The role of heterogeneity in the population ecology and resilience of marine predator species

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Summary

The marine environment is intrinsically linked to the biotic and abiotic processes that regulate the life support systems of the planet, including nutrient and hydrological cycling, climate patterns, geological processes, oxygen production, and nutritional resourcing. Long-term natural cycles in climate variation have pronounced impacts on weather systems, sea surface temperature and marine food webs. Spatial and temporal heterogeneity in these systems and processes can influence communities directly via modulation of survival, reproductive success, and the distribution of resources, and anthropogenic pressures can contribute to heterogeneity in natural systems, influencing bottom-up and top-down processes. For ecological communities regulated by top-down processes, climate-linked shifts in the distribution, population and community dynamics of predators are likely to have pronounced effects on ecosystem composition and function. The influence of environmental variability upon predator ecology is therefore an area of particular research focus.

In marine habitats, spatial and temporal heterogeneity in sea surface temperature has been associated with changes to reproductive phenology in predator and prey species, while spatial and temporal heterogeneity in resource availability may be associated with changes in the survival rates of animals across developmental stages. Likewise, heterogeneity in the approach to data collection, management and analysis may influence the interpretation of results and guide subsequent management decisions. To investigate the role of heterogeneity in marine predator ecology I focus on two apex predators in the Irish Sea: the grey seal (*Halichoerus grypus*) and the Manx shearwater (*Puffinus puffinus*). I explore how temporal heterogeneity of environmental conditions may affect reproductive phenology, how spatial and temporal heterogeneity of data collection and analysis methods affects estimates of population dynamics, and how heterogeneity in survival at different developmental stages can be reflected in population-level dynamics.

After providing an overview of the focus of my thesis in **Chapter one**, using multi-decade time series from eight major grey seal and Manx shearwater breeding sites, I use logistic population growth models and generalised additive models in **Chapter two** to explore how changes in the timing and progression of the grey seal pupping season are dependent on climatic drivers. In **Chapters three** and **four** I use matrix population models (MPM) to quantify the effects of data aggregation and substitution of missing model parameters upon estimates of population dynamics over multiple spatial and temporal scales. In **Chapter five** I then continue the application of MPMs to calculate indices of resilience in scenarios of perturbation, to explore the population-level effects of reduced survival in specific demographic groups, namely fledgling, juvenile and adult Manx shearwater.

My results suggest that contemporaneous heterogeneity in broad- and local-scale climate indices is less influential to reproductive phenology than intrinsic drivers, and that variation in survival rates of year-one animals is largely explained by fine-scale spatial heterogeneity. The substitution of demographic information when parameterising population models introduced biases and uncertainty into projections of population dynamics, and the simulated reduction of survival in juvenile animals appeared to have a potential latent effect on population stability – the consequences of reduced juvenile survival being realised as a reduction in recruitment to the breeding adult population.

Finally, in **Chapter six** I summarise the main findings of this mosaic of studies and discuss them in the context of existing research, to identify avenues for future research. These investigations highlight the need for intrinsic and spatial processes to be incorporated into

studies of climatic drivers of ecological change, and the importance of ensuring the accuracy and appropriate collection, management and analysis of data sources. They also illustrate the potential population-level effects of perturbations to survival in demographic groups which can be logistically difficult to monitor, and act as a reminder that the challenging option is often the one that is necessary.

Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed. [redacted]

Date..........01/02/2024..

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed.. [redacted]

Date..........01/02/2024..

I hereby give consent for my thesis, if accepted, to be available for electronic sharing

Signed......... [redacted]

Date..........01/02/2024..

The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

Signed..... [redacted]

Date..........01/02/2024..

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Acknowledgments

What a ride. I've seen enough responses from friends and acquaintances who have completed, and not quite completed, a PhD to know that that doing one myself was going to be tough, and it would probably have me questioning my life up to this point. I was not wrong. The last five and a bit years have been so much more challenging than I had anticipated, thanks in no small part to a couple of existential crises, one identity crisis, multiple bereavements, a really timely eviction and that global pandemic. There is no question that I would not have made it through on my own. There are so many people at Swansea who I would like to thank for your support, advice, chocolate, belly laughs and general kindness, but please don't be sad that your names are not here. You are all excellent, but these people are especially excellent:

I expect it could go without saying that Prof. Jim Bull has been a major source of support and guidance. Your approach to supervision was a good fit, and your patience and understanding throughout has been invaluable in allowing me to progress at the pace I needed. When it turned out that the first 18 months of my project would definitely be going in the sea your reassurance and guidance averted what could have been a real sticky situation, and when things were tough your advice was spot on. I really enjoyed the experience of helping in your third-year stats module, even the year it was mostly spent alone in a Zoom break-out room. I learned so much from those sessions, and it was a massive help to my own understanding.

I'm so grateful too for the steadfast support and friendship from Becky Phillips (now Hopper!). When I found out we'd be doing our PhDs together I was happy to be starting with someone I knew, and someone who was just as naive. Neither of us knew what this journey would become, but through everything I've been grateful to have someone there who understands. Our trips to conferences were so much fun, even when we did go to the talks, and I know I would have broken if you hadn't introduced me to self-care days. It's been a pleasure working alongside you on this, and it's a pleasure to continue working together in our careers.

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so grateful that you did. I can't wait til we can get back in that cold, cold line-up and share a wave again.

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Chapter one:

General introduction

Heterogeneity in the marine environment

The world's oceans cover more than 70% of the Earth's surface (Richardson et al., 2012) and are intrinsically linked to the biotic and abiotic processes that modulate the life support systems of the planet: nutrient and hydrological cycling, weather and climate systems, geological processes, oxygen production, and nutritional resourcing (Boyd and Hurd, 2009; Chahine, 1992; Doney et al., 2012; Watson, 1998). Long-term natural cycles in climate variation such as the Atlantic Multi-decadal Oscillation (AMO) and North Atlantic Oscillation (NAO) and El-Niño Southern Oscillation (ENSO) have pronounced impacts on weather systems, sea surface temperature (SST) and marine food webs (Mesquita et al., 2015; Stenseth et al., 2003). This spatial and temporal heterogeneity in environmental conditions and biological processes can influence marine organisms directly via changes to individual survival, the success and timing of reproduction, and the distribution of consumers and resources (Beaugrand et al., 2009; Bowen et al., 2020; Cavole et al., 2016; Drinkwater et al., 2003). Anthropogenic pressures can contribute to this heterogeneity, influencing bottom-up processes linked to increasing air and ocean temperatures and lowering of pH (Doney et al., 2009; IPCC, 2015), and top-down processes such as chemical and plastic pollution, habitat modification and overfishing (Alava et al., 2017; Kaiser et al., 2002; Macura et al., 2019; Pauly, 1998; Worm, 2015). The effects of natural and anthropogenic drivers on fundamental processes in the marine environment is an area of intense and diverse research, and the continuation of this, and the use of novel approaches to answer complex questions, is central to understanding the mechanisms of change in the marine environment, and the potential consequences for marine communities.

Environmental heterogeneity and marine predator ecology

Marine predators are a diverse guild of high-trophic-level animals representing a number of taxonomic groups including fish, seabirds, cetaceans and pinnipeds. Predators are reliant upon prey resources for nutrition and survival, so access to these resources is likely to have a profound influence upon predator trophic ecology and population dynamics (Barbraud et al., 2018; Cury et al., 2011; MacDonald et al., 2015; Øigård et al., 2013). Changes in the availability of organisms at lower trophic levels is largely driven by bottom-up processes affecting primary productivity (Frederiksen et al., 2006; Greve et al., 2005). Natural seasonal cycles of phytoplankton abundance can be influenced by local trends in sea temperature and nutrient availability, which in turn can be affected by broader-scale climate processes (Tiselius et al., 2016; Weijerman et al., 2005). Changes to phytoplankton abundance and distribution can affect consumer abundance, with effects being seen at higher trophic levels (Dulvy et al., 2008; Frederiksen et al., 2006), Moreover, asynchrony between prey availability and the energetic requirements of consumers (e.g. gestation and lactation in mammals, and egg production, incubation and chick provisioning in birds) may be critical in determining fitness and subsequent breeding success (Cherel et al., 2016; Hipfner, 2008). The outcome for predator populations may be determined by whether potential phenological shifts of prey and consumer can keep pace with each other.

The effect of climate-induced changes to primary producer abundance upon predator life history processes has been investigated for over 30 years. For instance, changes to trophic linkages in the North Sea between phytoplankton, zooplankton and the direct prey of the kittiwake (*Rissa tridactyla*)illustrate the connection between climate processes and predator reproduction and population size, via bottom-up effects to trophic processes (Aebischer et al., 1990). In the same region, a negative association has been observed between recruitment of lesser sandeel (*Ammodytes marinus*) and winter NAO index, highlighting the potential for changes to prey availability and indirect effects at higher trophic levels (Arnott and Ruxton, 2002). In the Celtic Sea, climate-linked environmental heterogeneity has produced less marked effects across trophic levels. Here, effects of NAO index and SST are apparent in the breeding success and population growth rate of some seabird species, with no effect detected in plankton community structure, and only weak climate signals across this food web (Lauria et al., 2012).

More recently, the effects of heterogeneity of physical processes (such as patterns of ocean stratification and mixing) and habitat characteristics upon predator-prey interactions and foraging strategies have been explored (Waggitt et al., 2018). Clupeid prey (i.e. low-trophic level fish including herring (*Clupea harengus*) and sprat (*Sprattus sprattus*)) in the northern Celtic Sea occurred more densely, and were distributed at shallower depths, in mixed water than in areas of stratified water. Patterns of ocean mixing are predicted to be influenced by changes in ocean current resulting from climate change (Doney et al., 2012; Li et al., 2020) and at a smaller scale from marine renewable energy (MRE) installations (Cazenave et al., 2016; De Dominicis et al., 2017). Temporal and spatial heterogeneity of stratification patterns arising from changes in habitat and environmental conditions, however these changes occur, may subsequently affect the distribution of marine predators like seabirds and marine mammals. Climate- and habitat-mediated variability in the abundance, richness and distribution of prey (namely marine fishes) are therefore primary mechanisms connecting heterogeneity in the marine environment with changes to predator trophic and population ecology, particularly in seabirds, marine mammals and predatory fish species (Florko et al., 2021; García Molinos et al., 2016; Hazen et al., 2013; Poloczanska et al., 2016; Sadykova et al., 2020; Searle et al., 2022; Weimerskirch et al., 2003). Changes in these mechanisms are driven by both natural and anthropogenic processes, and investigation of the relative contribution of these is key to understanding the drivers of temporal variation in resource availability, and the potential effect upon marine predator population dynamics. Previous research has alluded to the role of environmental variability in the population dynamics of some marine predator species, including pinnipeds (Bowen et al., 2020; Weimerskirch et al., 2003), seabirds (Daunt and Mitchell, 2013) and cetaceans (MacLeod, 2009; Moore and Huntington, 2008), as well as potential for changes in the spatial distribution of these (Hazen et al., 2013; Moore et al., 2022; Russell et al., 2015). However, the precise mechanisms underpinning these predicted patterns of change is not fully understood, and additional research into the linkages between variability in environmental conditions and regional and population-level trends in abundance and distribution is required, particularly at regional scales.

Environmental heterogeneity and population modelling

Monitoring of free-living populations can be conducted by collection of a broad range of information on the individual animals observed (Powell and Gale, 2015). In particular, the number of individuals (i.e. abundance), changes in abundance between consecutive observations (survival), and fecundity and reproductive success can be used to infer whether a population size is stable, increasing or contracting, and make basic predictions of population size (Morris et al., 1999; Newman et al., 2014). When combined with similar observations from different locations, it is possible to begin exploring spatial, temporal and demographic variation within a population, or between separate populations (Newman et al., 2014).

The basic model of population dynamics for an open geometric population (i.e. a population subject to immigration and emigration, for which growth occurs in discrete reproductive periods) can be described by the simple equation:

$$N_{t+1} = N_t + (B_t + I_t) - (D_t + E_t)$$

where N_t is the population size at time point t, and N_{t+1} is the population size at the next time point. B and D represent the number of births and deaths, respectively, and I and E represent the number of individuals migrating into (immigration) and out of (emigration) the population. An increase in population size is determined by the number of births and the level of immigration within a given time period (e.g. one year), and a decrease in population size is determined by the number of deaths and the level of emigration within the same year. For a closed population, this would be described simply without the inclusion of immigration and emigration.

In the context of investigating the association between spatial and temporal heterogeneity in environmental conditions and marine predator population dynamics, the processes associated with births and deaths are of particular interest. For births we are interested in the number of offspring produced per year (fecundity or reproductive rate), and for deaths we are interested not necessarily in the number of deaths, but rather the number of individuals *not* dying that year (i.e. survival rate).

Estimates of (e.g. annual) survival rate can be used to make predictions about future population size and trajectory, and this is therefore an important parameter in modelling population dynamics (Oli and Dobson, 2003; Sæther and Bakke, 2000). When survival can be estimated for specific sections of a population, for instance by dividing animals according to age, size, or developmental stage, the accuracy of population models can be greatly improved, because more detailed information about the population becomes available (Robinson et al., 2014).

One commonly applied approach to modelling population dynamics is via the classical Leslie matrix (Leslie, 1945) wherein a square transition matrix can be parameterised using stage-specific survival rates, expressing the rate at which individuals in a population are expected to transition from one developmental stage to another (Lefkovitch, 1965). Matrix population models (MPMs) such as these can be used to calculate the growth rate of a (theoretically) stable population, to estimate the age or stage structure of the stable population, and to explore the relative influence of particular stages upon population trajectory (Caswell, 2001; de Kroon et al., 1986). Moreover, if individuals can be tracked throughout the monitoring programme, confidence in the accuracy of the data can increase, and models can become more informative (Clobert and Lebreton, 1995).

With improving access to greater computer processing power, and the associated development of increasingly sophisticated statistical tools, the number of studies exploring spatial and temporal variability in vital rates (that is, rates of survival, development, reproduction and fecundity) has increased. A number of studies have identified a high degree of temporal correlation between survival rates in spatially segregated populations of the same species (Harris et al., 2005; Jenouvrier et al., 2009; Kilduff et al., 2015; Schaub et al., 2005), although it has also been suggested that spatial (between-population) variation in survival rate may be greater than temporal variation (Dobson and Jouventin, 2010; Paradis et al., 2000). Appropriate management decisions require accurate information, and where decisions incorporate the outputs of statistical models, these depend upon accurate data (Abadi et al., 2010), so determining the relationship between variation in demographic rates at multiple locations across a species' range, and the potential for missing model parameters (i.e. the vital rates discussed above) to be estimated, is central to maximising the usefulness of predictions of population trajectories. When modelling population dynamics, in the absence of robust observational data, substituting specific information from ecologically similar species, or from different populations of the same species, may be preferable to having missing model parameters. However, the effect of such substitution upon the outcomes from population models is not well documented in the literature.

Environmental heterogeneity and resilience

The concept of resilience has a number of contemporary applications, and common to these is a response to disturbance. In its modern use, the term originated in the fields of engineering and the physical sciences, where the presumption is that a single, optimum equilibrium exists in a system (Gunderson, 2000), and that permanent departure from this is undesirable. As a generalised term, resilience may also be applied in the natural world, where it broadly describes the capacity of a system to withstand perturbations without suffering significant degradation (Holling, 1973). In this context resilience is often discussed at the ecosystem or landscape scale, but in such large and dynamic environments it is possible for multiple equilibria to exist (May, 1977; Scheffer et al., 2001; Solow et al., 2003; Sutherland, 1974). Indeed, the transition between equilibria in response to perturbation may be seen as evidence of a resilient ecosystem, able to function by means of compensatory dynamics (Fischer et al., 2001; Ives and Carpenter, 2007) or it may be seen as evidence that the system is not sufficiently resilient that an equilibrium can be maintained (Capdevila et al., 2021; Holling, 1973).

From a purely human, utilitarian point of view, the response to disturbance may be considered in terms of the services that an ecosystem provides (Hammerschlag et al., 2019; Mantua, 2015; Worm et al., 2006). When considered in the context of a single optimum equilibrium, a significant disturbance that alters the processes and structures of an ecosystem may be detrimental to whoever is benefiting from these services (Kilduff et al., 2015), and under these circumstances we may only be concerned with a situation where those services resume at previous levels.

‘Ecological resilience’ (Holling, 1973) acknowledges that multiple equilibria could exist for any given system and considers the nature and magnitude of the disturbance and the response of the system, rather than simply the restoration of an ‘optimum’ state. To make sense of the processes involved in a system’s response to perturbation, and to be able to quantify, predict and manage subsequent changes, it may be useful to consider different components of resilience separately. Resilience as a concept can be complicated by subtleties between definitions and between fields (Angeler and Allen, 2016; Baho et al., 2017; Holling, 1996; Myers-Smith et al., 2012), which can lead to confusion or overly complicated terminology. In general terms, and to avoid confusion, resilience has been considered in this thesis as two related processes: resistance and recovery.

Resistance has been described as a component of ecological resilience rather than being truly analogous to it (Angeler and Allen, 2016; Walker et al., 2004) and is useful in measuring and assessing a system’s capacity to tolerate disturbance. A system with high resistance would be more likely to remain in a stable state following perturbation. Recovery is concerned entirely with the return to pre-disturbance conditions (Angeler and Allen, 2016), and although this definition does not consider multiple equilibria, by simplifying the concept it is possible to measure and quantify a system’s response to disturbance. A system with a high recovery rate would be more likely to return to equilibrium quickly following perturbation.

Although the research focus upon resilience in ecological systems has increased substantially since the 1980s, at the demographic and population level the topic remains is underexplored (Capdevila et al., 2020).

Thesis aims

As discussed above, our understanding of marine predator ecology could be improved by exploration of the population ecology and resilience of marine predators and the relationship with temporal and spatial heterogeneity of environmental conditions. Moreover, investigation of the effect that decisions in data analysis methods may have upon our ability to identify and explain patterns of change in marine predator populations could improve the usefulness of these analyses in understanding the underlying processes.

This thesis aims to explore patterns of temporal and spatial heterogeneity in environmental conditions, biological processes, and data analysis methods, and the potential role of this heterogeneity in the population ecology and resilience of marine predator species. To investigate this, I seek to answer the following research questions:

1. Do marine predator population dynamics and the timing of reproductive cycles respond to temporal heterogeneity of environmental conditions? If so, are responses observed uniformly across spatial scales?
2. Is our understanding of marine predator population ecology affected by spatial heterogeneity in the methods of collection, management and analysis of monitoring data?
3. Where specific and consistent data gaps occur, can these gaps be filled by substitution of equivalent information from elsewhere in a species' geographic range?
4. Are marine predator population dynamics affected by temporal and spatial heterogeneity in rates of survival at different developmental stages? If so can this heterogeneity be observed and quantified at the population level?

I chose two species for which high-quality population monitoring data sets are available, and for which the time series would include observations made over multi-generational time scales for the species in question. The Atlantic grey seal (*Halichoerus grypus*) and the Manx shearwater (*Puffinus puffinus*) are examples of species for which suitable datasets exist, and both species occur as breeding populations in the same region.

To explore the potential relationship between marine predator population ecology and temporal and spatial heterogeneity in environmental conditions and data analysis methods, I have investigated broad-scale climate indices (NAO, AMO), meso-scale habitat conditions (SST), and fine-scale habitat characteristics (geographic location), as well as intrinsic biological processes (reproductive timing), demographic observations (vital rates) and the effect of aggregation and substitution of data in analytical approaches.

Study species

Atlantic grey seal (*Halichoerus grypus*)

The Atlantic grey seal (hereafter simply ‘grey seal’) is distributed in three population centres: the northwest Atlantic, the northeast Atlantic and the Baltic Sea, and approximately 35% of the global population occurs around British coasts (SCOS, 2022). The grey seal is protected in the UK under the Conservation of Seals Act, 1970 and as an Annex II species (EU Habitats Directive: 92/43/EEC) is a primary qualifying feature of three Special Areas of Conservation (SAC) in Wales: Lleyn Peninsula and the Sarns/Pen Llŷn a’r Sarnau, Cardigan Bay/Bae Ceredigion, and Pembrokeshire Marine/Sir Benfro Forol. The breeding population in Pembrokeshire comprises the largest in southwest Britain (Bull et al., 2017a), and together with the Calf of Man represents approximately 3.5% of the regional population (SCOS, 2022; Stone et al., 2013). The species data on which this thesis is based are largely pup census counts from which annual survival rates and daily cumulative births could be calculated. These data were collected as part of established monitoring programmes at five breeding colonies within the Irish Sea: the Calf of Man, Bardsey, Ramsey, Skomer, and the Marloes peninsula.

Manx shearwater (*Puffinus puffinus*)

The Manx shearwater is a long-lived, medium-sized (Brooke, 1978a) Procellariiform seabird which breeds at island colonies in the north and northeast Atlantic, making annual migrations to the east coast of South America (Guilford et al., 2009). Approximately 90% of the global population breeds around the UK and Ireland (Mitchell et al., 2004), where nests are made in burrows, and a single chick is raised. Although the population appears to be stable and healthy, the high concentration of breeding in few locations has led the Manx shearwater to be Amber-listed, and a European species of conservation concern (Robinson and Ratcliffe, 2010). The species data on which this thesis is based were collected as part of established productivity and adult survival monitoring programmes at five colonies, discussed below: the Isle of Rum, Lighthouse Island (in the Copeland group), Bardsey, Skomer and Skokholm.

Figure 1.1. Atlantic grey seal hauled out at the Calf of Man

Figure 1.2. A Manx shearwater emerges from its burrow on the Calf of Man

Study sites

The eight locations of this study are primarily islands in the Irish Sea (Figure 1.3), with the exception of Rum (an island in the Inner Hebrides, Scotland), and the Marloes peninsula (a headland connected to mainland Wales). Breeding colonies of the grey seal or Manx shearwater are known to occur at all eight sites, with each species being the subject of study at five sites. A summary of the locations of grey seal and Manx shearwater breeding colonies, and the Chapters where they appear, is presented in Table 1.1.

Table 1.1. Locations of grey seal and Manx shearwater breeding colonies, and the Chapters in this thesis in which they appear.

