptions promotes inappropriate management solutions. *Oryx*, *51*(3), pp.506-512.

R Core Team (2016). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*, Vienna, Austria. URL https://www.R-project.org/.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ratcliffe, N., Bell, M., Pelembe, T., Boyle, D., Benjamin, R., White, R., Godley, B., Stevenson, J. and Sanders, S., (2010). The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. *Oryx*, *44*(1), pp.20-29.

Reed, J.M. and Dobson, A.P., (1993). Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology & Evolution*, *8*(7), pp.253-256.

Reed,J.M.,Mills,L.S.,Dunning,J.B.,Menges,E.S., McKelvey,K.S.,Frye,R.,Beissinger,S.R.,Anstett,M.C. and Miller,P.,(2002). Emerging issues in population viability analysis. *Conservation biology*, 16(1), pp.7-19.

Reiertsen, T.K., Erikstad, K.E., Anker-Nilssen, T., Barrett, R.T., Boulinier, T., Frederiksen, M., González-Solís, J., Gremillet, D., Johns, D., Moe, B. and Ponchon, A., (2014). Prey density in non-breeding areas affects adult survival of black-legged kittiwakes Rissa tridactyla. *Marine Ecology Progress Series*, *509*, pp.289-302.

Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S. and Schlax, M.G., (2007). Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate*, *20*(22), pp.5473-5496.

Riotte-Lambert, L. and Weimerskirch, H., (2013). Do naive juvenile seabirds forage differently from adults?. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1768), p.20131434.

Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P.A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A. and Corlett, R.T.,(2016). Saving the world's terrestrial megafauna. *Bioscience*, *66*(10), pp.807-812.

Rubolini, D., Romano, M., Boncoraglio, G., Ferrari, R.P., Martinelli, R., Galeotti, P., Fasola, M. and Saino, N., (2005). Effects of elevated egg corticosterone levels on behavior, growth, and immunity of yellow-legged gull (Larus michahellis) chicks. *Hormones and Behavior*, *47*(5), pp.592-605.

Russell, D.J., Brasseur, S.M., Thompson, D., Hastie, G.D., Janik, V.M., Aarts, G., McClintock, B.T., Matthiopoulos, J., Moss, S.E. and McConnell, B., (2014). Marine mammals trace anthropogenic structures at sea. *Current Biology*, *24*(14), pp.R638-R639.

Ryan Norris, D. and Marra, P.P., (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, *109*(3), pp.535-547.

Saether, B.-E., & Bakke, O. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, 81, 642–653. https://doi.org/10.2307/177366

Sæther, B.-E., R. Andersen, and H. C. Pedersen. (1993). Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the antarctic petrel, Thalassoica antarctica. *Behavioral Ecology and Sociobiology* 33:147–150.

Saether,B.-E.,Engen,S.,Lande,R.,Both,C.andVisser,M.E. (2002), Density dependence and stochastic variation in a newly established population of a small songbird. *Oikos*, 99: 331–337.

Sands,P., & Peel,J. (2012). Principles of international environmental law. Cambridge University Press.

Sandvik, H., Erikstad, K.E., Barrett, R.T. and Yoccoz, N.G., (2005). The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology*, *74*(5), pp.817-831.

Sanz-Aguilar,A.,Igual,J.M.,Tavecchia,G.,Genovart,M. and Oro,D., (2016). When immigration mask threats: The rescue effect of a Scopoli's shearwater colony in the Western Mediterranean as a case study. *Biological Conservation*, 198, pp.33-36

Saunders,S.P,Cuthbert,F.J and Zipkin,E.F (2018). Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology* 00:1-13

Schreiber, E.A. (2002). Climate and weather effects on seabirds. *Biology of Marine Birds* (eds E.A. Schreiber & J. Burger), pp. 179–215. CRC, Boca Raton.

Schaub, M., Abadi, F., (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152 (Suppl. 1), S227–S237

Smout, S., Rindorf, A., Wanless, S., Daunt, F., Harris, M. P., & Matthiopoulos, J. (2013). Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: a multi-species functional response for guillemots in the North Sea. *Journal of Applied Ecology*, *50*, 1071-1079.

SNIFFER (2006) , Scotland and Northern Ireland Forum For Environmental Research "*Practical guidance on applying the precautionary principle*".

Spiegelhalter, D., Best, N., Carlin, B. and van Der Linde, A. (2002). Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society*, Series B 64, 583–639.

Stamps, J. A. (1988). Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329–347.

Steiner, U.K. & Gaston, A.J. (2005) Reproductive consequences of natal dispersal in a highly philopatric seabird. *Behavioral Ecology*, 16, 634–639.

Stewart, G. B., Pullin, A. S., & Coles, C. F. (2007). Poor evidence-base for assessment of windfarm impacts on birds. *Environmental Conservation*, *34*(01), 1-11.

Sutherland, William J.(1996) From individual behaviour to population ecology. Vol. 11. Oxford University Press,.

Szostek, K. L., Schaub, M., & Becker, P. H. (2014). Immigrants are attracted by local pre-breeders and recruits in a seabird colony. *Journal of Animal Ecology*, *83*, 1015-1024.

Szostek, K.L. and Becker, P.H., (2015). Survival and local recruitment are driven by environmental carry-over effects from the wintering area in a migratory seabird. *Oecologia*, *178*(3), pp.643-657.

Tasker, M. L., Camphuysen, C. J., & Fossum, P. (1999). 3 Variation in prey taken by seabirds. Diets of seabirds and consequences of changes in food supply. No. 232. International Council for the Exploration of the Sea, 1999.