Study site	Chapter two:	Chapter three:	Chapter four:	Chapter five:
Isle of Rum			×	
Copeland Island			×	
Calf of Man	×	×		
Bardsey Island	×		×	
Ramsey Island	×	×		
Skomer Island	×	×	×	×
Marloes Peninsula	×	×		
Skokholm Island			×	

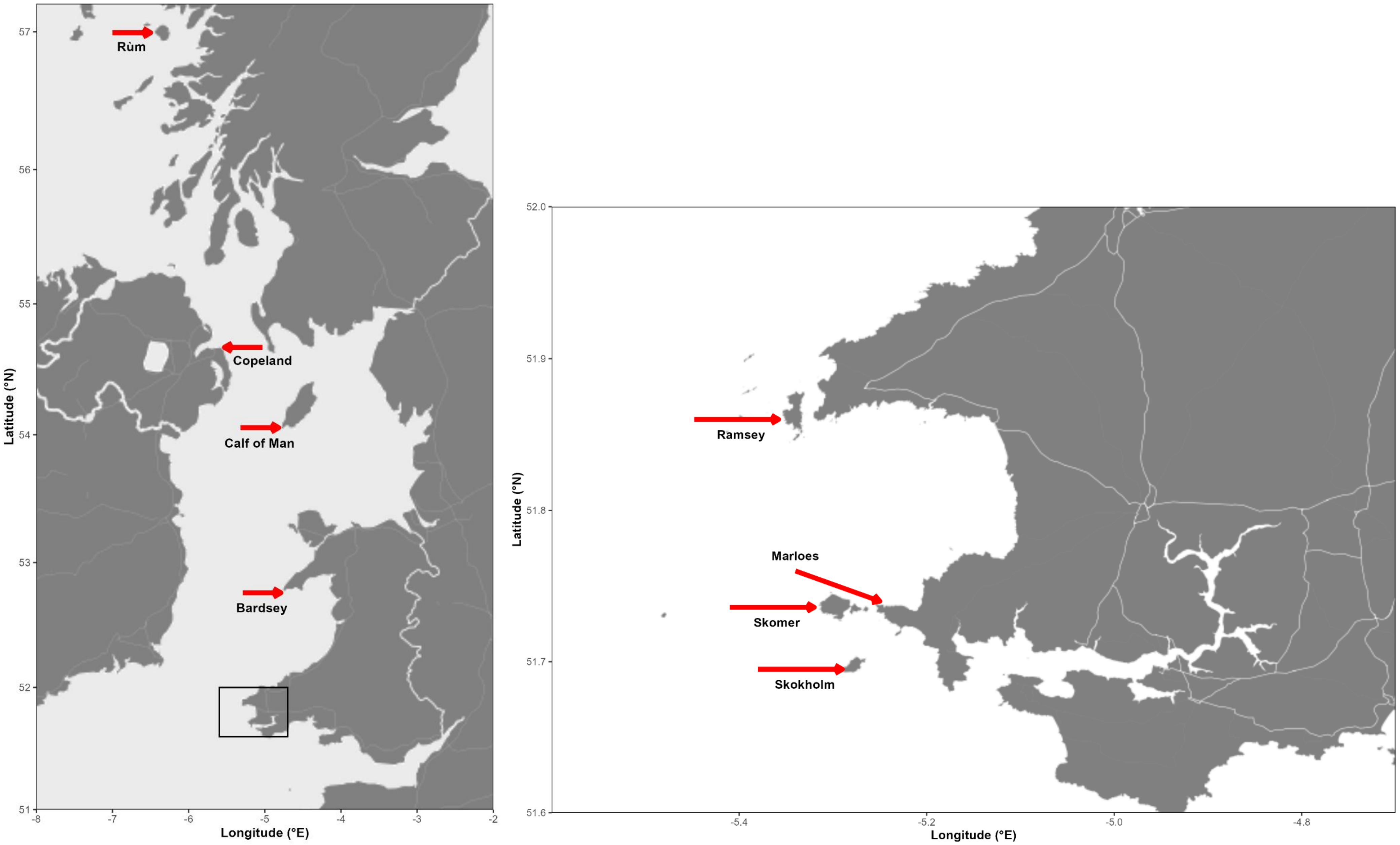

Figure 1.3. Location of study sites

Isle of Rum/Rùm (57.00°N, 6.21°W)

The Isle of Rum is a 10,500 ha island in the Inner Hebrides, with a permanent human settlement that is inhabited year-round, and a Manx shearwater colony estimated at approximately 120,000 (± 13,000) pairs (Newton et al., 2004). Despite the human settlement on the island, the Manx shearwater colony is largely undisturbed due to its remoteness, and covers approximately 150 ha in total (Murray et al., 2003). This is distributed across relatively discrete patches in the Cullin Hills, in contrast to the low-lying Copeland, Calf of Man, Skomer and Skokholm colonies. There are four sub-colonies on Rum where occupation is denser, alongside areas of more sparsely occupied habitat, which previous researchers have referred to as 'core' and 'fringe' sites, respectively (Murray et al., 2003). The core Hallival and Askival sub-colonies are largely connected by fringe habitat, such that they form one larger, roughly contiguous, area. The two other sub-colonies, Trollaval and Clough's Crag, are located separately on either side of the Hallival-Askival area, with Trollaval being surrounded by fringe habitat, and Clough's Crag appearing as just a finger of core habitat. There is a brown rat (*Rattus norvegicus*) population here, but its presence has not had the same deleterious effect as on the Calf of Man, and the population is monitored regularly to ensure it does not become a problem (Lambert et al., 2015).

Copeland Islands/Oileáin Chóplainn (54.67°N, 5.53°W)

The Copeland Islands are a group of three islands located in the North Channel off the coast of County Down, Northern Ireland. They comprise Lighthouse Island, Copeland Island and Mew Island, and the Copeland Bird Observatory is located on Lighthouse Island, where a Manx shearwater colony of approximately 3,000 breeding pairs is also present. Lighthouse island is approximately 40 ha (0.4 km^2) in size, and like other Manx shearwater colonies the presence of rabbits provides burrows in which birds can nest: it is estimated that more than half of the burrows on the island are inhabited by Manx shearwaters. Vegetation on Lighthouse Island is kept under control by a combination of rabbit grazing and human management, and the short sward benefits the Manx shearwater population by providing a suitable surface across which adults and fledglings are able to travel.

Calf of Man/Yn Cholloo (54.05°N, 4.82°W)

The Calf of Man is a small islet of approximately 250 ha to the south west of the main Isle of Man. Given its proximity to the main island, the Calf of Man has a history of cultivation, and a network of fields and field boundaries remains today. Much of the land adjacent to the coast is grassland, extensively covered by seasonal bracken growth. Further inland habitat includes swathes of heath, and a small area of wetland, as well as areas of grassland managed to provide foraging habitat for the breeding Chough (*Pyrrhocorax pyrrhocorax*) population. Historically, the shearwater population on the Calf of Man was significant enough for this to be the titular colony, but is now significantly smaller than the other colonies in this study, having declined significantly following the introduction of the brown rat (*Rattus norvegicus*) in the 17th century. The presence of shearwaters has been recorded in modern times (Mitchell et al., 2004), although breeding has only been observed more recently once a project to eradicate the rat population had commenced. Breeding burrows on the Calf of Man are largely confined to one area in the south of the island, although signs of breeding have been observed at other sites.

Bardsey Island/Ynys Enlli (52.76°N, 4.79°W)

Bardsey is a small island of approximately 178 ha located to the south-west of the Llŷn Peninsula in Gwynedd, North Wales, and located within the Lleyn Peninsula and the

Sarns/Pen Llŷn a'r Sarnau SAC. Much of the south of the island is relatively low-lying, with Mynydd Enlli at the north, with a summit at 167 m. Bardsey supports nationally important populations of Chough, Manx Shearwater and a number of scarce lichens, and its location at the east of the Irish Sea migration route makes it an important site for migrating birds. As well as the Bardsey Bird and Field Observatory, the island is inhabited for much of the year, and vegetation is managed by grazing of sheep and cattle.

Ramsey Island/Ynys Dewi (51.86°N, 5.34°W)

Ramsey Island (hereafter referred to simply as 'Ramsey') is approximately 260 ha in area, and is located approximately 1 km west of St. David's Head, at the northern point of St. Bride's Bay, Pembrokeshire. It is a National Nature Reserve (NNR) owned and managed by the Royal Society for the Protection of Birds (RSPB), and along with Skomer Island, the Marloes peninsula, and the north Pembrokeshire coast, accommodates the largest grey seal population in the southwest UK (Strong et al., 2006) and a recovering population of breeding Manx shearwaters (RSPB, 2022).

Skomer Island/Ynys Sgomer (51.74°N, 5.30°W)

Skomer is located less than 1 km to the western tip of the Marloes peninsula, and is the largest of a group of three low-lying islands off the coast of south Pembrokeshire (along with Skokholm and Middleholm). Skomer is the site of a grey seal pupping colony, and mothers haul out here to give birth and wean pups in sheltered bays and in caves around the island. The island is also occupied by the largest Manx shearwater colony, estimated at approximately 380,000 pairs in 2011 (Perrins et al., 2012) and almost 450,000 pairs in 2018 (Brown and Eagle, 2019a). The colony represents approximately half of the global breeding population and covers much of the 290 ha (2.9 km^2) island wherever the substrate allows for burrowing, although density varies across the island. Skomer is a Marine Nature Reserve (MNR) located within the Skomer Marine Conservation Zone (MCZ), the Pembrokeshire Marine/Sir Benfro Forol Special Area of Conservation (SAC), and along with Skokholm is part of the Skomer and Skokholm Special Protection Area (SPA).

Marloes Peninsula/Penrhyn Marloes (51.73°N, 5.24°W)

The Marloes peninsula is roughly delineated by a line drawn north from the small tidal islet of Gateholm at the western end of Marloes Sands. The coast of the Marloes peninsula (hereafter referred to simply as 'Marloes') is located within the Skomer MCZ, itself located within the Pembrokeshire Marine/Sir Benfro Forol Special Area of SAC, for which the grey seal is a primary qualifying feature (JNCC, 2015). Monitoring of grey seal pupping has been undertaken here since the 1980s, with regular, focussed monitoring commencing in 1992, across 21 sites facing either north, west, or south-west, with the latter aspect accounting for the majority of beaches.

Skokholm Island/Ynys Sgogwm (51.70°N, 5.28°W)

Skokholm is an island of approximately 106 ha (1.1 km^2) located around 4 km off the coast of Pembrokeshire and 3 km south of Skomer. Along with Skomer, Skokholm is a component of the Skomer and Skokholm SPA and the Pembrokeshire Marine/Sir Benfro Forol SAC. Like Lighthouse Island (Copeland), the Calf of Man and Bardsey, Skokholm is the site of a Bird Observatory, having received re-accreditation in 2014. Over 45,000 pairs of Manx shearwater breed on Skokholm, contributing to the significant local population alongside Skomer and Middleholm, and demographic monitoring of this population is conducted across three sites on the island. Given its proximity to Skomer and the Marloes peninsula, grey seals forage in the sea around Skokholm, although no records of pupping here are included in this thesis.

Thesis outline

This thesis explores patterns of spatial and temporal heterogeneity in environmental conditions in the Irish Sea, and the potential relationship with heterogeneity in demographic and population-level processes in breeding populations of grey seal and Manx shearwater. It then goes on to explore the consequences of heterogeneity in data analysis methods when interpreting the results of modelling population dynamics. Each chapter has been composed as a self-contained piece of research, with its own introduction, methods, and conclusion, and can be read independently alongside four **Appendices** which provide additional information for Chapters two to five.

In **Chapter one** I have given a contextual overview of heterogeneity in the marine environment. I introduce the themes of this thesis, in terms of exploring temporal and spatial heterogeneity in environmental conditions, and the potential ecological responses of free-living marine predator species to this heterogeneity. I then outline the principles of population ecology in the context of marine predator responses to environmental heterogeneity and provide an overview of approaches to modelling population dynamics. Finally, I discuss the concept of resilience as it relates to population-level responses to perturbation.

Chapter two uses a 29-year time series of grey seal monitoring at five locations in the Irish Sea to explore trends in the grey seal pupping season that have been observed between 1992 and 2020. I use daily-to-weekly observations of pup births to construct logistic growth curves for each year at each location, and from these I estimate the length, mid-point and maximum output (pup count) of each pupping season. I then investigate temporal and spatial trends in these parameters in the context of local environmental conditions and intrinsic characteristics as explanatory covariates. I found that the length of pupping seasons and the annual reproductive output from the monitored pupping sites were not affected by SST or by the timing of the previous pupping season. The timing of the pupping season (represented by the temporal mid-point of cumulative recorded pup births) was found to be affected by changes in SST and by the timing of previous pupping seasons, although effects and effect sizes were not consistent across breeding colonies.

Following on from the timing of the grey seal pupping season, **Chapter three** investigates spatial and temporal heterogeneity in grey seal pup survival and the potential effect of observations at the population level. This chapter builds upon a previous study by Engbo et al. (2020) and uses MPMs to look at the effect of spatial and temporal data aggregation of pup survival estimates upon estimates of population growth rate and subsequent simulation of population trajectories. This includes an additional fourth colony at the Calf of Man, as well as additional years of observation from sites at Skomer (24 additional years) and the Marloes peninsula (three additional years), and also seeks to address potential effects of density-dependence upon site-specific pup survival rates. Results indicated that grey seal pup survival rates exhibit spatial and temporal heterogeneity within and between the three main colonies in SW Wales (Skomer, Marloes and Ramsey), while pups at the Calf of Man colony exhibited higher survival probability, and greater consistency. Temporal heterogeneity of within-colony survival estimates was greater than that observed between colonies, and some evidence of density dependency was evident at the Ramsey colony, where subsequent research would be encouraged.

Chapter four extends the approach of the previous chapter by applying similar MPM methods to a 35-year time series of Manx shearwater survival in the Irish Sea and Inner Hebrides. This time, estimates of annual survival rates are available for fledglings in their first year of life (as per grey seal pups in **Chapter three**) at five breeding colonies, and for adult birds at two of these colonies. This provided me the opportunity to parameterise MPMs with variable survival estimates from two developmental stages (compared with one stage previously), and allowed me to investigate the effect of using substituted data for colonies where adult survival rates are not monitored. Results suggested that, although vital rates may be substituted from elsewhere in a species' range, local variability in survival rates can skew the outputs of MPMs, especially when substituting parameters for influential stages.

In **Chapter five** I continue the use of MPMs to investigate the population-level response to perturbations in stage-specific survival rates for the Manx shearwater. I use estimates of vital rates from the whole Manx shearwater time series at the Skomer breeding colony to construct MPMs for each year of monitoring. From here I simulate perturbations to stage-specific survival rates for fledgling, juvenile and adult birds by iteratively reducing rates by a given percentage. I use the resulting set of matrices to produce indices of resilience for these perturbation scenarios and explore the consequences to population dynamics. Results of this investigation indicated that perturbation to stage-specific survival rates in the Manx shearwater can elicit measurable population-level responses to disturbance. Responses were not consistent amongst resilience indices, however, as their magnitude and direction varied depending on which stage-specific survival rate was perturbed.

Finally, **Chapter six** summarises the findings of Chapters two to five in the context of the spatial and temporal heterogeneity in environmental conditions and biological processes discussed in **Chapter one**, and discusses heterogeneity in the approach to the planning, collection and analysis of data, including those on which this thesis was based, before identifying some of the subsequent limitations and discussing remaining knowledge gaps and avenues for future research.

In addition, in **Appendix five** I have included a condensed version of a manuscript that explores the spatial and trophic ecology of the Manx shearwater. The initial direction of my PhD project was to use stable isotope analysis to investigate patterns of migration from three colonies along a 600 km latitudinal gradient. I also planned to explore differences in chick provisioning and self-maintenance between years and between colonies, and relate potential trends to environmental drivers. I completed one field season before the COVID-19 pandemic began. By May 2020, a month before I was due to return to fieldwork, it became clear that travel restrictions would prevent me from continuing, and that I would need to begin exploring alternative avenues for research. My collaborators on Skomer, the Calf of Man and Rum very kindly agreed to continue collecting samples on my behalf, and although I was no longer able to complete my project as I had originally intended, it has enabled me to develop a small pilot study on which future research might be continued.

Collaborator contributions

Chapter two was conceived and designed by me, in consultation with Dr. James C. Bull (JCB). The data on which this chapter is based were provided to JCB by Natural Resources Wales (NRW), the Wildlife Trust of South and West Wales (WTSWW), the Royal Society for the Protection of Birds (RSPB), and Manx Wildlife Trust (MWT). JCB provided consultation on statistical approaches to data analysis, and provided feedback on draft manuscripts.

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Chapter four was conceived and designed by me, in consultation with JCB. Data were obtained from publicly accessible sources, with permission granted from NRW, NatureScot (formerly Scottish Natural Heritage), WTSWW, Matt J. Wood (MJW) of the University of Gloucestershire, Bob Swann (BS) and access to additional data from Bardsey Island was provided by Steve Stansfield (SS) of Bardsey Bird and Field Observatory (BBFO). Additional information on monitoring procedures was also provided by SS. JCB provided consultation on statistical approaches to data analysis, and provided feedback on draft manuscripts.

Chapter five was conceived and designed by me, in consultation with JCB. Data were obtained from publicly accessible sources, with permission granted from NRW, NatureScot, WTSWW, MJW, BS and access to additional data from Bardsey Island was provided by SS of BBFO. JCB provided consultation on statistical approaches to data analysis, and provided feedback on draft manuscripts.

Chapter two:

Environmental drivers of grey seal pupping phenology in the Irish Sea

Abstract

The causes and consequences of phenological shifts associated with global climate change have become an area of particular research focus across multiple ecosystems and regions. For ecological communities in which top-down processes have a strong regulating effect, climate-mediated shifts in the distribution and dynamics of predators are likely to have pronounced effects on species assemblages and ecosystem function. However, environmental drivers of these shifts at the fine and broad scale, and interactions with intrinsic processes are not well understood. I therefore aimed to explain the potential relationship between local and broad-scale environmental heterogeneity and the population dynamics of marine top predators.

The grey seal is a charismatic and well-studied example of a marine apex predator species and an important indicator of the wider effects of climate change. Using multi-decade time series from five major pupping sites in the Irish Sea, I explore how changes in the timing and progression of the grey seal pupping season are dependent on climatic drivers. I use a logistic population growth model to estimate parameters of the timing, duration and productivity of annual pupping seasons. I then use these parameters as response variables in generalised additive models (GAMs) to test the hypothesis that local and regional scale environmental processes are drivers of change in the timing and progression of the grey seal pupping season. Finally I investigate whether patterns of between-colony pupping phenology are replicated at all locations, and explore patterns of spatial heterogeneity in changes to the timing of the pupping season.

Seasonal sea surface temperature (SST) was found to influence pupping season timing at two locations, while intrinsic processes were drivers of phenology at a four of the sites. No association was identified between temporal heterogeneity in environmental conditions and

the duration or total reproductive output of the pupping season at any location. Regional indices of climate, the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO), were not found to influence any of the pupping season parameters.

Introduction

Changes in phenology – the cyclic timing of life-history events such as breeding – can have consequences from individual to population and community level, affecting connectivity, rates of reproduction and survival, and ecosystem function (Carson et al., 2010; Miller-Rushing et al., 2010; Thackeray et al., 2016). Phenological change has been attributed to a number of drivers, including global climate change, (Chambers et al., 2014; Poloczanska et al., 2016; Thackeray et al., 2016, although see Visser and Both, 2005 and Burthe et al., 2012 on the challenge of quantifying this) population density (Votier et al., 2009), resource availability and individual physiological status (Maniscalco and Parker, 2018), and interactions between these processes (Rotella et al., 2016). The ways in which species respond to environmental changes are complex and can vary considerably, and will largely be determined by a species' ecological and physiological characteristics (Poloczanska et al., 2016). As well as temporal shifts of life-history events, responses may also include changes to the duration of these events, for instance the lengthening or shortening of the breeding season (Halupka and Halupka, 2017; Møller et al., 2010).

Much has been discussed on the proximal consequences of phenological change across ecosystems and taxa (Anderson et al., 2013; Beard et al., 2019; Sydeman et al., 2015; Thackeray et al., 2016), which include disruption to predator-prey, plant-consumer and plant-pollinator relationships, and shifts in the timing of migration and breeding. Identifying and measuring longer-term consequences, and disentangling ecological and evolutionary processes, present a greater challenge (Cleland et al., 2007; Ji et al., 2010; Visser and Both, 2005).

In marine mammals, changes in breeding phenology have been proposed as evidence of system shifts in the Indian, Southern, and Atlantic Oceans (Cordes and Thompson, 2013; Weimerskirch et al., 2003). These changes may reflect commonality amongst taxa for tracking climate-mediated patterns of prey abundance and optimal environmental conditions: pinnipeds in particular tend to exhibit a high degree of synchrony in the timing of parturition (Atkinson, 1997). Alternatively, population-level shifts in demographic structure associated with climate change have been suggested as a regional driver of variation in breeding phenology (Bull et al., 2021). Births occurring after the peak pupping season (which will vary according to region) have been associated with reduced mass at weaning, and lower rates of juvenile survival (Bowen et al., 2015; Maniscalco and Parker, 2018). In long-lived iteroparous species that raise one offspring annually (i.e. classical K-selected species), a short-term reduction in productivity alone is unlikely to have immediate population-level effects, but protracted reductions in productivity may influence rates of recruitment.

Timing of birth can be broadly dictated by the timing of copulation since the length of gestation often does not vary a great deal. In some species, there may be variability in the period between copulation and birth, either via sperm storage (Holt and Fazeli, 2016) or embryonic diapause (Ptak et al., 2012). The latter of these involves a delay in implantation of the fertilised egg into the uterine wall and is observed in most seal species (Atkinson, 1997), likely being the mechanism by which temporal plasticity in breeding is achieved. While broad-scale temperature change has been linked to changes in pupping phenology, the exact physiological mechanism for this is unclear (Renfree and Fenelon, 2017), and the magnitude and characteristics of change across spatial scales and between populations remains under-investigated.

The grey seal is a large member of the Phocid family, and occurs in three population centres across the north Atlantic (SCOS, 2022). The largest colonies in the UK are concentrated in Scotland and the English North Sea, with a smaller number of colonies located in the Irish Sea. In the latter, grey seal population monitoring has been conducted at sites in Wales, Ireland, and the Isle of Man, in some cases extending back to the early 1990s. Productivity has appeared stable in these colonies until around 2010 when annual pup estimates began to rise dramatically in two Welsh colonies (Bull et al., 2017a, 2017b; Morgan et al., 2018), with more modest increases observed at two more.

Despite a general understanding of the changes to breeding patterns that are occurring at Irish Sea grey seal colonies, a detailed exploration of the direction and magnitude of change is required to contextualise patterns between colonies and through time. While changes to the timing and length of the grey seal pupping season and to annual rates of pup production, have been observed in Irish Sea colonies, local and broad-scale environmental factors as a driver of change, and the time scales over which changes may occur, have yet to be investigated in detail. The Irish Sea population extends towards the southern end of this species' range (SCOS, 2022), making this region ideal as an early indicator of responses to environmental change. The effect of intrinsic factors such as local population density and the timing of previous pupping seasons also warrants consideration. The degree of movement between colonies and the potential for metapopulation dynamics within the Irish Sea is not well understood, and the responses to environmental change at each of these colonies requires investigation to understand how local patterns fit into their regional context. To understand the role of climate in seal pupping phenology across the Irish Sea, the aims of this study are to:

1. Quantify patterns in site-specific grey seal productivity and the timing and duration of the pupping season to identify potential for temporal shifts;
2. Test the hypotheses that a) potential changes in the timing of the pupping season are connected with variation in local environmental conditions, and b) intrinsic factors such as productivity (i.e. population density) and timing of previous pupping seasons influence the timing of subsequent seasons;
3. Investigate multi-colony patterns in grey seal pupping phenology, to identify whether these patterns are replicated at all pupping colonies;
4. Explore the ecological consequences of potential heterogeneity in between-site changes to pupping phenology.

Methods

Data collection

Data for this study were collected between 1992 and 2018 (actual monitoring period varies between sites) at five known pupping sites in the Irish Sea. In Pembrokeshire, the Marloes peninsula, Skomer Island and Ramsey Island colonies are located within approximately 15 km of each other, while Bardsey Island (Gwynedd), and the Calf of Man (Isle of Man) exist as discrete colonies. These three colony clusters are distributed almost equidistantly from north to south (Calf of Man, Bardsey, Pembrokeshire), offering the opportunity to explore the additional influence of latitude. Monitoring protocols varied slightly between colony (detailed below), but at all sites the number of new pups encountered at each survey was recorded, allowing a cumulative pup count to be calculated through the season.

Calf of Man

Pup counts were conducted almost daily by volunteers during the month of October between 2009 – 2018, with additional ad-hoc observations made by island Wardens before and after the arrival of volunteers. Observations as part of formal monitoring were made on land from 14 predefined vantage points, with varying elevations, around the island as part of ongoing monitoring of seal productivity, behaviour and identification of individual adults (Andrew et al., 2019; Stone et al., 2013).

Bardsey Island

Monitoring on Bardsey follows a less structured protocol than at other colonies, and has varied between years. From 2010 to 2015 a weekly land-based count was conducted by a dedicated surveyor, whereas before and after this, maximum monthly counts were recorded by wardens as they went about their other duties, so no formal protocol was followed. Additional observations were recorded from the sea throughout the year, and this dataset includes the years 2009 – 2017.

Ramsey Island

Along with seals associated with nearby SMCZ, Ramsey Island contributes towards the Pembrokeshire grey seal population, which is the largest in the Irish Sea and southwest UK (Stringell et al., 2014). Population monitoring in this study occurred during the 2008-2018 seasons, according to the protocol described in (Strong et al., 2006) and was conducted between July and the following January.

Skomer and Marloes

The island of Skomer and the nearby Marloes peninsula provide sheltered beaches and caves for adult female grey seals to give birth and nurse pups until weaning. Beaches on Skomer were surveyed from cliff tops every 1-2 days between August and November, and caves were accessed when conditions allowed. Surveying on the Marloes peninsula was conducted along a predefined route, every 2-3 days, between August and December. For both sites a standardised protocol was followed (as detailed in Lock *et al*., 2017 and Büche and Stubbings, 2018). To identify whether seals breeding at Skomer and Marloes exhibit similar patterns of phenology (i.e. within the SMCZ), pup count estimates here were analysed as discrete data sets.

Environmental data

To test the hypothesis that local environmental change influences the timing of parturition, the timing of the pupping season was investigated in the context of environmental data obtained from publicly accessible repositories, over a monthly, seasonal (three-month) and annual scales. Local sea surface temperatures (SST) were obtained from the UK Met Office HadISST1 dataset (Met Office, 2022; Rayner et al., 2003) and processing of environmental data is discussed below.

Data processing

Grey seal productivity data

Initial analysis of cumulative pup count data was conducted using a non-linear mixed-effects model, to allow survey year to be modelled as a random effect. Here, pup count was included as the response variable in a self-starting logistic model with cumulative days as a fixed predictor, and temporal auto-correlation assumed:

daily pup count ~ cumulative day + survey year

The self-starting method allowed the initial values required by the non-linear model to be calculated automatically, simplifying the process. Logistic curves produced from this model (see below) were then plotted against cumulative pup counts for each survey year . This analysis and comparison was repeated for each colony, and three parameters from the modelled curves were used as proxies for pupping season features:

- Curve asymptote (the maximum value on the curve for the given data), was used to model total pup count for each season;

- Point of inflection (the point on the logistic curve at which the upward trajectory switches from accelerating to decelerating) was assumed to model the mid-point of the pupping season;
- Scaling parameter (the gradient of the logistic growth phase) was used as a proxy for the length of the pupping season.

Season mid-point (expressed as days since July 1st) rather than the first instance of a pup being observed was used as the measure of pupping season timing, as this is less prone to error. The true first pup of the season may be missed, either because monitoring was not yet underway, wasn't conducted that day, or because the pupping occurred out of sight of monitoring patrols. Similarly, using the median point in the season reduces the influence of outliers, for example if one pup was born much earlier than the rest of the cohort. Modelled pup count (asymptote), pupping season mid-point (point of inflection), and pupping season length (scaling parameter) were then visualised by fitting to generalised additive models, with year as a smoothing term. In the context of environmental change and seal pupping phenology, the parameter of greatest interest here is the mid-point of the pupping season, since this can be used to describe the timing of the pupping season.

Environmental data

All environmental data were obtained on a monthly scale, and used to calculate broader seasonal periods, since the observed trends occur over the course of years, rather than months. Data were divided into Winter (Dec, Jan, Feb), Spring (Mar, Apr, May), Summer (Jun, Jul, Aug) and Autumn (Sep, Oct, Nov) of the same year as the pupping season, and Autumn (Sep, Oct, Nov) of the previous year.

SST data (Rayner et al., 2003) are divided into 1° squares. Data in the nearest squares to the study colonies were tested for correlation (Pearson's) to ensure that season mid-point in each colony could be analysed against the same SST data, to allow for direct comparison between colonies. The nearest square to each of the colonies is as follows:

- Calf of Man: 4.5°W, 54.5°N
- Bardsey: 4.5°W, 52.5°N
- Ramsey: 5.5°W, 51.5°N
- Skomer: 5.5°W, 51.5°N
- Marloes: 5.5°W, 51.5°N

Data analysis

Relative to other colonies, which follow a consistent approach to monitoring during a discrete field season, monitoring of seal productivity at Bardsey is less structured, and because the island is used throughout the year, observations may be recorded at any time. This has resulted in a data set with inherent biases, which has been included for completeness and context, but which should be regarded with caution. Observations from the Bardsey colony are therefore not included in statistical analyses or interpretation of wider patterns.

The Calf of Man, Ramsey, Skomer and Marloes colonies were modelled separately to maximise the analysis period for each, and generalised additive models (GAM) based on a gamma error distribution with log link function were used. Pupping season mid-point ('mid') at each location ('colony') was modelled against population density, timing of the previous pupping season, and SST across seasonal (three-month) and annual (12-month) divisions. Model fit was assessed by comparison of AIC values, and the formula of the best fitting model structure was as follows:

$$mid_{t0} \sim pup\ count_{t0} + autumn\ SST_{t0} + winter\ SST_{t-1} + mid_{t-1}$$

Where mid_{t0} is the mid-point of the ‘current’ pupping season, $pup\ count_{t0}$ is the estimated pup production taken from the logistic curve fitting (see above: ‘*Data processing: Grey seal productivity data*’), $autumn\ SST_{t0}$ is the mean SST measured across September, October and November of the current year, $winter\ SST_{t-1}$ is the mean SST measured across the preceding December, January and February, and mid_{t-1} is the mid-point of the preceding pupping season. Since the pupping season in the Irish and Celtic Seas occurs between late summer and late autumn, the mid-point of the season is expressed as days after July 1.

All data processing and analysis was undertaken in R statistical software 4.1.3 (R Core Team, 2022). Initial analysis via non-linear mixed effects models was conducted using the ‘nlme’ package (Pinheiro et al., 2020) and GAM analyses were conducted using the ‘mgcv’ package (Wood, 2011).

Results

Logistic model fitting

For all colonies, births of pups recorded between July and August of each survey year provided the best fit between observed counts and modelled curves. Figure 2.1 provides an example of this fit. The full set of observed cumulative pup counts overlaid onto modelled logistic curves is presented for all years and all colonies in **Appendix one**.

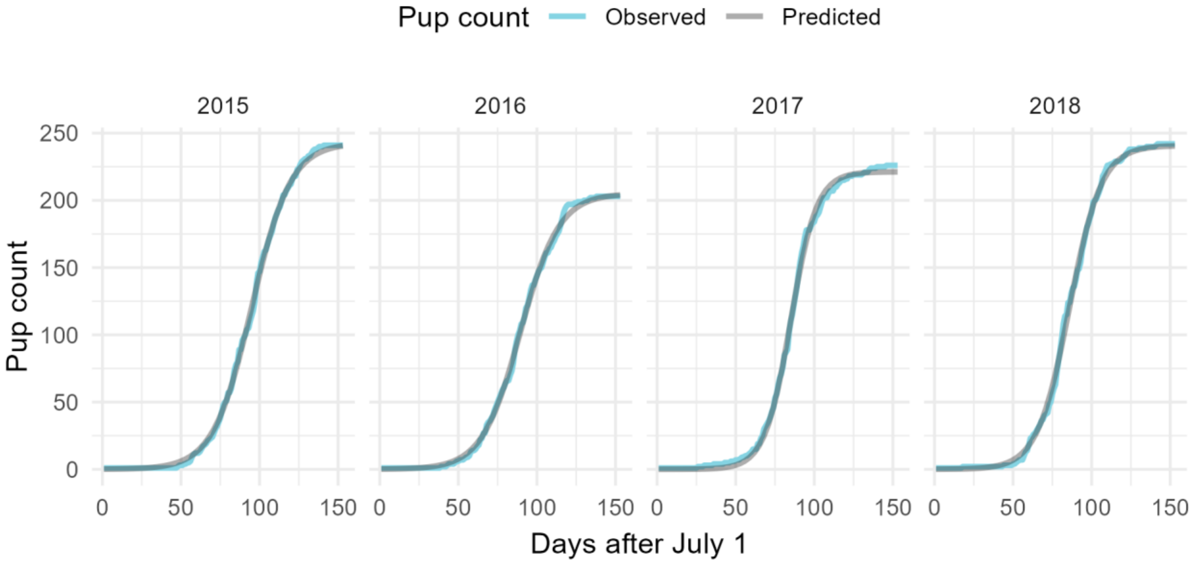


Figure 2.1. Illustrative sample of observed pup counts (blue line) and modelled logistic curves (grey lines) from the most recent four surveys (2015-2018) conducted at the Skomer colony in the study period (1992-2018).Parameter estimates

Although there are clear differences in modelled logistic parameter estimates between pupping colonies, some similarity in the patterns of total estimated pup count, season length, and season mid-point can be seen across colonies (Figure 2.2). Estimated pup count appears to be stable at most colonies, while season length and pupping season mid-point appear to fluctuate at most colonies. Given the additional records available from the Skomer and Marloes colonies (27 years compared to between 10 and 14 years at the other three colonies), patterns here are easier to detect than at other colonies.

Annual total pup count

In the Skomer and Marloes colonies productivity appears to have increased steadily across the duration of the monitoring period, particularly at Marloes, where the trend has been broadly positive since the mid-1990s (Figure 2.2**Error! Reference source not found.**a). Following a clear but short-term decline at the start of the monitoring period at the Ramsey colony, productivity here appears to have increased rapidly, from an estimate of 140 pups in 2008 to almost 600 pups in 2018. The increase has been slower, but more consistent at the Calf of Man colony, but appear to be relatively static on Bardsey Island.

Pupping season length

Pupping season length appears to fluctuate in the Pembrokeshire and Bardsey colonies, with a peak in around 2010, (Figure 2.2b) but little synchronicity despite the Pembrokeshire colonies being located so close to each other. The Calf of Man colony shows a relatively linear trend of shortening over the recorded period, but with a much lower variation when compared to the other colonies (see narrow 95% CI ribbon). Estimates of pupping season length from Bardsey show a high degree of variability between years, but broadly exhibit a similar trend to the other colonies over the same time period.

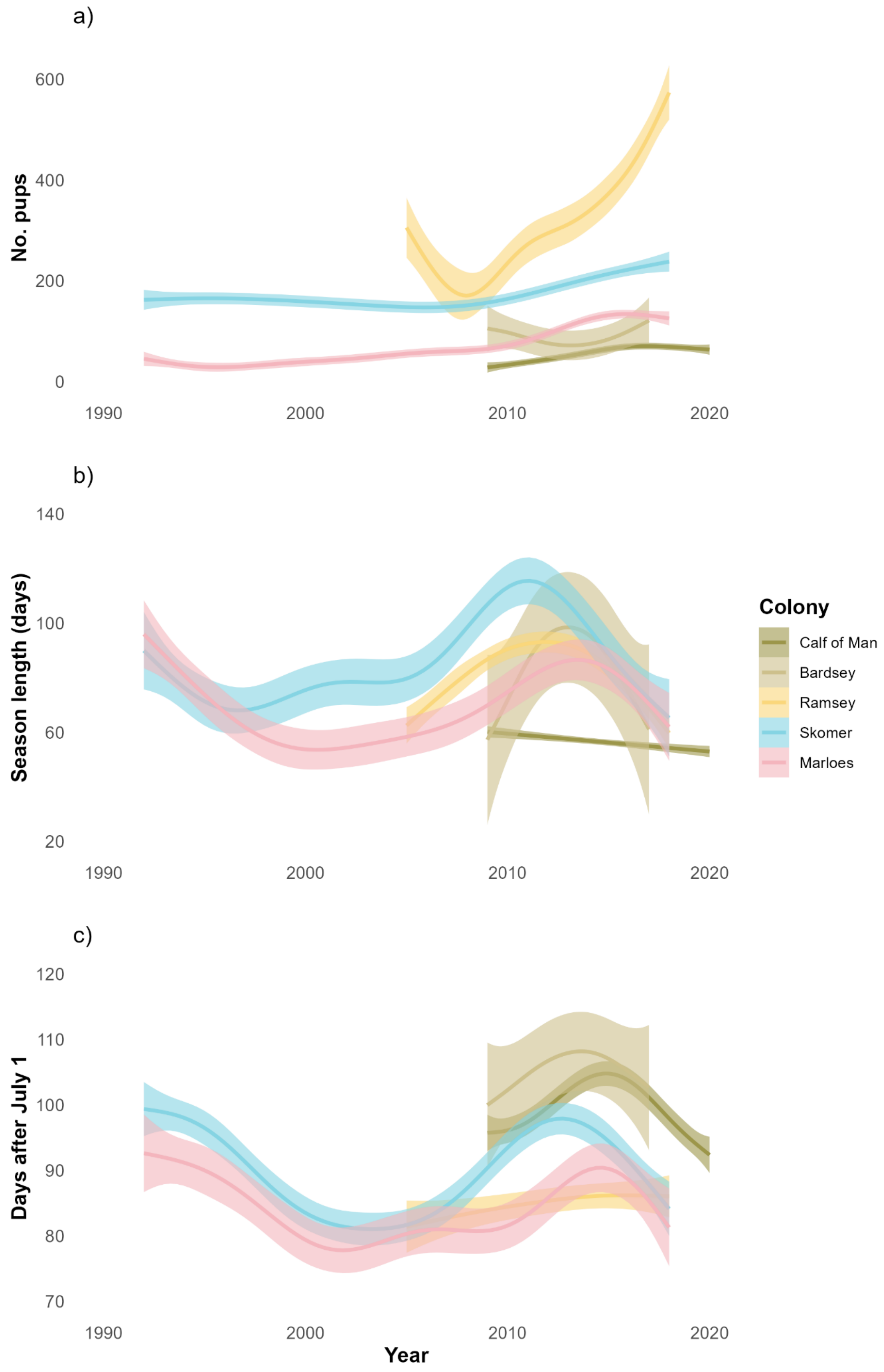


Figure 2.2. GAM-fitted temporal trends in a) annual estimated pup count, b) pupping season length and c) pupping season mid-point, estimated from observations at the Calf of Man, Bardsey, Ramsey, Skomer and Marloes grey seal pupping colonies between 1992 and 2020. Shaded ribbons indicate 95% CIs.

Pupping season midpoint

Pupping season midpoint appears to follow very similar trends in all colonies where datasets are concurrent, but peaks in the time series only coincide between Marloes and Bardsey (Figure 2.2c). These patterns are broadly consistent with published results. Mean season mid-point was 14.8 days earlier at the most southerly colony (Marloes: 23rd September) compared to the most northerly colony (Calf of Man: 8th October), with a mean within-colony range of 17.6 days (Table 2.1).

The greatest range of pupping season mid-points (i.e. earliest recorded versus latest recorded) was between Marloes (13th September) and Bardsey (26th October): a difference of 43.2 days. Given that these estimates are 13 years apart, and from colonies where ad-hoc observations are recorded, this range should be interpreted with caution.

Table 2.1. Grey seal monitoring periods, and movement of the pupping season midpoint (expressed as days after July 1), for the five colonies studied.

Site	Latitude	Monitoring period (no. years)	Earliest (year)	Latest (year)	Mean	Range
Calf of Man	54.05° N	2009 – 2018 (10)	92.5 (2020)	105.71 (2016)	99.16	13.03
Bardsey	52.76° N	2009 – 2017 (9)	96.4 (2010)	117.52 (2014)	104.92	21.15
Ramsey	51.86° N	2005, 2008 – 2018 (12)	80.20 (2005)	89.08 (2016)	84.97	8.90
Skomer	51.74° N	1992 – 2018 (27)	78.58 (2004)	100.56 (2013)	89.90	21.98
Marloes	51.74° N	1992 – 2018 (27)	74.33 (2001)	97.41 (2014)	84.32	23.09

Environmental drivers of pupping season phenology

SST in the grid-squares corresponding to the Pembrokeshire colonies (Skomer, Marloes and Ramsey) and the Calf of Man were found to be highly positively correlated ($r = 0.988$, $t = 115.52$, d.f. = 322, $p < 0.001$) so analyses for all colonies was based upon SST data from the grid square corresponding to the Pembrokeshire colonies (5.5°W, 51.5°N). Although observations of seal pupping on Bardsey were not consistent enough to be included in formal analysis, SST in the Bardsey grid-square was compared with others for completeness, and was found to be similarly highly-correlated (Calf of Man:Bardsey $r = 0.996$, $t = 204.21$; Pembrokeshire:Bardsey $r = 0.997$, $t = 219.4$. In all cases d.f. = 322 and $p < 0.001$).

Results of the GAM analysis of pupping season mid-point against estimated pup count, autumn and winter SST and the mid-point of the previous pupping season were not consistent. No single variable had a significant explanatory effect at all colonies, although the mid-point of the ‘previous’ season did have a significant effect upon the mid-point of the ‘current’ season at three of the four colonies.

At the Calf of Man, the timing of preceding pupping season appears to influence the timing of the subsequent pupping season ($F = 5.446$, $p = 0.012$) although uncertainty remained ($r^2 = 0.51$). Likewise, a great deal of the variability in the timing of pupping at the Ramsey colony was unexplained ($r^2 = 0.44$) but SST during the pupping season (i.e. autumn) did have an effect ($F = 3.467$, $p = 0.023$). At the Skomer colony, SST during the preceding winter ($F = 3.262$, $p = 0.011$) and the previous pupping season mid-point ($F = 27.11$, $p < 0.001$) had the greatest effect upon timing of pupping ($r^2 = 0.73$), and likewise at Marloes previous pupping season mid-point ($F = 2.513$, $p = 0.010$) and estimated pup count ($F = 2.164$, $p = 0.037$) had the largest effect upon the mid-point of the pupping season ($r^2 = 0.46$).

The summary output of the colony-specific GAMS is presented in Table 2.2, and the modelled parameters for each colony are illustrated in Figure 2.3.

Table 2.2. GAM summary of relationship between pupping season mid-point and environmental and intrinsic variables.