Tavecchia, G., Pradel, R., Genovart, M. and Oro, D. (2007), Density-dependent parameters and demographic equilibrium in open populations. *Oikos*, 116: 1481–1492.

Thomas, C. D., and W. E. Kunin. (1999). The spatial structure of populations. *Journal of Animal Ecology* 68:647–657

Thomas, C.D. and Hanski, I., (1997). Butterfly metapopulations. In *Metapopulation biology* (pp. 359-386). Academic Press.

Tims,J., Nisbet, I.C., Friar, M.S., Mostello, C. & Hatch, J.J. (2004). Characteristics and performance of Common Terns in old and newly-established colonies. *Waterbirds* 27: 321–332.

Tranquilla, L.A.M., Montevecchi, W.A., Fifield, D.A., Hedd, A., Gaston, A.J., Robertson, G.J. and Phillips, R.A., (2014). Individual winter movement strategies in two species of Murre (Uria spp.) in the Northwest Atlantic. *PloS one*, *9*, p.e90583.

Turchin,P. (1995). Population regulation: old arguments and a new synthesis. *Population dynamics: new approaches and synthesis*, 19-40.

Valone, T.J. & Templeton, J.J. (2002) Public information for the assessment of quality: a widespread social phenomenon. *Proceedings of the Royal Society B*, 357, 1549–1557

Valone, T.J. (1989) Group foraging, public information, and patch estimation. *Oikos*, 56, 357–363.

van der Kooij, J., Scott, B. E., & Mackinson, S. (2008). The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. *Journal of Sea Research*, *60*, 201-209.

van Deurs, M., van Hal, R., Tomczak, M.T., Jónasdóttir, S.H. and Dolmer, P., (2009). Recruitment of lesser sandeel Ammodytes marinus in relation to density dependence and zooplankton composition. *Marine ecology progress series*, *381*, pp.249-258.

Van Drunen, S.G., Schutten, K., Bowen, C., Boland, G.J. and Husband, B.C.,(2017). Population dynamics and the influence of blight on American chestnut at its northern range limit: Lessons for conservation. *Forest Ecology and Management*, *400*, pp.375-383.

Velando, Alberto, Álvaro Barros, and Paloma Moran. "Heterozygosity–fitness correlations in a declining seabird population." *Molecular ecology* 24.5 (2015): 1007-1018.

Votier, S. C., Bearhop, S., Witt, M. J., Inger, R., Thompson, D., & Newton, J. (2010). Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology*, *47*, 487-497.

Votier, S.C., Birkhead, T.R., Oro, D., Trinder, M., Grantham, M.J., Clark, J.A., McCleery, R.H. and Hatchwell, B.J., (2008). Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *Journal of Animal Ecology*, *77*(5), pp.974-983.

Votier, S.C., Fayet, A.L., Bearhop, S., Bodey, T.W., Clark, B.L., Grecian, J., Guilford, T., Hamer, K.C., Jeglinski, J.W., Morgan, G. and Wakefield, E., (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), p.20171068.

Votier, S.C., Grecian, W.J., Patrick, S. and Newton, J., (2011). Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine biology*, *158*(2), pp.355-362.

Votier, S.C., Hatchwell, B.J., Beckerman, A., McCleery, R.H., Hunter, F.M., Pellatt, J., Trinder, M. and Birkhead, T.R., (2005). Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters*, *8*(11), pp.1157-1164.

Votier, S.C., Heubeck, M. and Furness, R.W., (2008). Using inter-colony variation in demographic parameters to assess the impact of skua predation on seabird populations. *Ibis*, *150*, pp.45-53.

Wade,P.R. (1998). Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, *14*(1), 1-37. https://doi.org/10.1016/j.biocon.2011.04.0142005

Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Grémillet, D., Jackson, A.L. and Jessopp, M.J., (2013). Space partitioning without territoriality in gannets.*Science*, *341*, pp.68-70.

Walsh, P.M., Halley, D.J., Harris, M.P., del Nevo, A., Sim, I.M.W., & Tasker, M.L. (1995). Seabird monitoring handbook for Britain and Ireland. Published by JNCC / RSPB / ITE / Seabird Group, Peterborough.

Wanless, S., Frederiksen, M., Daunt, F., Scott, B.E. and Harris, M.P.,(2007). Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Progress in Oceanography*, *72*(1), pp.30-38.

Wanless, S., Frederiksen, M., Walton, J. and Harris, M.P., (2009). Long-term changes in breeding phenology at two seabird colonies in the western North Sea. *Ibis*, *151*(2), pp.274-285.

Wanless,S., Murray,S. & Harris,M.P.(2005) The status of northern gannet in Britain & Ireland in 2003/04. *British Birds* 98, 280–294.

Watkinson, A.R. and Sutherland, W.J., (1995). Sources, sinks and pseudo-sinks. *Journal of Animal Ecology*, pp.126-130.

Weimerskirch,H. (2001). Seabird demography and its relationship with the marine environment. Biology of Marine Birds (EA Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, FL, 115-136.

Wernham C., Toms M., Marchant J., Clark J., Siriwardena G. & Baillie S. (2002). The Migration Atlas: Movements of the Birds of Britain and Ireland. T. & A.D. Poyser, London.

Wooller, R. D., & Coulson, J. C. (1977). Factors affecting the age of first breeding of the kittiwake Rissa tridactyla. *Ibis*, *119*(3), 339-349.

Wright, P.J., Orpwood, J.E. and Boulcott, P., (2017). Warming delays ovarian development in a capital breeder. *Marine biology*, *164*(4), p.80.