Colony	Parameter	edf	Ref df	F	p	r^2	Deviance explained (%)
Calf of Man	Pup count	<0.001	2	<0.001	0.410	0.51	58.9
	Autumn SST	<0.001	2	<0.001	0.920		
	Winter SST	<0.001	2	<0.001	0.703		
	Previous mid-point	**1.406**	**2**	**5.446**	**0.012**		
Ramsey	Pup count	<0.001	2	<0.001	0.927	0.44	51.0
	Autumn SST	**0.878**	**2**	**3.467**	**0.023**		
	Winter SST	0.219	2	0.137	0.295		
	Previous mid-point	<0.001	2	<0.001	0.953		
Skomer	Pup count	<0.001	2	<0.001	0.872	0.73	74.8
	Autumn SST	<0.001	2	<0.001	0.420		
	Winter SST	**0.862**	**2**	**3.262**	**0.011**		
	Previous mid-point	**1.290**	**2**	**27.110**	**<0.001**		
Marloes	**Pup count**	**1.191**	**2**	**2.164**	**0.037**	0.46	50.5
	Autumn SST	0.509	2	0.485	0.176		
	Winter SST	<0.001	2	<0.001	0.788		
	Previous mid-point	**0.746**	**2**	**2.513**	**0.010**		

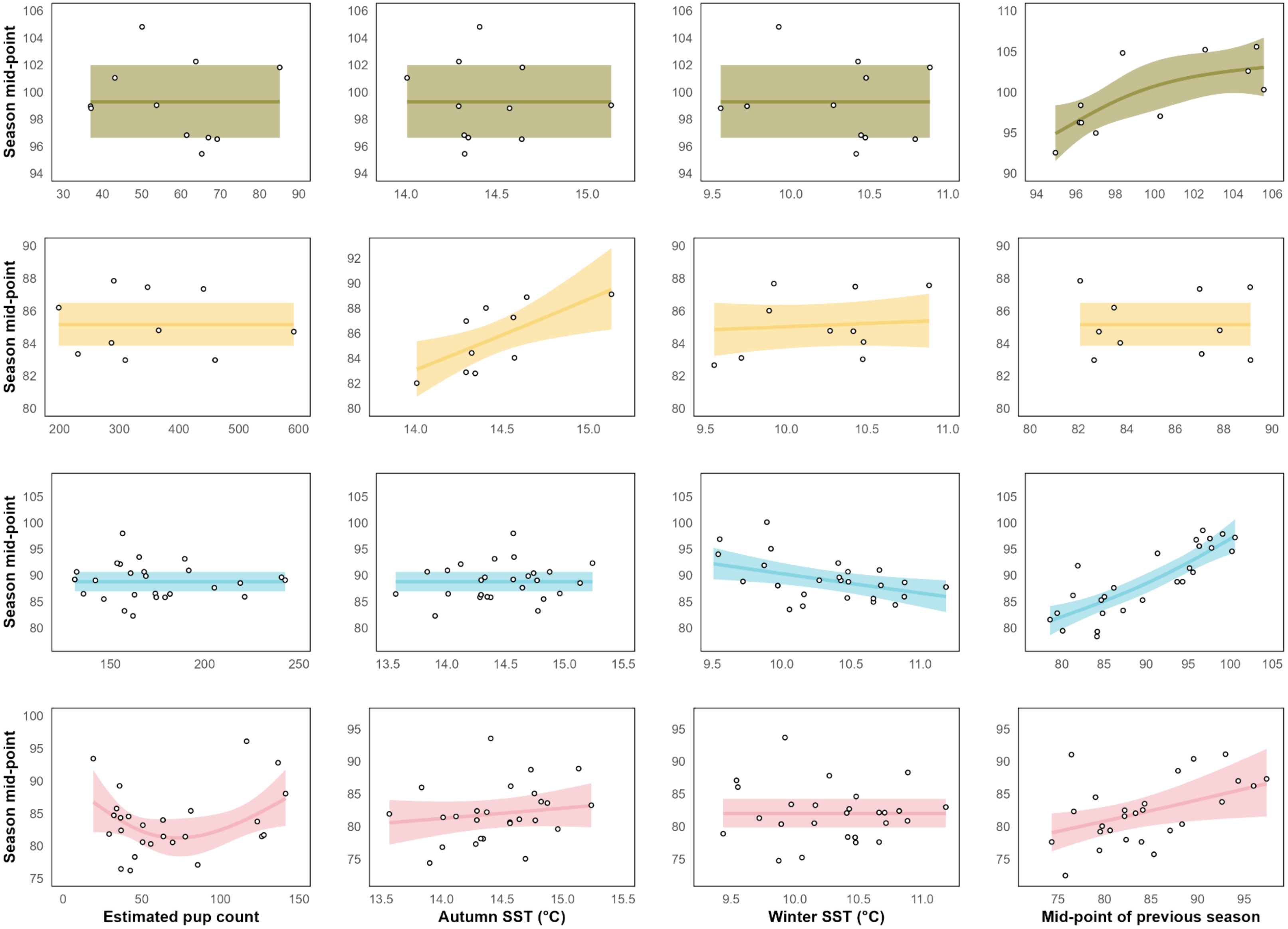


Figure 2.3. Relationships between the mid-point of the grey seal pupping season (measured as days after July 1) and estimated pup count, autumn and winter SST, and mid-point of the previous year's pupping season, for (from top to bottom) the Calf of Man, Ramsey, Skomer and Marloes colonies.

Discussion

Links between environmental change and phenological change have been inferred across species and systems (Chmura et al., 2019; Halupka and Halupka, 2017; McLean et al., 2016; Weimerskirch et al., 2003), but this connection is not universal or predictable, with some species/systems displaying resistance to change, inconsistent responses, or weak evidence of a direct link (Atkinson et al., 2015; Keogan et al., 2018; Orgeret et al., 2022). The results of this study found that, despite a similar magnitude and direction of environmental variability across the Irish Sea, phenological responses to these changes are not uniform between colonies, even over a relatively small spatial scale, and regardless of latitude. Similar patterns of change in season length at the Pembrokeshire colonies may reflect their proximity to each other. The timing of the peaks and the actual length of the pupping season at these colonies were not aligned, however, which suggests that the processes influencing the length of the pupping season are not shared between colonies, despite their geographical proximity. The timing of grey seal pupping in the UK is understood to proceed in a clockwise direction, beginning at the southwest of the country (SCOS, 2022), and results of these analyses are broadly consistent with this. Within the Irish Sea, this means that more northerly colonies (e.g. the Calf of Man) tend to pup later than colonies located further south (e.g. in Pembrokeshire). The results of preliminary investigations support this view, with mean season midpoint occurring 14.8 days earlier at the most southerly colony (Marloes: 23 September) compared to the most northerly colony (Calf of Man: 8 October). However, no consistent significant effect of SST upon pupping phenology was observed.

Of the four colonies included for formal analysis, a relationship between pupping phenology and SST was identified only at the Ramsey and Skomer colonies, but this relationship was not consistent, since the effect was observed from mean SST calculated across autumn months (Ramsey) and winter months (Skomer). The influence of pupping phenology in previous years had the most consistent effect, as later pupping in one year tended to influence later pupping in the following year, at the Calf of Man, Skomer and Marloes colonies. The timing of the pupping season appeared to be largely insensitive to population density, since Marloes was the only location where the estimated pup count had an effect on pupping phenology.

Despite the proximity between the colonies at Skomer and Marloes (<1 km) and Ramsey (~15 km), the mid-point of the pupping season at Ramsey and Marloes is, on average, around six days earlier than at the Skomer colony. The timing of the pupping season at the Calf of Man and Marloes colonies appears unaffected, relatively, by changes in SST, but in warmer years pupping occurred earlier at the Skomer colony, and later on Ramsey. This pattern was observed when only concurrent observations from each colony were considered (i.e. 2005 and 2008-2018 in Ramsey; 1992-2018 in Marloes), suggesting that the differing length of these datasets was not having an influence. If phenological change is occurring at one colony, but not at another nearby, or if responses to environmental change are not consistent at all colonies, this may have implications for relative breeding success between these colonies. Changes that occur in warmer years at the Skomer colony may encourage earlier, more successful weaning and greater survival probability (Bowen et al., 2015; Maniscalco and Parker, 2018; Pomeroy et al., 1999). This may also bring pups born at the Skomer colony in line with those born at the Marloes and Ramsey colonies which may already have a competitive advantage if their earlier weaning is synchronous with greater resource availability. If future SST trends upwards, above the patterns of variability observed in this study, then pups at the Skomer colony, where a response to change has been identified, may continue to wean earlier, and a competitive advantage may develop here if the timing of the pupping season at nearby colonies remains static.

The effect of temperature upon the phenology of ecological processes is well established across taxa and organisational levels (de Bettignies et al., 2018; Ficetola and Maiorano, 2016; Poloczanska et al., 2016; Sydeman et al., 2015), and population size and density may also drive change (Bowen et al., 2020; Coulson, 1981; Votier et al., 2009). Where within-community responses are heterogeneous ecological interactions may be affected (Burthe et al., 2012; Thackeray et al., 2016; van Beest et al., 2022), although phenological responses to environmental change are by no means universal. For instance, responses to variation in SST in planktonic food webs may not be as marked or as consistent as in other communities (Atkinson et al., 2015) and in seabirds a broad insensitivity to changes in SST has been observed (Keogan et al., 2018). If responses are weak or lacking, resource-consumer relationships may become weakened, and where asynchrony occurs between groups competing for resources, a competitive advantage may arise for the group that is able to track change (or parity) in the resource. Where such asynchrony is expressed at an inter-colony (i.e. intra-population) scale then population dynamics may be altered.

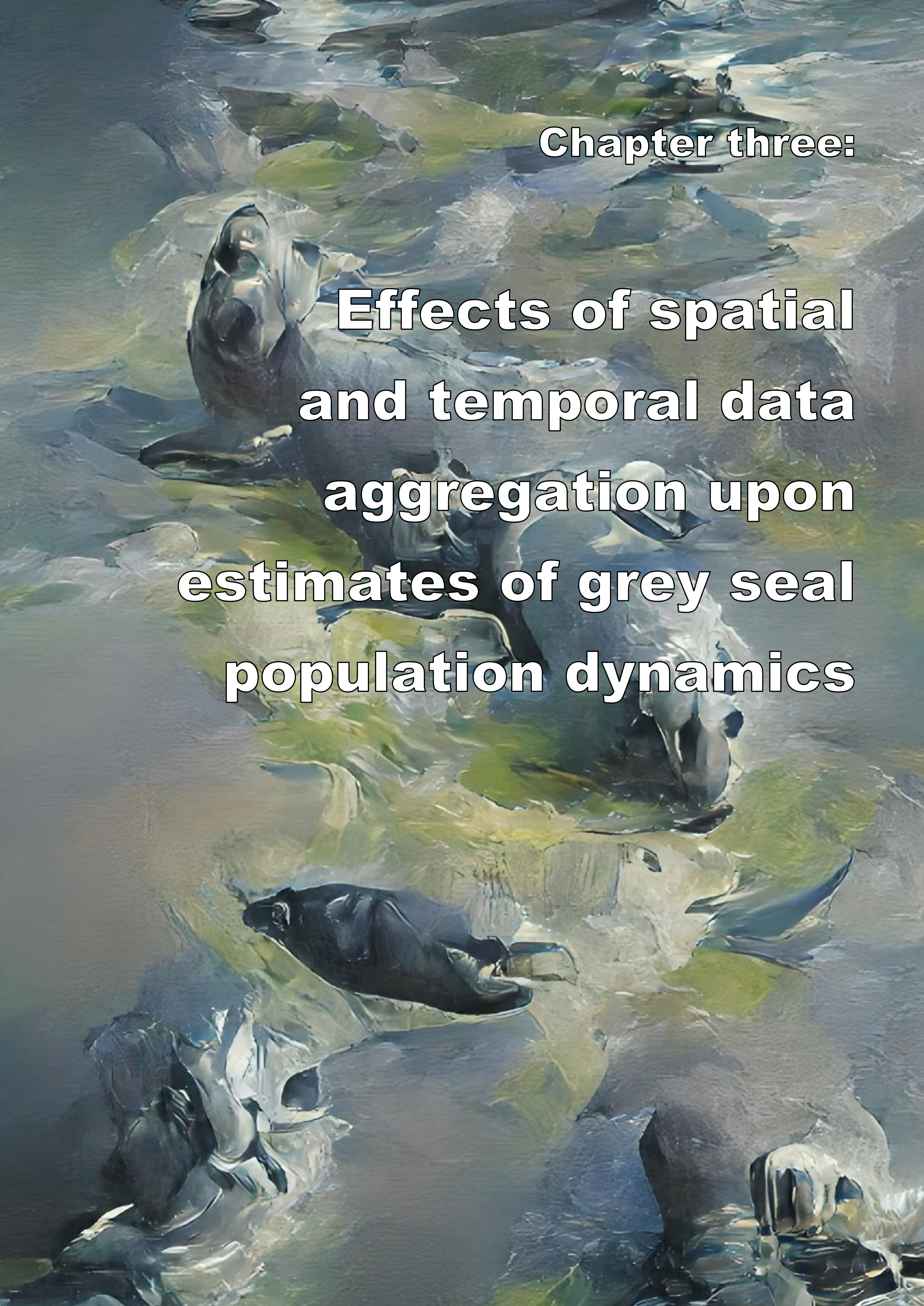
If environmental variability and the timing of earlier pupping seasons influences pupping phenology at a colony level, results from the current study are still unable to determine the response to such drivers at the individual level, or indeed the relative contribution to observed trends. The assumption here is that the phenological response occurs across the whole breeding population, but this does not take account of the age or experience of the mothers. Younger and less experienced females tend to breed later, and with lower rates of survival/recruitment amongst pinniped and other mammal species (Boltnev and York, 2001;

Bowen et al., 2006; Maniscalco and Parker, 2018; Peláez et al., 2017; Wolcott et al., 2015). Further, since older females tend to breed earlier, the apparent advancing of the pupping season in warmer years may be driven by an increased likelihood of older females to breed in warmer years, effectively altering the age structure of the population (Bull et al., 2021), rather than a wholesale shift in the pupping season.

In summary, despite within-colony variability in the mid-point of the pupping season, with some colonies exhibiting reasonably well-defined cycles, much of this variability could not be explained by concomitant changes in local environmental conditions and broad-scale indices. At two colonies (Ramsey and Skomer), a relationship was observed between environmental conditions and the timing of the pupping season, when SST during the previous year's autumn (Ramsey) and winter (Skomer), and previous pupping season mid-point, were considered. While this ostensibly supports the hypothesis that changes to reproductive timing are connected to changes in environmental conditions, these patterns are not replicated in all colonies. Indeed, this relationship could not be defined at the neighbouring Marloes colony, less than 1 km to the east of Skomer. The effects of such a localised phenological response has the potential to modify interactions between colonies. If earlier weaning at some colonies facilitates earlier access to resources (i.e. prey), this may result in a competitive advantage over later-born pups nearby. In contrast, pups born and weaned later in the season (for instance those at colonies exhibiting less phenological plasticity) may have a competitive advantage if resources become available later, leaving earlier-weaned pups experiencing a shortage..

The patterns described above indicate that it is possible to document and model phenological change in grey seal pupping seasons. However, the biological mechanisms underpinning such change, and the potential consequences for the wider grey seal population, are not well understood, and further research on the intrinsic factors influencing the timing of parturition in grey seals would enable any environmental component to be better isolated.

Established monitoring programmes in the Republic of Ireland, Scotland and east coast of England (SCOS, 2023) provide the opportunity for the observations discussed above to be investigated at other known breeding centres. This would allow potential patterns of phenological change to be identified at other locations within the species’ range, to identify the extent and direction of change across the wider population. Moreover, research into temporal patterns at a wider spatial scale could enhance our understanding of the consequences of phenological change upon interactions between colonies, particularly in the context of the existing temporal cline in pupping season that is believed to occur around the coast of the UK.



Chapter three:

Effects of spatial and temporal data aggregation upon estimates of grey seal population dynamics

Abstract

Census counts are a common method of estimating population size for conservation management, providing a snapshot of the population that may be contextualised by previous and subsequent censuses.. In all censuses, sampling method, landscape characteristics, monitoring schedule, observer experience, and sample size may affect the accuracy of estimates. Further, the spatial scale over which observations are interpreted may introduce local-scale biases to inferences made at the population level, with possible implications for management decisions. Matrix population models (MPM), based upon stage-specific survival rates derived from census counts, provide methods with which population dynamics can be estimated and projected. When MPMs are parameterised with vital rates estimated from specific sites or colonies, then a spatial component can be introduced, and the influence of particular sampling sites on broader scale estimates can be investigated. Previous research on the effects of data aggregation decisions on population-level estimates has focused on a limited spatial scale, but the effects of similar aggregation of data over regional scales or greater is lacking.

To explore the impact of aggregating data over different spatial scales I used a 29-year time series of grey seal (*Halichoerus grypus*) pup survival estimates from the Irish Sea to parameterise MPMs at three spatial scales. Data were collected from 70 beaches in four known breeding centres in SW Wales and the Isle of Man. Annual pup survival rates were calculated from established census survey campaigns conducted throughout the pupping seasons, and these were compared between years, and across pupping sites, colonies and at the regional scale. Survival probability was observed to be highly variable (and poorly correlated) between beaches, with observations at less-frequently used beaches likely to

introduce variability and uncertainty into wider scale population estimates. The choice of sampling sites, and the spatial scale over which observations are aggregated, is important in obtaining accurate population estimates, and will have downstream impacts upon the calculation of survival rates, and the projection of population trajectories.

Introduction

Human activity is widely acknowledged as a driver of change in marine ecosystems (Defra, 2005; Halpern et al., 2008). This observation has been made possible only by ongoing monitoring of habitats, and the communities that inhabit and characterise them. Monitoring of abundance and distribution of species is a common way to identify and assess changes in population dynamics and community composition, and accurate monitoring is critical to effective management (Hiers et al., 2016; Kowalewski et al., 2015). However, exhaustive monitoring is precluded by limited resources, and cryptic species, such as those in the marine environment, make this more difficult. Life-history processes such as sexual or stage-dependent segregation mean that when individuals are observed they may represent only a small portion of the population. It is important to understand, therefore, that abundance estimates can only capture a snapshot of the population at the spatial and temporal point of sampling (Powell and Gale, 2015). The tools employed to monitor wild populations must therefore be able to use information on only part of the population to facilitate inferences on the wider population or sub-population of interest.

Counting individuals over a specific period, such as for the duration of a breeding season, is the first step in estimating vital rates like survival and reproductive output, which can form the basis of more complex and informative analyses to guide management planning. Matrix population models (MPMs), for instance, use probabilities of survival and rates of fecundity to make estimates of current and future population size and structure (Caswell, 2001). MPMs can also be used to calculate several metrics with which to quantify demographic and life-history processes (Capdevila et al., 2020; Caswell, 2018; Ingrisch and Bahn, 2018). Spatial and temporal heterogeneity, and the quality of data used to parameterise MPMs will affect their accuracy, so these factors need to be considered in the early stages of data collection and analysis. Alongside this an appropriate temporal and spatial scale is critical to ensure that inferences drawn from MPMs are representative of the subject population.

The grey seal is an excellent subject on which to test the effects of spatial and temporal heterogeneity in parameterising MPMs, as this species is predictable in the timing and location of breeding, is large enough to monitor from a distance, and its pupping habits make it possible to track the fate of most observed offspring. In the UK pupping occurs at semi-discrete colonies, distributed broadly in regional population clusters, with a high degree of within population temporal synchrony in pupping (SCOS, 2022). Pup production is not uniform across the range, having reached an asymptote at many Scottish colonies, while still increasing at others, and some areas exhibiting variability or a decline, with no overall trend apparent (Russell et al., 2019; SCOS, 2022, 2021).

Grey seals have been the subject of much historical exploitation and persecution, to the point that they were extirpated from most of Europe, and declined to around 2,000 to 4,000 individuals in the UK by the start of the 20th Century (Lambert, 2002), although no reliable records of historical population size actually exist (SCOS, 2018). The Grey Seals (Protection) Act, 1914 was the first statutory protection extended to a mammal in the UK, and subsequent legislation and conservation management has addressed the decline to the point that the population in the UK is increasing. This has renewed historical human-seal conflict, with grey seals being blamed for damage to fishing gear and perceived competition affecting fish stocks, driving discussions of culling programmes (Cook et al., 2015; Strong et al., 2006). Appropriate management to avoid population decline and minimise conflict with human communities requires reliable monitoring data and population estimates. Census monitoring needs to be conducted efficiently and consistently to maximise data quality, but this is time-consuming, requires surveyors to be specially trained, and can be dictated by external factors such as weather. Similarly, monitoring may vary between sites, depending on accessibility, population size, and frequency of visits. The way in which census data are collected and handled can influence the conclusions that can be made from population models, so the peculiarities of the monitoring process need to be understood by whoever compiles the data before analysis. Notable observations and patterns of uncertainty also need to be dealt with consistently to reduce bias in the data.

This chapter explores how estimates of grey seal population dynamics may be affected by the scale at which monitoring data are aggregated before analysis. Across 70 monitoring locations, in four sampling areas, and over 29 years, this chapter aims to:

1) Investigate how the spatial scale over which observations are summarised influences estimates of annual pup survival rate and population dynamics;
2) Explore the effect of population density on pup survival, and test the assumption that survival declines as population size increases;
3) Estimate the sample size required from each of the pupping colonies to obtain a reliable estimate of overall pup survival;
4) Test the hypothesis that the source and accuracy of data affects how projections of future population dynamics are obtained from matrix population models; and
5) Compare these observations with a previous investigation of the subject by Engbo *et al.* (2020), based upon a shorter time series and fewer sampling areas.

Methods

Grey seal populations have been monitored in Pembrokeshire since the 1940s. Observations of varying consistency have been made subsequently, but at the Marloes and Skomer sites regular, standardised monitoring began in 1992 (Lock et al., 2017). Standardised monitoring has also been ongoing on Ramsey since 1992, albeit with less regularity until 2008, when annual monitoring was initiated (Morgan et al., 2018). Similarly, the long-term monitoring project at the Calf of Man has been operating since 2009, although observations had been recorded less consistently before this (Stone et al., 2013).

Monitoring of seal pup production was conducted by Wardens and volunteers in four sampling areas (hereafter referred to as 'colonies') in south west Wales and the Isle of Man. The three Welsh colonies lie within the Pembrokeshire Marine/Sir Benfro Forol Special Area of Conservation (SAC), designated under the European Habitats Directive (Council Directive 92/42/EEC), for which the grey seal is a primary qualifying feature (JNCC, 2015; Lock et al., 2017). The Manx colony is located on the Calf of Man, located within the 'Calf and Wart Bank' Marine Nature Reserve, designated under the Wildlife Act (1990), with the grey seal as a feature of interest.

Colony-specific monitoring methods

Calf of Man

Pupping at the Calf of Man occurs on sheltered beaches (hereafter referred to as 'sites', to include locations where pupping occurred in caves), largely at the north and south of the island, since east and west coasts are dominated by sheer cliffs with few suitable haul-outs. Monitoring is undertaken in two modes: ad-hoc observations made by up to three island wardens during the course of their daily duties between March and the end of November, and targeted monitoring by up to three volunteers during the peak pupping season, between late September and early November (Andrew et al., 2019). Pup counts were conducted from pre-determined vantage points, with the majority of survey effort concentrated on 13 sites. Sites are clustered at the north (n = 6) and south (n = 7) of the island, with each cluster monitored on alternating days to minimise disturbance.

Ramsey

Ramsey has recently observed a rapid increase in pup production (Morgan et al., 2018; Strong et al., 2006)and monitoring here was conducted at nine sites, located either on the eastern coast, or in sheltered bays on the western coast. As there are fewer sites on Ramsey, monitoring was conducted every three days, from cliff tops only, as described by Strong et al. (2006), and no caves were monitored. No pups were marked on Ramsey, so tracking the development and survival of pups was dependent upon the same experienced fieldworkers conducting all monitoring through the season. Pup counts on Ramsey were multiplied by a site-specific correction factor, based on earlier ground-truth surveys, to adjust for differences in the field of view at each site, and to mitigate double-counting when fieldworkers moved between fixed observation points (Morgan et al., 2018). Where adjusted values were not whole numbers, the nearest integer was used.

Skomer and Marloes

Skomer Island ('Skomer') is located less than 1km from the western tip of the Marloes peninsula, and lies within the Skomer Marine Conservation Zone (Skomer MCZ) at the southern tip of St Bride's Bay. Grey seal pups were monitored at 21 beaches and caves on Skomer, located largely at the eastern end of the island, where conditions are more sheltered.

Monitoring on Skomer and Marloes followed methods described by Poole (1996) and Alexander (2015). At these colonies fieldworkers recorded pups largely from a clifftop vantage point, or at beach- or water-level when site characteristics allowed or required these approaches. At accessible sites, pups were dye-marked to assist with identifying individuals and simplify cliff-top monitoring through the season (Büche and Stubbings, 2018; Lock et al., 2017). Monitoring of beaches was undertaken every one to five days, with more well-used sites being visited more frequently, so that pups could be recorded soon after birth. Monitoring in caves occurred only if breeding behaviour by females had been observed in the vicinity. Caves were visited when weather, sea conditions and tides allowed, and when cows were absent to minimise disturbance and ensure fieldworker safety, so these sites were visited less frequently.

Estimating pup production and survival rates

At all colonies, pups were assigned to a developmental stage based upon those described by Baines *et al.* (1995 after Radford *et al*., 1978). Pups of 0-2 days' age were assigned to stage I, and pups that reached stage IV (16-20 days) were assumed to survive to independence. For each site the number of pups counted across the season was divided by the number of pups that survived to independence, giving a per-annum survival rate between 0 and 1 for each site. On Ramsey, where a site-specific correction factor was applied, in nine out of the 72 observations the adjusted estimate of survivors was greater than the initial pup count, so a survival probability of 1 was assumed.

Spatial and temporal scale of monitoring

With the inclusion of monitoring records from the Calf of Man, and additional years of observation from Skomer and Marloes since Engbo *et al.* (2020), monitoring activities have yielded 811 estimates of pup survival, across 70 sites. Whereas Engbo *et al.* (2020) investigated inter-colony patterns in pup survival within the Pembrokeshire Marine SAC, the inclusion of the Calf of Man has allowed us to explore patterns at a broader spatial scale. It has therefore been possible to explore survival estimates and concomitant effects upon population dynamics at the regional level, as well as at colony- and site-level, as previously. These records were collected over 29 years (1992-2020), although observations coincide in all four colonies for only seven years (2009-2015).

Data analysis

Density dependence of pup production was explored to test the hypothesis that pup survival declines as population density increases (Harwood, 1978; Thomas et al., 2019). Here, site-level annual survival estimates were modelled against site-level pup abundance for each colony, and investigated with generalised linear models to identify any potential relationship, with the binary fate of pups (i.e. dead/alive) as the response variable.

I calculated mean annual survival probability, weighted by the number of pups recorded at each site, for each of the four colonies. I then tested for a trend in mean survival probability via linear regression, with time as a predictor. Finally, I estimated the amount of variation in pup survival that could be explained by time, site and colony via hierarchical partitioning of variance,. I also investigated between- and within-colony variation in estimated survival probabilities by examining the density distribution of annual survival estimates at all sites, to, and the variation in survival between sites and years (i.e. within colonies). These were compared with previous density distributions in which Skomer was represented by just five years, rather than the 27 years here.

I conducted a sensitivity analysis to determine the amount that estimated survival probability at each site influences the estimate of the overall mean, by systematically removing each site from calculations of the overall mean. We then used linear regression to test whether sensitivity was associated with the number of pups recorded at each site, since monitoring effort tended to be greater at more well-used sites, i.e. those where more pups were recorded. If sensitivity is related to pup count (and therefore monitoring effort), this could be a source of bias in survival estimates.

Following this, I investigated simple temporal variation in survival probability against pup population size, and conducted pairwise Kendall rank correlation tests for all pairs of sites with at least five records, to identify collinearity in survival between sites. The Kendall rank test was chosen due to the non-normality of survival estimates (being bounded at 0 and 1), and the likelihood of ties. I also investigated the sample size required for colony-specific records to be used to calculate a reliable estimate of overall mean survival probability. This was achieved by randomly sampling from records and calculating a mean using sample sizes ranging from n = 5 to n = 40, at intervals of five samples. I repeated this process 1,000 times for each colony, and for all colonies combined, and calculated how often the means of these samples were within 10% of the estimated mean of all observations. This overall ‘true’ mean was calculated for years where monitoring coincided at all four colonies.

Parameterising MPMs

The process for parameterising MPMs follows that described by Engbo *et al.* (2020). One generic matrix was built using stage-specific vital rates published in Thomas et al. (2019). These rates comprised survival estimates (φ) at seven life stages (birth to age 1 ($\varphi_p = 0.48$), pre-breeding: ages 1-5 ($\varphi = 0.95$) and breeding: age 6+ ($\varphi = 0.95$)) and fecundity ($\alpha = 0.90$). A 50:50 sex ratio was assumed, and therefore fecundity was multiplied by 0.50 to give a female-only fecundity rate of $\alpha = 0.45$. The generic matrix was the basis upon which modelling could be conducted over different spatial scales, and this was achieved by iteratively replacing φ_p with the survival estimates obtained from observations at the pupping colonies. This provided a site-specific transition matrix for every year of monitoring.

Pup survival estimates from the monitoring programmes described above represent survival from birth to weaning ('stage IV': approximately 20 days). These rates were converted to estimates of survival from birth to age 1 by multiplying by a ‘survival’ coefficient, based upon the estimate of mean year-one survival (0.48) from Thomas et al. (2019) divided by the mean rate of survival to weaning from the observations of this study (0.75) to give a coefficient of 0.64. Based on the generic matrix, MPMs were constructed at each of four spatial scales by substituting pup survival rates in the generic matrix with estimates of survival calculated from observations at respective scales. Estimates at site (n = 70), colony (n = 4), and ‘population’ (n = 1) level were obtained by calculating the per-annum mean rate across the respective scale, weighted by the number of seals at each site.

Estimating population dynamics

Population growth rate (λ: lambda) was calculated from each MPM and used to quantify the potential influence of variation in pup survival rates on population dynamics. Lambda values were then compared across spatial scales to assess the potential bias introduced by aggregating observations. Population trajectory was estimated via stochastic methods, using MPMs from all sites, as projecting the population from a single site in a single year would produce a deterministic estimate. Variability can be introduced by using multiple matrices throughout the projection, as an analogue to natural heterogeneity. Projection was initialised with a starting population structure based on that used by Engbo *et al*. (2020), updated to include the Calf of Man. It was assumed that juveniles numbered approximately three times the number of pups or breeding adults, with the number of pups (n = 767) calculated from the most recent year in which observations coincide at all colonies (2015). As noted by Engbo *et al*. (2020) the actual starting values are not critical as the projections are of an asymptotic nature. Two subsets of ten MPMs were then projected for 20 years, with each subset based upon the ten highest and ten lowest site-specific mean survival rates. These site-specific survival rates were calculated for all available years, to ensure that projections were able to account for inter-annual variation.

All data processing and analyses were conducted using R statistical software v. 4.2.0 (R Core Team, 2022). All calculations, lambda values and projections from MPMs were conducted using the 'popdemo' R package (Stott et al., 2021) and the hierarchical partitioning of variance to explore the influence of time, site and colony on heterogeneity in pup survival was conducted using the ‘hier.part’ R package (Mac Nally and Walsh, 2004).

Results

Estimated rates of productivity and survival varied over the course of the observation period, and were not consistent between or within the four colonies. Survival probability on Ramsey tended to be lower than at the other three colonies (Figure 3.1a), and this is reflected in the mean pup survival estimates across the four colonies (Ramsey = 0.555, SE = 0.004; Marloes = 0.708, SE = 0.001; Skomer = 0.749, SE = 0.001; Calf of Man = 0.920, SE = 0.001. Overall mean = 0.746, SE = 0.0003). Within-colony (i.e. between-site) variability is greater in Marloes than in Skomer, despite the geographical proximity of the two sampling areas.

Influence of spatial scale on summary estimates of pup survival and population dynamics

Density distribution of site-specific survival probabilities (Figure 3.1b) illustrates the differences in pup survival patterns between colonies. Survival rates at the Calf of Man colony are consistently higher than at the Pembrokeshire colonies, while rates at the Ramsey colony are concentrated below 0.50. The distribution of survival rates differs between colonies, and the pattern for the subset of years in which observations coincide across all colonies (2009-2015) does not change markedly from the full time series, but instead appears to exhibit greater variability, illustrated by the distribution of higher densities being exaggerated in the paler shaded areas (2009-2015 subset) in Figure 3.1b.

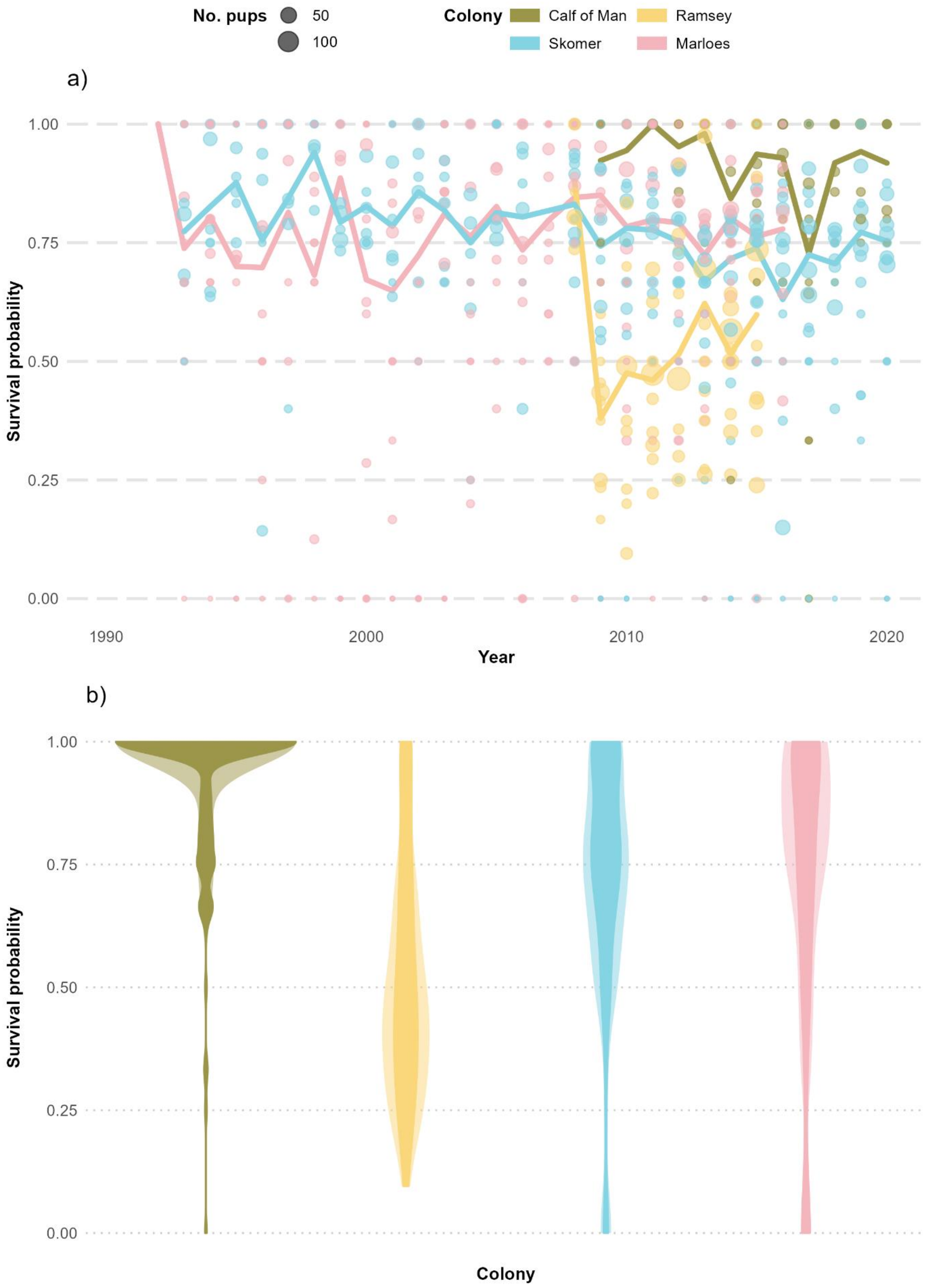


Figure 3.1: Estimates of grey seal pup survival at four colonies in the Irish Sea. Panel a) illustrates temporal variability in survival estimates from 1992 to 2020. Individual points indicate within-colony sampling observations, point size corresponding to sample size, and solid lines corresponding to mean annual survival estimate for respective colonies. Panel b) illustrates the density distribution of site-specific pup survival probabilities for the same Irish Sea colonies. Full-colour areas indicate observations from the whole time series, while lighter-shaded areas indicate only the years in which observations coincide across all colonies (2009 to 2015).

No additional observations were included at Ramsey since Engbo *et al.* (2020) so results here are identical to the original study. Three additional years of monitoring observations were included from Marloes, 24 additional years from Skomer, and 12 additional years from the Calf of Man, which was not previously investigated. No temporal trend was observed at either Ramsey ($\beta = -0.009$, $F_{1,6} = 0.144$, $p = 0.718$), Marloes ($\beta = 4.86 \times 10^{-5}$, $F_{1,23} = 0.001$, $p = 0.982$), or the Calf of Man colony ($\beta = -0.006$, $F_{1,10} = 1.187$, $p = 0.305$). At the Skomer colony there was a slight negative trend in survival probability, which can be observed in Figure 3.2, although the effect size is likely to be biologically negligible ($\beta = -0.005$, $F_{1,25} = 18.98$, $p < 0.001$).

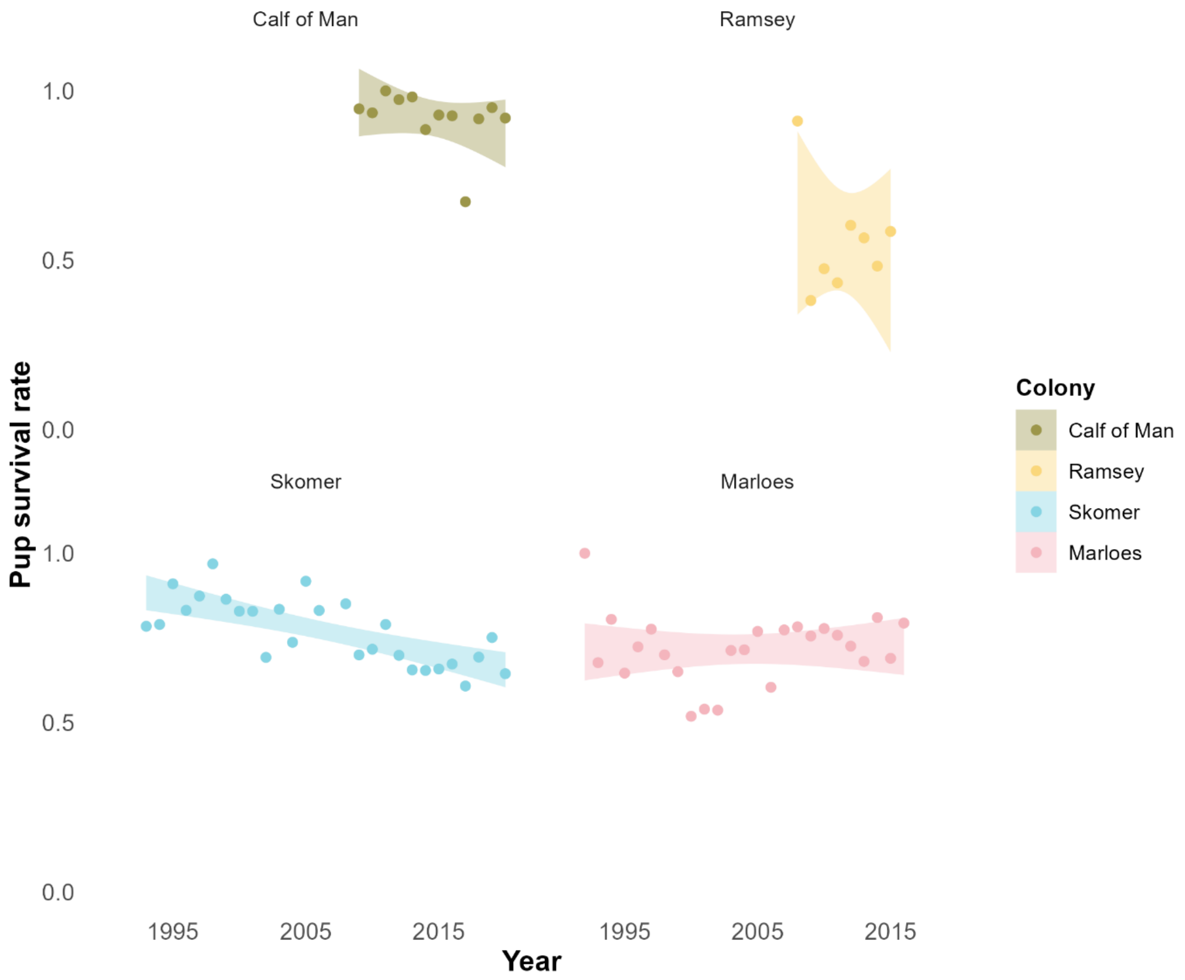


Figure 3.2: Temporal trends in estimated mean annual pup survival rates at the colony level between 1992 and 2020. Points indicate mean annual survival rates at the colony level and shaded ribbons indicate 95% confidence limits from simple linear regression of mean annual survival rate (calculated across monitoring beaches) against year.

Effect of population density on pup survival

No consistent trend in pup survival relative to population density was apparent at three of the pupping colonies, but site-level survival did appear to vary negatively with abundance at the Ramsey colony (Figure 3.3). However, the results of the quasibinomial GLM were not significant (β = 0.005, t = 1.102, p = 0.275), and the small sample size (n = 8) would require additional data collection to allow a robust analysis of these patterns.

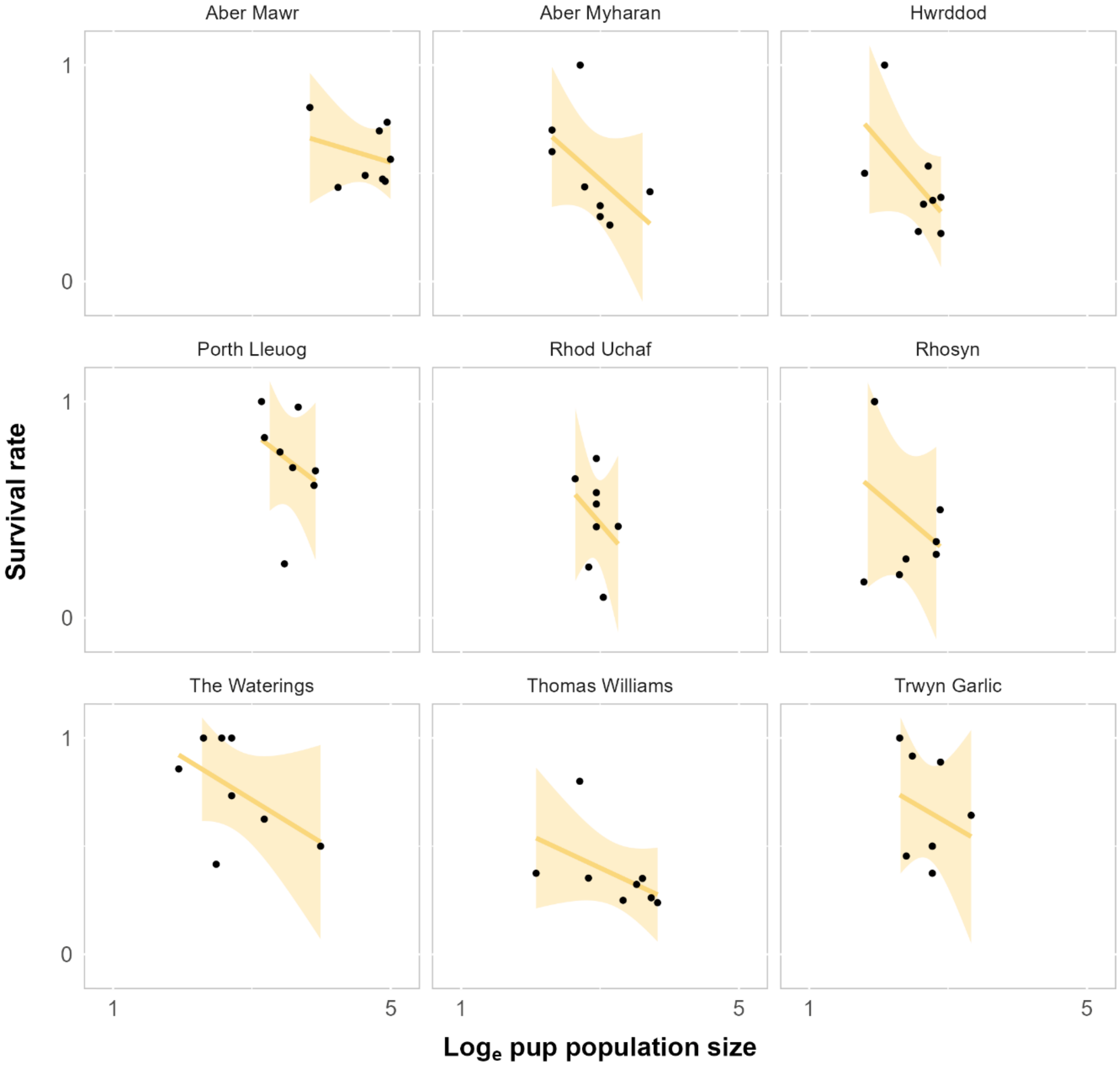


Figure 3.3: Comparison of pup survival against abundance at the Ramsey colony, where all sites appear to be exhibiting density-dependent decline in annual survival during years of greater pupping abundance. Note the log scale on the x-axis to accommodate greater abundance at the Aber Mawr site.

An analysis of sensitivity suggested that removing any given site from calculations of overall mean pup survival may change estimates by between -0.006 (-0.76%) and 0.009 (1.22%). The estimated abundance of pups (Figure 3.4) at each site did not have a strong effect upon sensitivity across the whole sampling range (grey line: $r^2 = 0.04$, $F_{1,61} = 3.696$, $p = 0.059$), which suggests that pup population size would not be expected to affect survival estimates when considered across the Irish Sea.

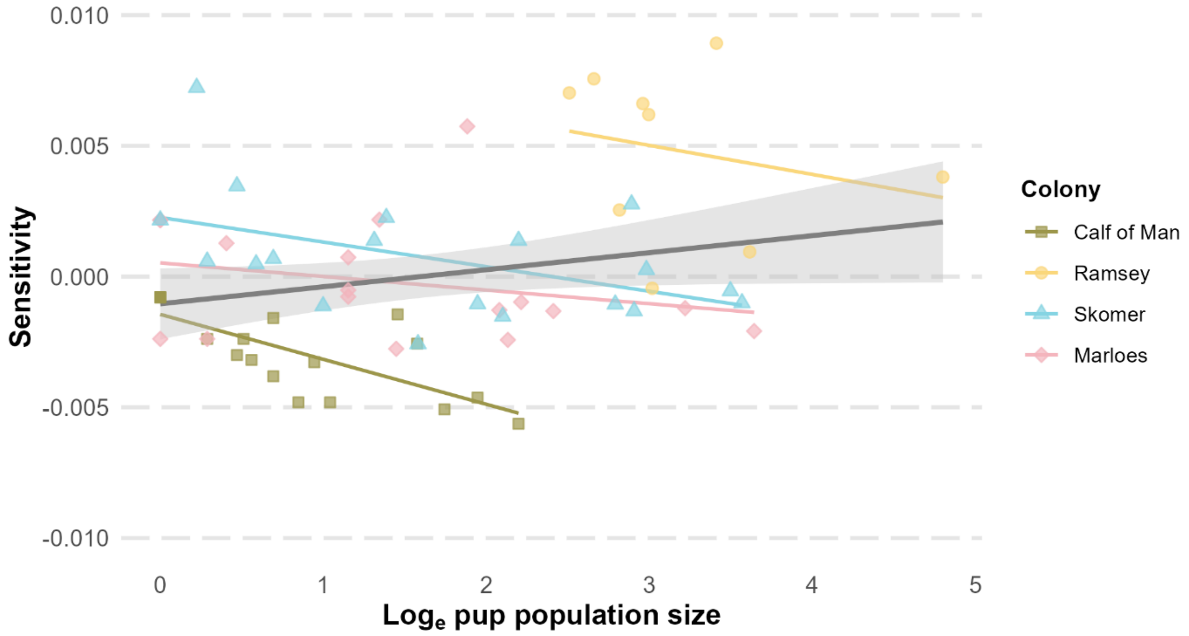


Figure 3.4: Relationship between sensitivity (the relative influence site-level mean survival estimates on the overall mean survival estimate) and pup population size, when considered across the whole sampling range (black line) and at individual breeding colonies (coloured lines). Grey ribbon indicates 95% confidence interval around estimate for whole sampling range. Note the log scale on the horizontal axis to accommodate particularly high population estimates at the Ramsey colony.

However, when considered at the colony level, a small negative relationship between sensitivity and pup population size did appear at all colonies, and colony-level effect sizes are presented in Table 3.1. Sensitivity varied significantly between colonies ($r^2 = 0.59$, $F_{4,58} = 23.06$, $p < 0.001$), where pup survival rates at Ramsey exhibited greater sensitivity than rates at other colonies.

Table 3.1: Summary of colony-specific relationships between pup population size and sensitivity.

Parameter	Estimate (SE)	SE	t-value	p-value
Intercept	*-0.002*	*0.0006*	*-3.825*	*< 0.001*
Log_e pup population	-0.001	0.0002	-3.267	0.002
Colony - Ramsey	0.010	0.0011	9.026	< 0.001
Colony - Marloes	0.003	0.0007	4.634	< 0.001
Colony - Skomer	0.004	0.0007	5.875	< 0.001

Estimates of population growth rate (lambda: λ) derived from MPMs using the 'popdemo' package (Stott et al., 2021) indicated that lambda tended to reduce as the pup population increased, although this was not a statistically significant effect ($r^2 = 0.80$, $F_{1,2} = 12.65$, $p = 0.07$). The source and accuracy of data used was also critical in making reliable estimates of population dynamics (Figure 3.5).

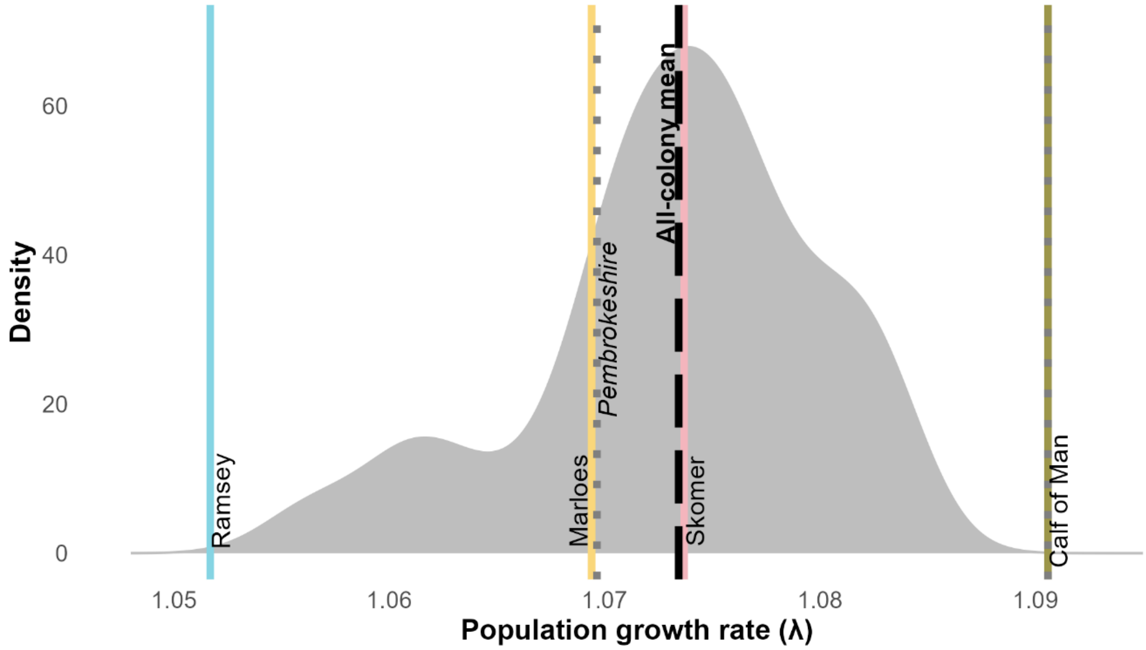


Figure 3.5: Density distribution of lambda values for all sites, where aggregated estimates are indicated at the colony (solid coloured lines), region (grey dotted lines) and whole range level (black dashed line). Note that the region- and colony-level lines for the Calf of Man are identical since this region has only one colony.

The Calf of Man exhibited the highest growth rate (λ = 1.091) followed by Skomer (λ = 1.074), Marloes (λ = 1.069) and Ramsey (λ = 1.052), which appears to bring the regional mean down (Pembrokeshire λ = 1.065) compared to the mean of all colonies (λ = 1.071). These growth rates correspond to an annual population increase of 9.1%, 7.4%, 6.9% and 5.2% for the Calf of Man, Skomer, Marloes and Ramsey, and an estimated 6.5% and 7.1% annual increase across the Pembrokeshire region and whole study area, respectively.

Variance in pup survival estimates did appear to reduce as pup abundance increased (Figure 3.6a), and most of the variance in survival (68%) could be explained by site-level differences (Figure 3.6b). This was alongside colony- (25%) and region-level effects (5%), and temporal factors (2%). Pair-wise Kendall rank correlation analysis suggested a weak temporal relationship between pairs of sites (mean τ = -0.013, SE = 0.009; mean p = 0.471, SE = 0.007).

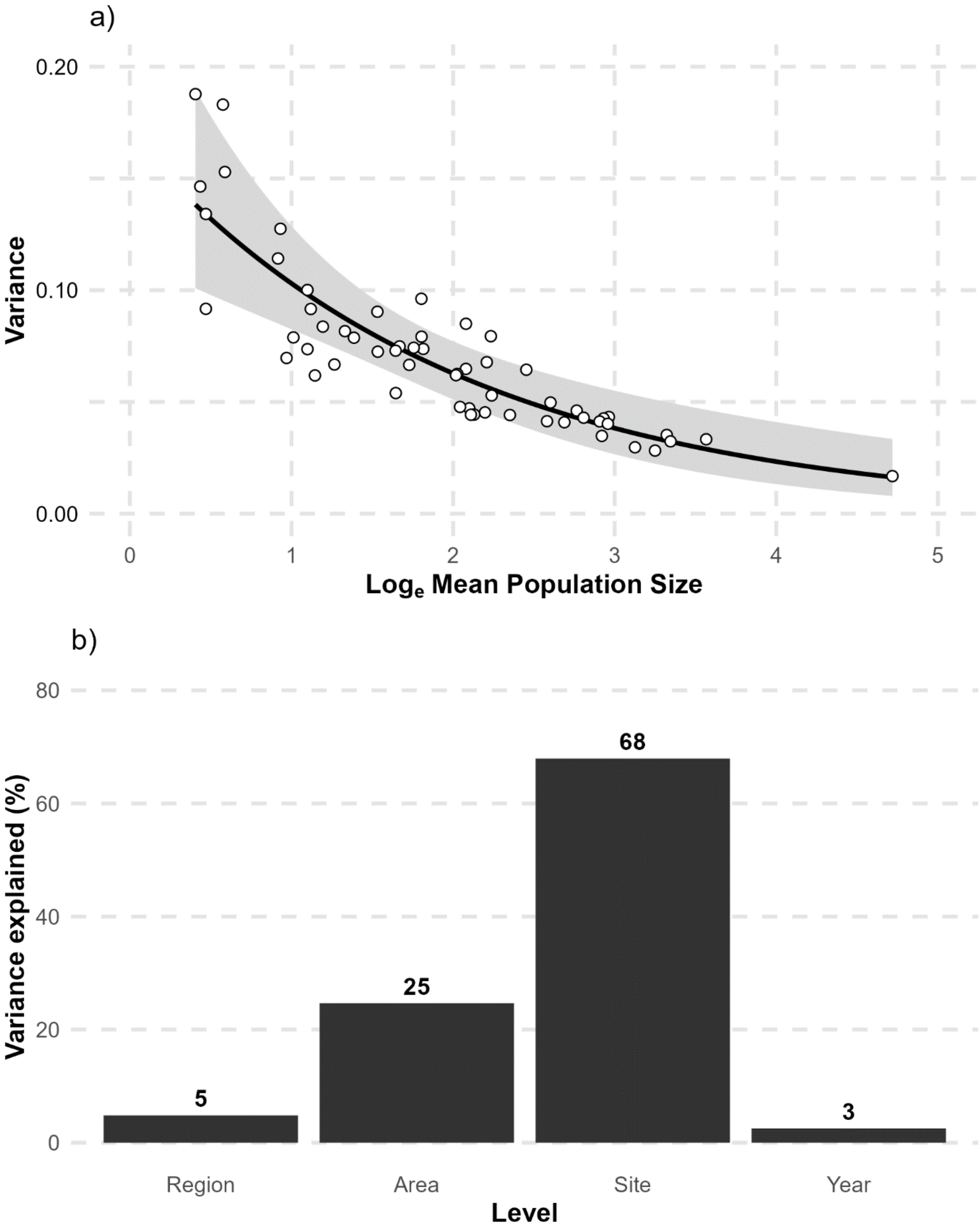


Figure 3.6: Variance in survival estimates appeared to be influenced by population size (or sample size) increased and the spatial and temporal scale over which estimates were calculated. Panel a) indicates the relationship between variance and population size as plotted from a simple generalised additive model of mean population size against variance. Panel b) illustrates the explained variance when considered across regional, area (colony) and site (beach) level, and across years.

Estimated colony-specific sample size required to obtain a reliable overall estimate

The proportion of estimates of overall mean pup survival rates that fell within 10% of the true value (0.732), when bootstrapped from between five and 40 samples of colony-specific records, varied between colonies (Figure 3.7). For 80% of estimates to provide an overall mean survival rate at the desired precision, at the five-sample interval employed during this analysis n = 10 for the Calf of Man, n = 25 for Ramsey, n = 20 for Skomer, and n = 35 for Marloes with at least 25 samples required from the full set of observations.

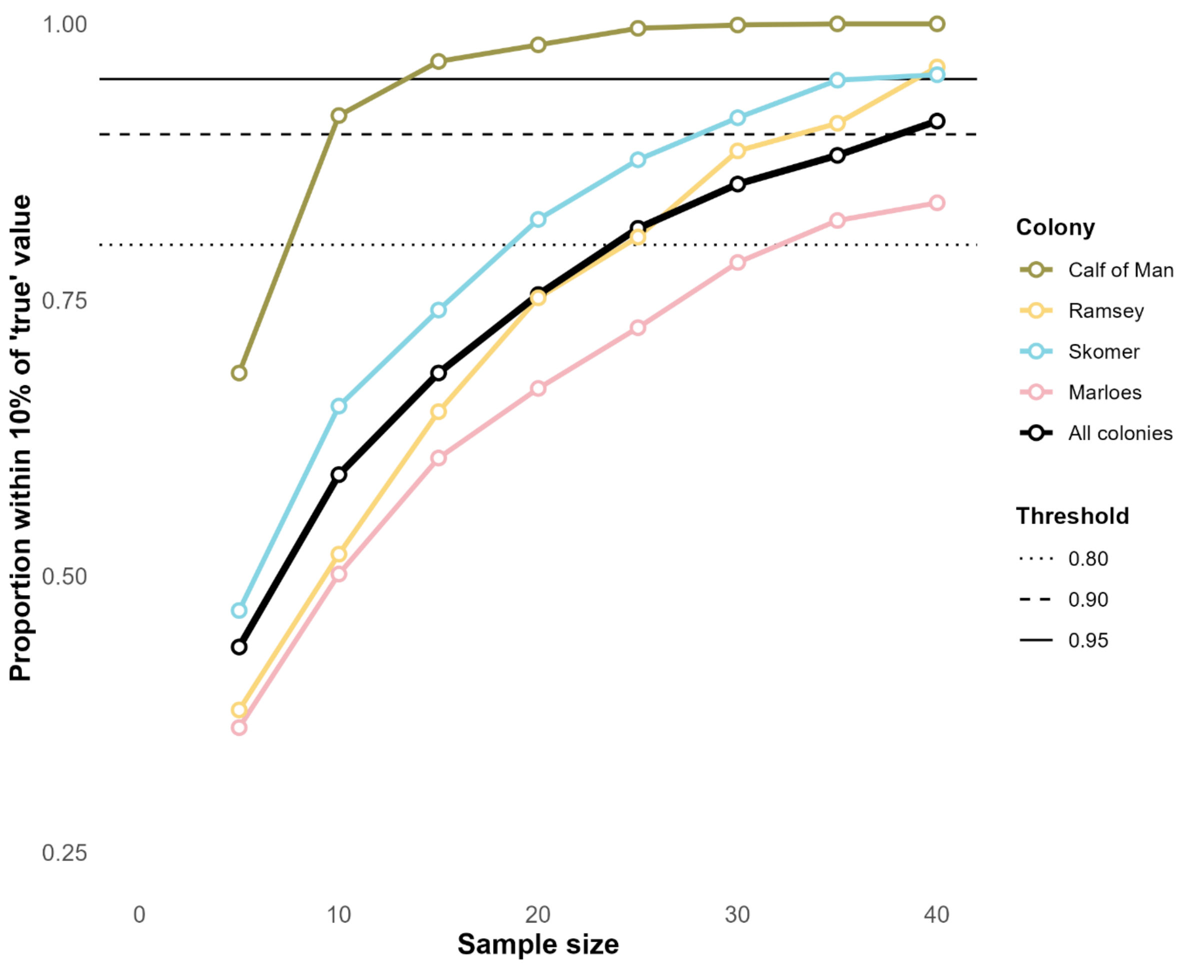


Figure 3.7: Proportion of estimates of overall mean pup survival rates that fall within 10% of the true value, with bootstrapped samples (n = 1,000) taken from colony-specific records greater than 0.80, 0.90 and 0.95. When thresholds are higher, the sample size required to replicate the 'true' mean also tends to be higher.

Effect of data source and accuracy on MPM projections of population trajectory

Population growth rate estimates of 1.05, 1.07, 1.07 and 1.09 (respectively corresponding to increases of 5%, 7%, 7%, and 9% per year) were calculated from pup survival rates aggregated across sites within each of the four colonies: Ramsey, Marloes, Skomer, and Calf of Man, respectively. Pup survival estimates aggregated from subsets of sites with the ten highest and ten lowest mean site-specific pup survival, produced estimates of population growth rates of 1.01 and 1.10 (1% and 10% increase), respectively. Figure 3.8 illustrates the 20-year trajectory of populations when based upon these two subsets. To illustrate regional differences trajectories are presented separately for the Pembrokeshire (Figure 3.8a) and Calf of Man (Figure 3.8b) colonies, alongside trajectories sampled across all colonies (Figure 3.8c). Population growth rates calculated from MPMs based on these subsets ranged between 0.95 (Howney Stone, Marloes) to 1.10 (Bull Hole, Skomer), corresponding to a 5% annual decline and a 10% annual increase, compared to an overall mean of 1.07 (i.e. a 7% annual increase). Survival rates at the Calf of Man colony were consistently high, compared with much greater variability at the other three colonies, which has led to the separation of trajectories in Figure 3.8c. If broad-scale (e.g. regional) population trajectories are summarised from a subset of vital rates originating from colonies with particularly high pup survival (whether as a result of optimal conditions, or a consequence of lower sample size (Figure 3.6a)), this may bias population estimates across the observed range. Likewise for population trajectories derived from sites with pup survival rates at the lower end of the scale.

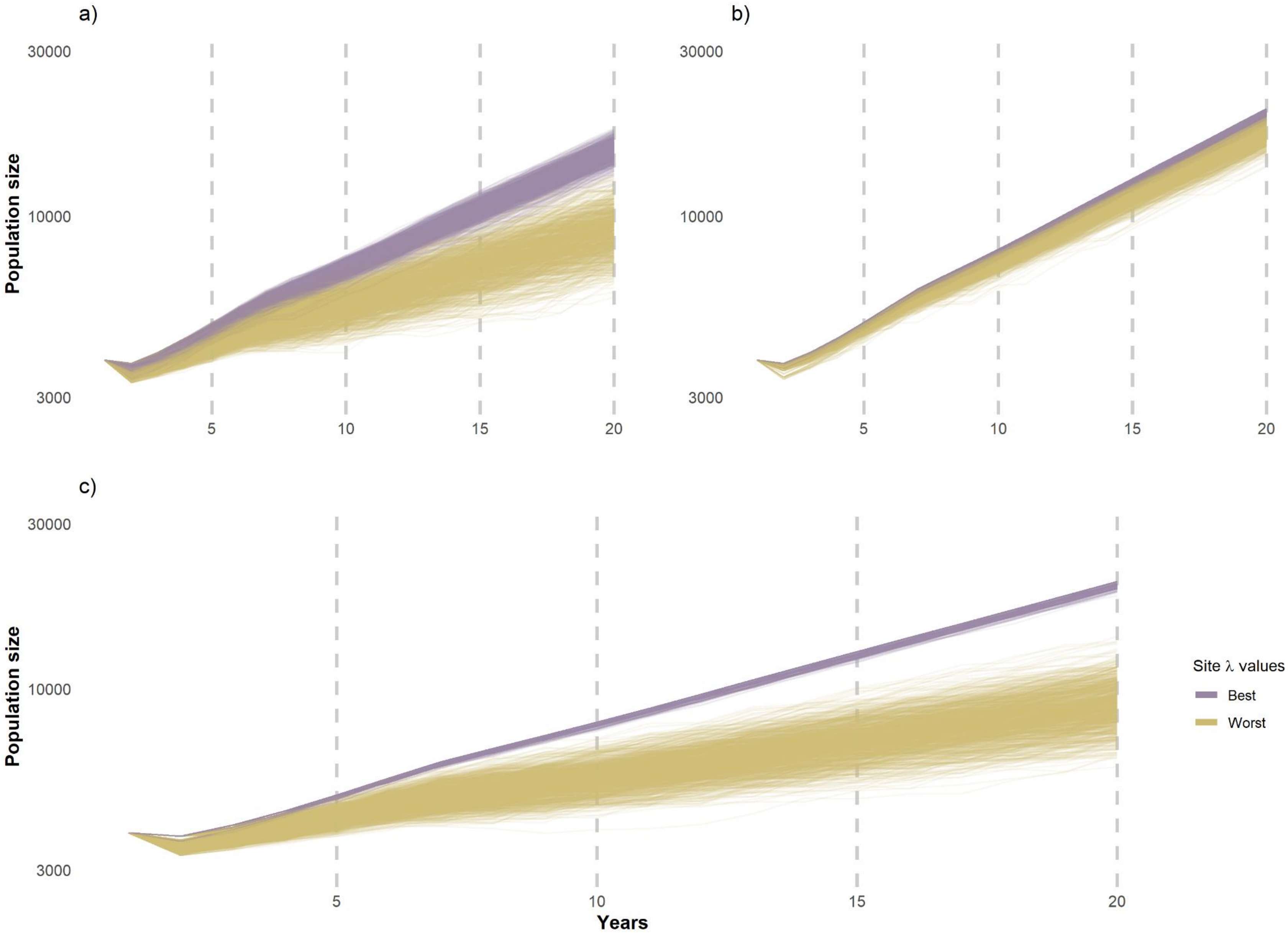


Figure 3.8. Twenty-year population trajectories estimated from MPMs, based on the ten ‘best’ and ten ‘worst’ sites (i.e. those with the highest and lowest values of lambda), at a) the Pembrokeshire colonies, b) the Calf of Man and c) across all colonies.

Discussion

Consistent monitoring is central to a robust understanding of patterns of change across taxa and habitats, and data collection at suitable spatial and temporal scales is critical to accurately characterise patterns of change. To explore the effect of heterogeneity in data collection and management affects interpretation of population models, I examined estimates of pup production and survival at four colonies in the Irish Sea. I investigated how the spatial aggregation of monitoring records may affect estimates of pup survival, population growth rate and projections of population size. The results of this investigation indicate that grey seal pup survival rates exhibit marked spatial and temporal heterogeneity within and between the three main colonies in SW Wales, whereas pups at the Calf of Man colony exhibited greater, and more consistent, survival probability. Despite this moderating influence, within-colony heterogeneity in survival estimates (i.e. differences between pupping sites) was greater than that observed between colonies.

Influence of spatial scale on summary estimates of pup survival and population dynamics

Estimating colony-level survival rates from highly variable rates at site-level, in the pursuit of simplified model parameters, risks information loss and the introduction of aggregation bias (Clark and Avery, 1976; Shafran-Nathan et al., 2017). However, management and conservation of grey seals in the UK is implemented across 14 broad-scale Management Units (MU). Each MU encompasses multiple pupping colonies, many of which are within SACs, and seven of these list grey seal as a primary qualifying feature: five in Scotland, one traversing the Scots-English border, and one in Wales (JNCC, 2022; SCOS, 2022). Since grey seal pup survival exhibits temporal heterogeneity at the site level, and grey seals are managed across hundreds of square kilometres, aggregation of monitoring data to inform management decisions is unavoidable. Similar challenges are faced in selecting appropriate spatial scales over which to define and investigate cetacean populations around the UK and Republic of Ireland. Individual MUs for these animals cover a greater area than MUs for grey seal, because for some species these are believed to be part of a single population, particularly common dolphin (*Delphinus delphis*), white-sided dolphin (*Lagenorhynchus acutus*), Risso's dolphin (*Grampus griseus*) and minke whale (*Balaenoptera acutorostrata*). MUs for these species extend as one contiguous region around the UK and Republic of Ireland, and as far east as the coasts of Denmark, Sweden and Norway (IAMMWG, 2015).

The total pup production for the period where observations coincide across all colonies (2009-2015) was almost seven times higher at Ramsey (n = 2043) than at the Calf of Man (n = 304). Ramsey in particular has exhibited a much larger increase in pup production over the observation period compared to other colonies (see **Chapter 2**). The spatial variability in pup production and survival rates that is illustrated here for four Irish Sea colonies reflects just a small portion of the UK grey seal population (SCOS, 2022; Thomas et al., 2019). This study estimated 764 pups in Pembrokeshire (Ramsey, Skomer and Marloes combined) and 51 pups at the Calf of Man for 2014, compared to around 60,000 across the UK (SCOS, 2017), increasing to around 68,000 in 2019 (SCOS, 2022). Similar variability in pup production and population density occurs in sub-populations around Scotland and the English North Sea coast, which represent the majority of the UK population estimate, approaching 160,000 (SCOS, 2022). While population density and rates of pup production and survival vary across the species' range, the magnitude, direction and spatial distribution of such variation is not uniform. Indeed, population estimates are themselves based upon assumptions of survival rates across the range, since exhaustive censusing of pupping sites is not possible.

Effect of population density on pup survival

The lower survival probability of pups on Ramsey is unlikely to be simply due to the shorter time series. Survival estimates on Skomer did not change markedly when the time series increased from the four years of the original study (Engbo et al., 2020) to 27 years in this analysis. Moreover, the period for the original analysis overlapped for Skomer (2012-2015) and Ramsey (2008-2015). Pup survival has previously been assumed to be density-dependent, with survival rates expected to reduce as pup numbers increase (Harwood, 1978; Thomas et al., 2019). Given the greater abundance and consistently lower pup survival (and lower mean population growth rate: $\lambda = 1.051$, $SE = 0.006$) at Ramsey when compared to the other colonies ($\lambda = 1.071$, $SE = 0.004$), density-dependent processes may be moderating survival rates here. At 31 out of 70 monitored sites, observations from this study align with the hypothesis, and for Ramsey in particular, every one of the nine monitored sites showed the same negative (albeit non-significant) relationship between pup survival and annual abundance. At 24 sites, survival rates appear to increase with population density, and at 15 sites, observations were either consistent throughout the time series (i.e. no interannual change in survival rates), or survival estimates were only made in a single year, so a trend could not be ascertained. However, this does not mean that pup-survival at these sites is not density-dependent, but instead may simply be an indication that these pupping locations have not yet reached carrying capacity (Lande et al., 2002; Svensson et al., 2011).

Sensitivity analysis indicated that estimates of mean pup survival can be affected by the inclusion or omission of certain sites. Here, estimates increase or decrease by up to 1%, depending on which sites are included. This is a reduction from the ±1.45% change observed during previous analyses (Engbo et al., 2020), suggesting that the inclusion of an additional colony (Calf of Man) and a longer time series from Skomer, has reduced the relative influence of site-specific survival rates when estimating means over a greater spatial scale. When pupping site was not considered, the small effect of pup population size upon sensitivity suggested that survival estimates from high-output beaches and less populated beaches may be assumed to be similarly representative. However, when estimated at the colony level, the effect of pup population size upon sensitivity became apparent, which suggests that site-specific differences in population should be accounted for with a suitable weighting incorporated into colony-wide survival estimates.

Estimated colony-specific sample size required to obtain a reliable overall estimate

The results of this investigation also indicate that projections could over- or under-estimate population trajectories if models are parameterised with estimates from sites where pup survival rates are consistently higher or lower, or exhibit more variability, than broad-scale patterns. This location-specific sensitivity may explain why the sample size required to achieve an accurate estimate of pup survival varied between colonies. However, the inclusion of an additional 18 years of observations from the Skomer colony since Engbo *et al.* (2020) suggests that confidence in smaller sample sizes (i.e. fewer individuals) may improve when the sampling duration increases. Nevertheless, monitoring at a greater number of sites is favoured as being more representative of the population than fewer sites being monitored for longer.

Effect of data source and accuracy on MPM projections of population trajectory

Understanding the effect of monitoring protocol and environmental heterogeneity upon estimates of pup survival is vital to ensure that biases are minimised and that sampling decisions can provide accurate assessments and predictions of population trajectory. Likewise, it is important to account for spatial heterogeneity when constructing models from data aggregated across multiple sampling sites as this variability can influence parameter estimates depending on how monitoring data are summarised. The trajectories presented here highlight the effect of modelling from unrepresentative estimates. Pup survival rates at the Calf of Man colony are consistently higher than at other colonies, so predictions modelled from these data could give a falsely optimistic view of population trajectory. Likewise, models from Ramsey, where survival rates are lower and less consistent, and population growth rate is lower, could give the impression that the wider population may be approaching carrying capacity. But the models above didn't account for changes in vital rates during other developmental stages, as transition probabilities were held static for juvenile and adult seals.

Changes in age- or stage-specific survival rates are central to variability in population dynamics from one time-step to the next (Caswell, 2001), particularly in stages (like breeding adults) that make a greater contribution to the population than others. This is observable across numerous taxa including bats (O'Shea et al., 2011), cetaceans (Arso Civil et al., 2019), pinnipeds (Thomas et al., 2019) and reptiles (Doak et al., 1994; Heppell, 1998), and sex-specific differences in survival rate can also add complexity to modelling estimates of population dynamics (Arso Civil et al., 2019). Short-term differences in the accuracy of monitoring observations may not be immediately problematic, but if these compound over time, subsequent projections may increasingly depart from real-world population trajectories.

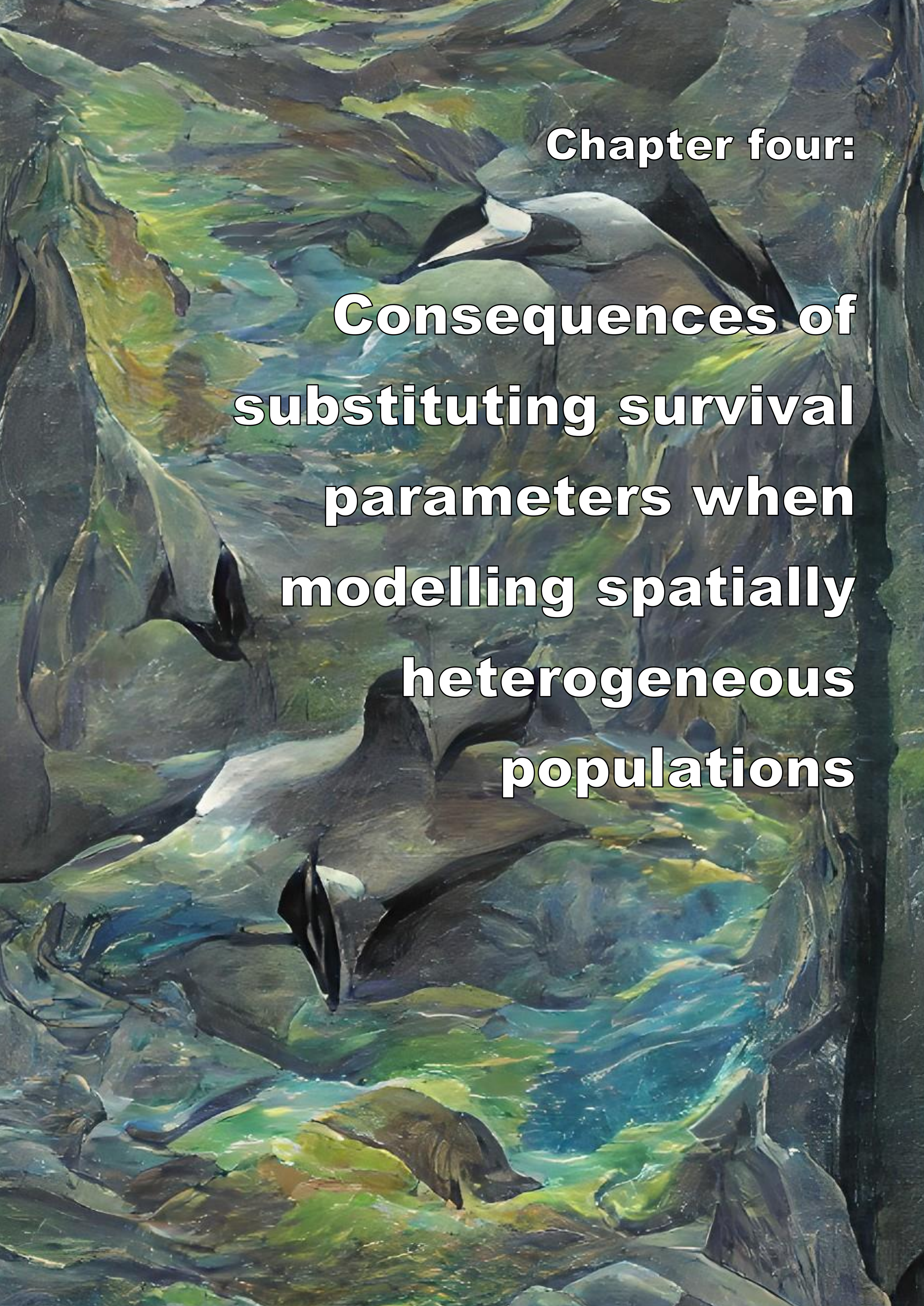
These results highlight the need to avoid, where possible, generalising predictions of population dynamics based upon estimates from a limited geographical range. Within-colony variation in pup survival rates may be driven by colony-level processes (Russell et al., 2019) which include topographical heterogeneity, exposure, and (less likely) food availability (Engbo et al., 2020; Hall et al., 2001; Smout et al., 2011; Twiss et al., 2003). Similarly, behavioural differences affecting interactions between mothers and pups may have an influence on pup growth rate (Twiss et al., 2012), with subsequent effects upon survival to independence (Bowen et al., 2015). Density-dependent processes are also likely to influence pup production and survival in grey seals (Thomas et al., 2019), as with other pinniped species (Holser et al., 2021; Pacoureau et al., 2017), but patterns of density dependence are not consistent across the colonies investigated here.

These analyses illustrate how decisions on the collection, handling and processing of life-history observations can have an effect upon the inferences that follow. In this case, aggregating observations over multiple spatial scales changed estimates of survival probability in grey seal pups. In turn, these estimates affected the accuracy of the MPMs on which they were based, and the metrics of population dynamics derived from them. For these reasons it is critical that caution is exercised when making predictions of population dynamics from the outputs of models built with spatially limited data, particularly in species with a large and heterogeneous distribution. My observations highlight the importance of monitoring species at as wide a range of sites as logistics and resources allow, to ensure that observations are representative of the diversity and spatial variation in survival probabilities and site characteristics. Incorporating estimates of survival for other demographic stages into these MPMs could provide greater accuracy to predictions of population trajectory, and could allow a fuller understanding of the effects of spatial and temporal variation in survival rates upon population dynamics. This would also allow a greater understanding of the relative contribution of each age stage to overall population trajectory. However, this information was not available for the colonies investigated above, and the logistical challenge of obtaining sufficient data for robust modelling, from multiple age stages, in such a wide-ranging and cryptic species, is recognised.

Regular monitoring of wildlife, habitats, and environmental conditions enable us to track changes in the natural world, and allows us to recognise patterns that may give cause for concern, but accurate information is critical to facilitate appropriate and successful responses. Management decisions based upon flawed inferences (i.e. those coming from non-representative monitoring) are themselves likely to be flawed, and could lead to costly programmes being initiated, or to missing opportunities to identify and mitigate declines. Not only could this affect the efficacy of current management schemes, but could also jeopardise the credibility of future management decisions. Future investigations of population dynamics should therefore consider spatial and temporal heterogeneity in methods of data collection and management, and should transparently take account of the uncertainties in the estimates of demographic rates on which population models are based. Our understanding would also benefit from exploration of potential drivers of pup survival at finer and broader temporal and spatial scales (e.g. beach topography and aspect, daily to weekly meteorological conditions, and incorporating additional breeding colonies from across the species’ range).

Chapter four:

Consequences of substituting survival parameters when modelling spatially heterogeneous populations



Abstract

In population biology studies of nesting vertebrate species vital rates such as survival and fecundity are often calculated from study plots, where nests and offspring can be consistently and systematically revisited, and rates estimated with confidence. In K-selected species such as seabirds, adults can be a particularly important demographic stage, but monitoring methods and logistical challenges at some colonies can preclude the collection of high quality, consistent data. In cases where vital rates are not possible to estimate, these may be sought from elsewhere in the species' range to model population dynamics, but there is no guarantee that vital rates at one location will be mirrored at another. Moreover, the effect of substituting vital rates in population models has seldom been the primary focus of research, since the priority in this context has often been on monitoring the management outcome, rather than improving the analytical decision process.

Using a 35-year time series of survival rates from five Manx shearwater (*Puffinus puffinus*) colonies, I investigated the consequences of substituting missing adult survival estimates with estimates from other locations when parameterising matrix population models. I found that models parameterised with directly observed data may have underestimated the population growth rate, giving a mean annual population decline of 4.55%, in contrast to regular censuses indicating a sustained population increase. I also found that substituted estimates of adult survival from the British Trust for Ornithology (BTO) Retrapping for Adult Survival (RAS) scheme may produce population trajectory estimates with a high degree of uncertainty. Population growth rate estimates from models parameterised with substituted values ranged from a 0.05% annual decline to a 2.20% annual increase, reflected in diverging simulated trajectories. The use of substitute data may be necessary in cases where resources, logistics

or genuine scarcity preclude estimates of survival being calculated, but it is critical that replacements are considered carefully so that model outputs do not inform inappropriate management decisions.

Introduction

Monitoring the size of a wild population is a common way to detect and evaluate changes in the abundance of species through time (Croxall et al., 2012; Engbo et al., 2020; Thomas et al., 2019), but simple counts of individuals are rarely adequate to investigate complex processes (Grosbois et al., 2009). Moreover, exhaustive sampling of individual animals is often precluded by limited resources, and further difficulties are introduced when species have cryptic lifestyles (Arneill et al., 2019). Even when individuals are observed, life-history processes that may result in spatial or temporal segregation of particular groups mean that any set of observations will only capture a snapshot of the population at the point of sampling. The structure of the population and spatial and temporal heterogeneity in demographic rates may be masked by incomplete observations so the tools employed to make predictions of population dynamics and trajectories, need to account for these gaps to allow reliable inferences to be made from resource-limited monitoring (Newman et al., 2014; Thomas et al., 2019).

When taken across a given time series, counts of individual animals used to estimate population size allow vital rates like survival and reproductive output to be estimated. Estimates of these vital rates at particular life stages can then be used to infer age-specific fecundity and probabilities of survival. Matrix population models (MPMs) are able to connect these processes to facilitate predictions of current and future population size and structure, and can be extended to derive metrics with which to quantify responses to perturbation (Capdevila et al., 2020; Caswell, 2018; Ingrisch and Bahn, 2018). Despite their potential usefulness in this respect, MPMs are only as reliable as the data used to construct them. For instance, sampling from low-population sites may be more prone to inter-annual variability, and inferring patterns at one site based on observations at another structurally or geographically different site may over- or under-estimate vital rates. Spatial and temporal heterogeneity of data collection, and variations in data consistency, will therefore affect the accuracy of estimates derived from MPMs (Engbo et al., 2020). Even with suitable tools, and careful consideration of how data are collected and analysed, an appropriate spatial and temporal resolution is critical. This is to ensure that inferences drawn from MPMs are representative and sufficiently accurate to improve our understanding of the population, and therefore appropriate to inform management decisions.

The Manx shearwater is an excellent subject on which to explore the effects of demographic heterogeneity and variability in sampling methods upon MPMs, as the species is predictable in the timing and location of breeding, and its nesting habits allow the fate of offspring to be tracked easily. The Manx shearwater raises one offspring per season and shows strong site fidelity, returning to breed in the same nesting burrow (Arneill et al., 2019). Breeding occurs at multiple discrete colonies around the UK and Ireland (Mitchell et al., 2004), with very rare movement of breeders between colonies (Harris, 1972; Leonard, 2005). Population dynamics at the Manx shearwater colonies in Pembrokeshire are particularly well suited for investigation, as the population is large and stable, numbering approximately 300,000 pairs in censuses between 1997 and 2018 (Perrins et al., 2019, 2012), and reliable demographic observations have been collected for over 30 years (Wilkie et al., 2019). Partial census attempts have been made here since the 1950s (Alexander and Perrins, 1980; Corkhill, 1973; Orians and Leslie, 1958; Smith et al., 2001), and full-island count estimates extend back to the late 1990s (Perrins et al., 2019, 2012; Smith et al., 2001). These most recent censuses, in 1997-

98, 2011 and 2018, provide a baseline of population size, concurrent with demographic observations, against which to compare model outputs and projections.

The details and drivers of colony-specific dynamics are not well understood in structured populations like the Manx shearwater (Breton et al., 2006; Horswill and Robinson, 2015). In this species particularly, post-fledging dispersal, and the resulting distribution of sub-adults prevents annual survival rates from being accurately estimated for the first year life stage. Subterranean nesting and nocturnal activity at the colony also makes monitoring of mature birds difficult.

Demographic monitoring is conducted at four breeding colonies around Britain and Ireland: Rum (Hebrides, Scotland), Copeland (County Down, Northern Ireland), Bardsey (Gwynedd, Wales), and Skomer/Skokholm (Pembrokeshire, Wales). Monitoring of fledgling survival has also been conducted at the colonies on Sanda (off Kintyre, Scotland) and Canna/Sanday (Hebrides, Scotland), but short time series, low sample sizes, and heavy predation have made these smaller colonies too complex to include in broader investigations. Annual survival rates of fledglings (productivity) have been estimated at all sites, but survival rates for adult birds are estimated only at the Skomer/Skokholm colony. This presents an opportunity to explore three fundamental aspects of Manx shearwater population ecology to investigate the role of demographic patterns on population-level processes, so the aims of this chapter are to:

1. Identify whether patterns in demographic rates vary between colonies or sub-populations, and whether this is reflected as trends in local population growth rate;
2. Investigate whether colony-specific demographic rates are replicated across the species' breeding range, and the extent to which rates can be substituted to fill gaps;

3. Explore local patterns in stage-specific survival rates and the potential effects upon long term population dynamics with projections of future population trajectories.

In this chapter I will explore these questions using observational data gathered between 1986 and 2021, to parameterise a series of MPMs. Models will be constructed for each year of observation at each breeding colony, with missing parameters being substituted with data obtained from the literature. These will then be investigated alongside equivalent MPMs constructed from more complete observations, and compared against a series of summary models, constructed from data aggregated at three spatial scales, across the whole time series. Following this, variability in colony- and site-specific survival rates will be projected to compare the long term effect of variability in survival rates.

The aim of this investigation is to better understand the patterns of heterogeneity in demographic rates, particularly survival rate, between breeding colonies, and the potential effect that this heterogeneity may have on broad-scale estimates of population dynamics. In addition, I aim to clarify the effect that substituting demographic information from one location may have upon estimates of population trajectory at another location, to provide a case study from which future research avenues may be explored.

Methods

Data collection: estimating survival rates

Survival estimates were calculated from chicks/fledglings and adult birds monitored annually in study burrows at the five breeding colonies. These data were obtained both directly from researchers monitoring Manx shearwater colonies, and from data published by the JNCC, Wildlife Trust for South and West Wales, and Bardsey Bird and Field Observatory (Brown and Eagle, 2019b; JNCC, 2021; Stansfield, 2020; Wilkie et al., 2019). At the Skokholm, Bardsey and Rum colonies, monitoring was undertaken over multiple sites, distributed across the colony, whereas monitoring at Skomer and Copeland was confined to one single study site. Study burrows comprise either a natural or artificially excavated nest chamber, covered by a removable roof, to allow repeated monitoring of the burrow throughout multiple seasons.

The annual rate of survival from laid egg to fledged bird (fledgling survival rate) was calculated simply as the proportion of birds that survived to independence, relative to the number of eggs observed within each study site. Fledglings were considered as birds that were either observed to be ready or near-ready to depart the colony at the end of the breeding season based upon the proportion of down in the plumage (Stansfield, 2020), or were assumed to have survived and departed before they could be recorded, based upon healthy growth through the season, and having reached a wing length of at least 200 mm (Brown and Eagle, 2016).

Adult survival was only calculated directly at the Skokholm and Skomer colonies. Here, birds are routinely ringed as part of ongoing monitoring, and adult survival rates were estimated as the proportion of ringed mature birds that survived from one year to the next. On Skomer this was calculated from the number of birds encountered, adjusted for the probability of detection and to account for survival rates in previous years. On Skokholm, this was calculated more simply, and similarly to fledgling survival, considering only the number of marked birds encountered in one year, as a proportion of marked birds encountered in the previous year. Kendall's rank correlation analysis (selected to account for the 0-1 bounding of the data, and the occurrence of ties) indicated that the two calculation methods were very highly correlated ($\tau = 0.986$, $z = 7.055$, $p < 0.001$, $df = 24$), so the estimates derived from the two methods are here considered directly comparable.

Data analysis

Data selection and preliminary analysis

To test for between-site trends in vital rates in corresponding years, I conducted a pairwise Kendall's rank correlation analysis between fledgling survival rates at all sites. Kendall's rank correlation was chosen to account for the non-normal proportion data, relatively small sample size, and the potential for tied observations. At sites where adult survival rates were estimated from observations, Kendall's rank correlation was also calculated for fledgling survival, and adult survival, between colonies (fledgling vs fledgling, adult vs adult), and on fledgling survival and adult survival within colonies (fledgling vs adult). This was conducted both within concurrent years, and with a one-year lag in adult survival, to address possible effects on fledgling survival in the following year.

I used binomial generalised additive models (GAM) to investigate potential non-linear temporal trends in fledgling and adult survival estimates at each colony. Survival rates were considered as binary variables (n alive, n dead) in models, rather than as decimal values, and ‘year’ was the only predictor, included as a smoothing term. I also used GAMs to investigate the relationship between the variability of fledgling survival rate and sample size at each site, and the relationship between variability of fledgling survival and the number of sampling sites at each colony.

Matrix model parameterisation

Manx shearwater development was split into six stages, each representing one year of development: one year as fledgling, four years as juvenile, and one year as adult, repeating for the remainder of the lifespan. Each stage was assigned a transition probability, based upon annual survival rates from one developmental stage to the next, and estimated fecundity rates were included for all stages in which breeding has been observed. This structure is illustrated as a generic diagram in Figure 4.1.

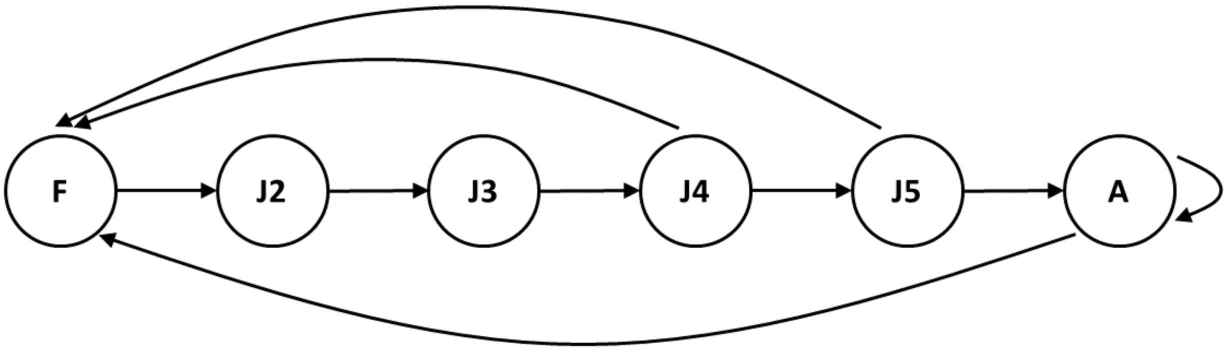


Figure 4.1. Simplified transition diagram representing Manx shearwater life cycle. Text inside circles represents annual age stages (F = Fledgling, comprising whole of first year; J2 to J5 = Juvenile in 2nd to 5th year, respectively; A = Adult), right-pointing arrows indicate development, left-pointing (curved) arrows indicate fecundity, and reflex arrow indicates adult survival.

Year one: fledgling survival

The three developmental stages of the first year (egg, chick, and fledgling) were combined into one survival estimate, since productivity in birds is considered as the proportion of individuals which survive from parturition (egg-laying) to independence (fledging). This was included in the matrix model as a single rate of survival from egg to fledgling.

Fledgling survival estimates implicitly incorporate variability about the observed value, as a result of uncertainty about the actual fate of birds. In some cases, fledgling survival estimates may be slightly inflated if absent near-fledged birds are assumed to have survived in the absence of evidence to the contrary. Similarly, where monitoring of chick development and fledgling survival is not exhaustive in a colony, fledgling survival rates may be higher or lower than those observed but are assumed to balance out overall.

Years two to five: juvenile survival

Manx shearwaters spend their second and third years of life away from land entirely and begin to return to their natal colony in the fourth and fifth years, prospecting for mates and burrows in which to breed. Since juveniles were not monitored directly here, and without identification from a known time point (usually leg rings/bands for birds), empirical survival estimates were not possible to obtain for juveniles. A small number of limited-scale observations do, however, suggest an overall juvenile survival rate (i.e. the four years from fledgling to adult) of approximately 0.33 (Brooke, 1977). The annual survival rate for juvenile birds was therefore taken as $\sqrt[4]{0.33} = 0.76$, for all four years.

Year six onwards: adult survival

The majority of Manx shearwaters begin returning annually to the colony in their sixth year, when they reunite and breed with established partners, usually occupying the same burrow each year. Where adult survival was estimated from observations, this rate varies between years. In colonies where adults were not monitored, adult survival rates were estimated in two ways: the survival rate published by the British Trust for Ornithology (BTO) Retrapping Adults for Survival (RAS) scheme (given as 0.92 (BTO, 2015)), and mean adult survival calculated from colonies where monitoring took place, only for corresponding years (see model structures below for details).

Adult survival estimates are expected to be a minimum annual survival rate, since birds are assumed to have died unless they are directly observed. Birds which are assumed to have died, but which are later observed alive will increase the survival estimate, but it is only possible for the estimate to be reduced by the observation of a recorded bird being found dead later in the same season. Given the size of the colonies where adult survival rates are estimated, and the sampling effort involved, this scenario is unlikely.

Fecundity

Most Manx shearwaters begin breeding in their sixth year, and an annual reproductive rate of 0.84 is estimated for each pair (Perrins et al., 1973).This was halved to obtain an estimate of fecundity of 0.42 for mature females: infidelity (and potentially higher fecundity) in males is unlikely given the high investment and co-ordination in parental care (Gillies et al., 2022), although this can never be ruled out . Some breeding has also been observed in earlier years, albeit at a much lower rate, and one small-scale meta-study found that approximately 4% of birds breed in each of the fourth and fifth years (Harris, 1966). Again, this was halved in each case to give a fecundity estimate of 0.02 for juveniles at these stages.

Model structure

To examine the effect of collecting data from particular stage-specific survival rates upon the overall population growth rate, and the value of collecting this accurately, two model structures were considered, based upon survival estimates from different sources.

Structure one: Directly observed data

To investigate cases when observational data are available for multiple developmental stages, a 'Direct' model was parameterised using fledgling and adult survival estimates from only Skomer and Skokholm, with no observations from other colonies. Since fledgling survival can be estimated within the season, this parameter was available for all years of observation. Adult survival estimates were not available for the first and last years of the time series, since these rates are calculated over consecutive years. Moreover, observations were limited to those years in which monitoring was conducted at both colonies to make direct comparisons possible, which reduced the time series from 29 years to six years (2013-2018).

Structure two: Substitute data

Fledgling survival rates estimated from observations at all five colonies were included in the matrix models and these vary between years and colonies. Adult survival rates were included as observed values where available (i.e., from Skomer and Skokholm), and missing values from other colonies were substituted. The mean estimated survival rate from the BTO RAS scheme, held constant at 0.92 throughout was selected as the substitute adult survival rate. The 'Substitute' model simulates a scenario in which published data are assumed to be representative of rates across the study range, and used to fill gaps in observations. In some cases, the substituted data may come from a variety of sources, and it may not be clear over what geographical range or time series they were estimated, although in the case of the BTO RAS data, this is known.

Spatial and temporal heterogeneity

As well as parameterising individual matrices for each monitoring site and each year of monitoring at the respective colony, summary matrices were also constructed to estimate population characteristics across one temporal and three spatial scales. At the temporal scale, estimates of mean fledgling survival were calculated for each year, across all colonies and sites combined (for simplicity referred to as the ‘population’, and comprises only the colonies where monitoring was conducted), providing a single matrix for each year of monitoring. Spatially, survival estimates were summarised across all years, to create a single matrix of survival estimates at population-, colony- and site-level. Site-level fledgling survival estimates were compared in years where monitoring was undertaken at all sites (2013 only) and considered against the overall mean fledgling survival estimate for that monitoring period. This was used as a measure of sensitivity, to understand how estimates at each monitoring site may influence the estimate of overall mean fledgling survival.

Estimating population characteristics

Long-term population growth rates were estimated as the dominant eigenvalue (λ) from each matrix, at every spatial and temporal level. Overall population trajectory was then projected via iterative stochastic simulation. Projecting the population from a single matrix would produce a deterministic estimate of population trajectory, but variability can be introduced as an analogue to natural heterogeneity by using multiple matrices throughout the projection. I introduced this variability by projecting the population 1,000 times from the site-level matrices that produced the ten highest and ten lowest estimates of population growth rate, to produce a 'best case' and 'worst case' projection.

The initial population structure used in the projections was taken as the mean asymptotic stable structure (*w*) across monitoring sites.. The stable structure was calculated from a transition matrix and is a vector comprising the proportion of individuals at each developmental stage in the population, when the population is stable. Each starting structure (s_i) was scaled such that $\|s_i\| = 1$, to allow comparison between subsequent trajectories. Comparisons were then made between projections from the Direct and Substitute models to investigate the effect of estimating population trajectory from remotely-sourced survival rates.

Results

Fledgling survival at all colonies

The results of the GAM described above suggests an inconsistent temporal influence in fledgling survival (Table 4.1). Although no clear trend was apparent at most colonies, an overall positive trend was identified at Copeland (Figure 4.2), analogous to a quadratic relationship (edf = 1.96, $p < 0.001$, GAM). Whereas Skokholm appears to be relatively stable (edf = 1, $p = 0.043$, GAM), Skomer, Bardsey and Rum exhibited a more non-linear, fluctuating variability in fledgling survival rates. Summary statistics from all GAMs are presented in Table 4.1. In the years where monitoring of fledgling survival at Skomer and Skokholm overlaps (2013-2019) estimates at Skokholm are also consistently higher than those at the Skomer colony, approximately 3 km to the north.

Table 4.1. Parameter estimates and model summary statistics for GAMs of fledgling survival against time (year), at each of the colonies.

Colony (n years)	**Parameter**	**Smoothed terms**			**P**	**adj. r^2**	**Deviance explained (%)**
		edf	**ref df**	**χ^2**			
Rum (8)	Year	5.705	5.962	89.19	<0.001	0.30	48.1
Copeland (7)	Year	1.961	1.998	51.91	<0.001	0.94	95.1
Bardsey (8)	Year	3.689	4.506	36.59	<0.001	0.62	68.4
Skomer (29)	Year	5.288	6.142	28.64	<0.001	0.13	28.9
Skokholm (8)	Year	1	1	4.10	0.043	0.10	20.9

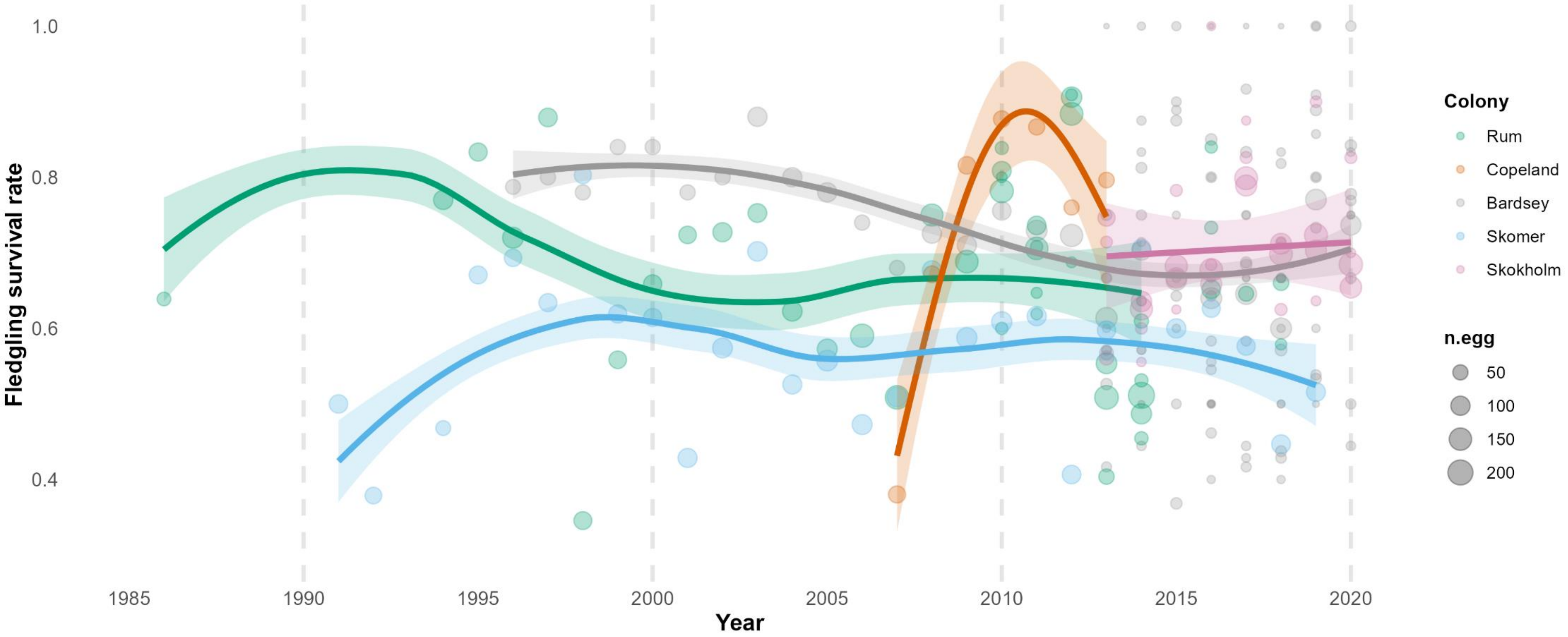


Figure 4.2. Fledgling survival estimates calculated from GAMs across the total monitoring period (1986-2020) at the Rum, Copeland, Bardsey, Skomer and Skokholm breeding colonies. Points indicate site-level mean fledgling survival rate, with points sized relative to sample size. Solid lines indicate colony-level mean estimated by GAMs, with 95% confidence intervals (shaded ribbons)..

Fledgling and adult survival rates at Skomer and Skokholm

Adult survival estimates were relatively consistent across the Skomer (mean = 0.879, SE = 0.011, n = 26) and Skokholm (mean = 0.857, SE = 0.018, n = 8) colonies, while fledgling survival rates was more variable (Skomer: mean = 0.563, SE = 0.022, n = 29; Skokholm: mean = 0.713, SE = 0.023, n = 9)..Adult and fledgling survival rates at the Skomer and Skokholm colonies did not display any association with each other, either in concurrent years (Skomer: $\tau = 0.068$, $p = 0.628$, df = 24; Skokholm: $\tau = -0.200$, $p = 0.719$, df = 4), or when adult survival was offset by one year (Skomer: $\tau = 0.055$, $p = 0.692$, df = 24; Skokholm: $\tau = -0.067$, $p > 0.99$, df = 4). Likewise, generalised additive models of adult survival rates with time as a smoothing term indicated no clear trends in the whole time series.

Table 4.2. Model summary statistics for GAMs of adult survival against time, at the Skomer and Skokholm colonies for the whole time series and for years in which monitoring coincided .

Colony (n)	**Parameter**	**Smoothed terms**			**P**	**adj. r^2**	**Deviance explained (%)**
		edf	**ref df**	**χ^2**			
Whole time series (Skomer: 1993-2018, Skokholm: 2014-2021)							
Skomer (26)	Year	1.967	1.999	29.54	<0.001	0.13	18.1
Skokholm (8)	Year	1.837	1.973	24.17	<0.001	0.38	49.5
Coinciding years only (2014-2018)							
Skomer (5)	Year	1	1	1.86	0.173	-0.25	5.72
Skokholm (5)	Year	1.673	1.893	4.15	0.180	-0.28	22.1

Sensitivity of mean fledgling survival estimate

The sensitivity of the mean estimate of fledgling survival (0.623, SE = 0.002) to variation in site-specific survival rates ranged between +0.015 to -0.025. Sensitivity values correspond to the difference to the overall mean that would result from a site being removed from monitoring. Removal of sites with positive sensitivity values would increase the overall mean, and vice versa. Relative fledgling survival estimates at each monitoring site are shown in Figure 4.3.

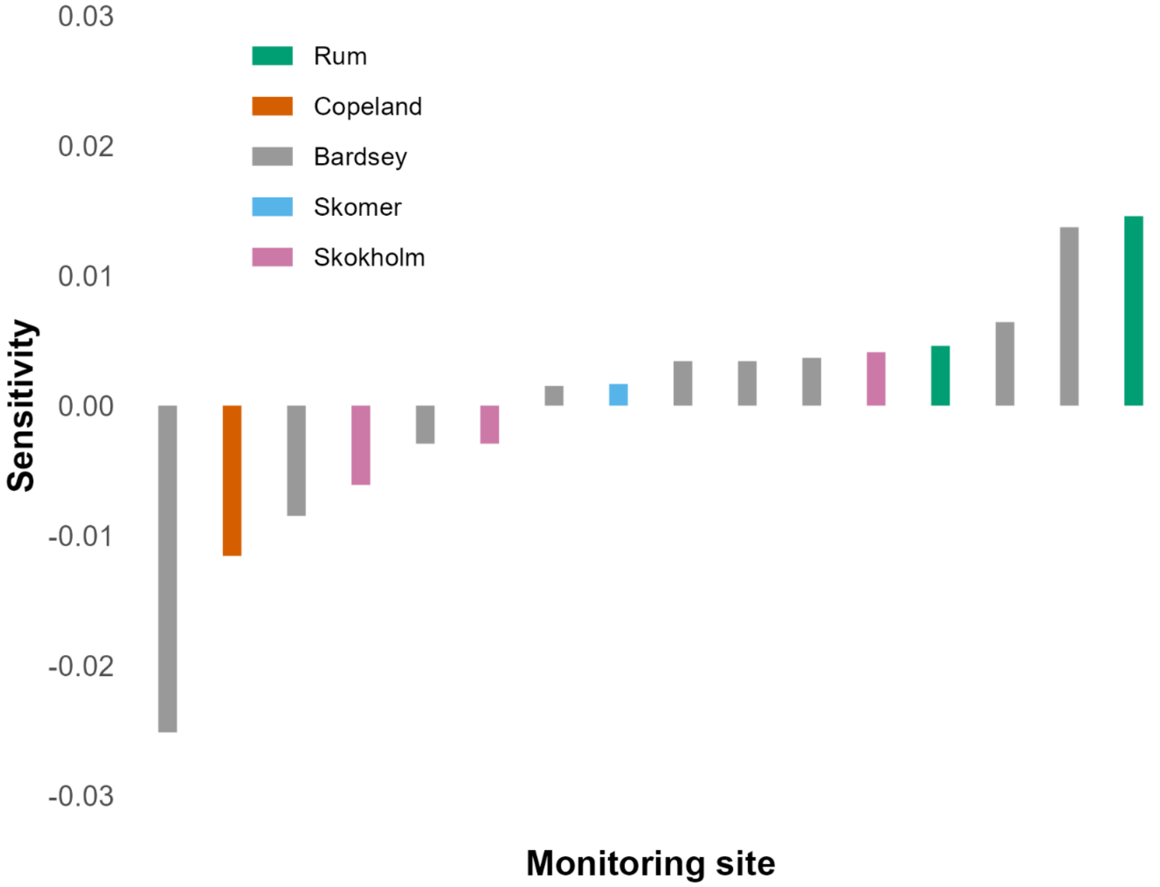


Figure 4.3: Sensitivity of the overall estimate of mean fledgling survival to within-colony variability between monitoring sites. Calculation of sensitivity is based upon only one year since monitoring at all colonies only coincided in 2013. Note that the Copeland and Skomer colonies only contain one monitoring site.

Spatial patterns of variability in fledgling survival

Fledgling survival estimates varied between sites and colonies, with some sites exhibiting relative stability between years compared to others. Much of this disparity is likely due to differences in population size between sites (Figure 4.4), since variance reduced with population size (F = 44.04, edf = 1.849, ref. df = 1.977, p < 0.001, GAM), although variance was unaffected by the number of within-colony sites monitored annually (β = 0.002, SE = 0.016, z = 0.114, p = 0.910, df = 3).

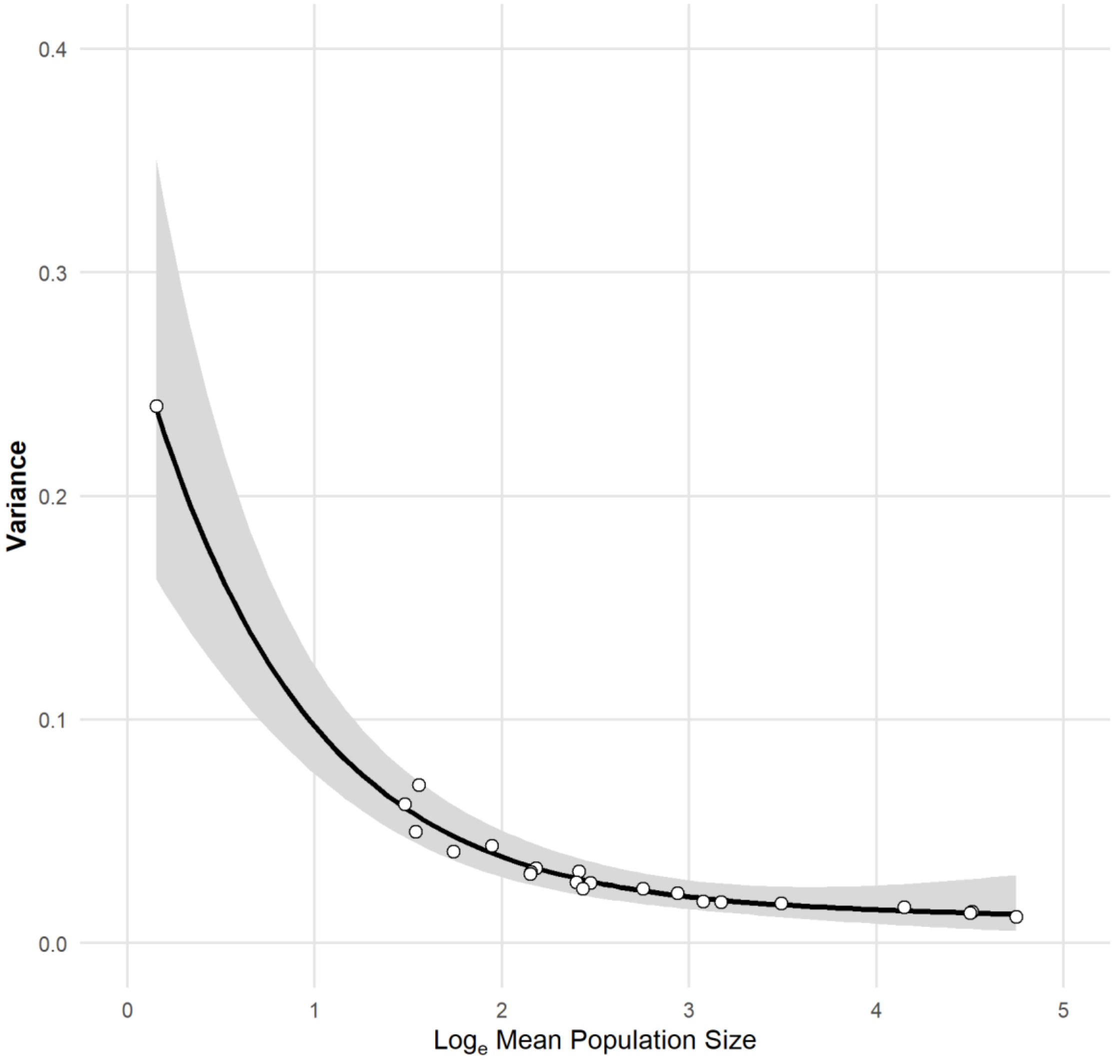


Figure 4.4: The relationship between variance and population size as plotted from a simple generalised additive model of mean population size at the colony-level against variance in fledgling survival estimates. Here variance in fledgling survival estimates reduces as population size reduces.

57.3% of the variation in fledgling survival estimates was explained by the effect of nesting site, with 32.3% of variation accounted for at the colony level, and temporal effects accounting for 10.4% (Figure 4.5).

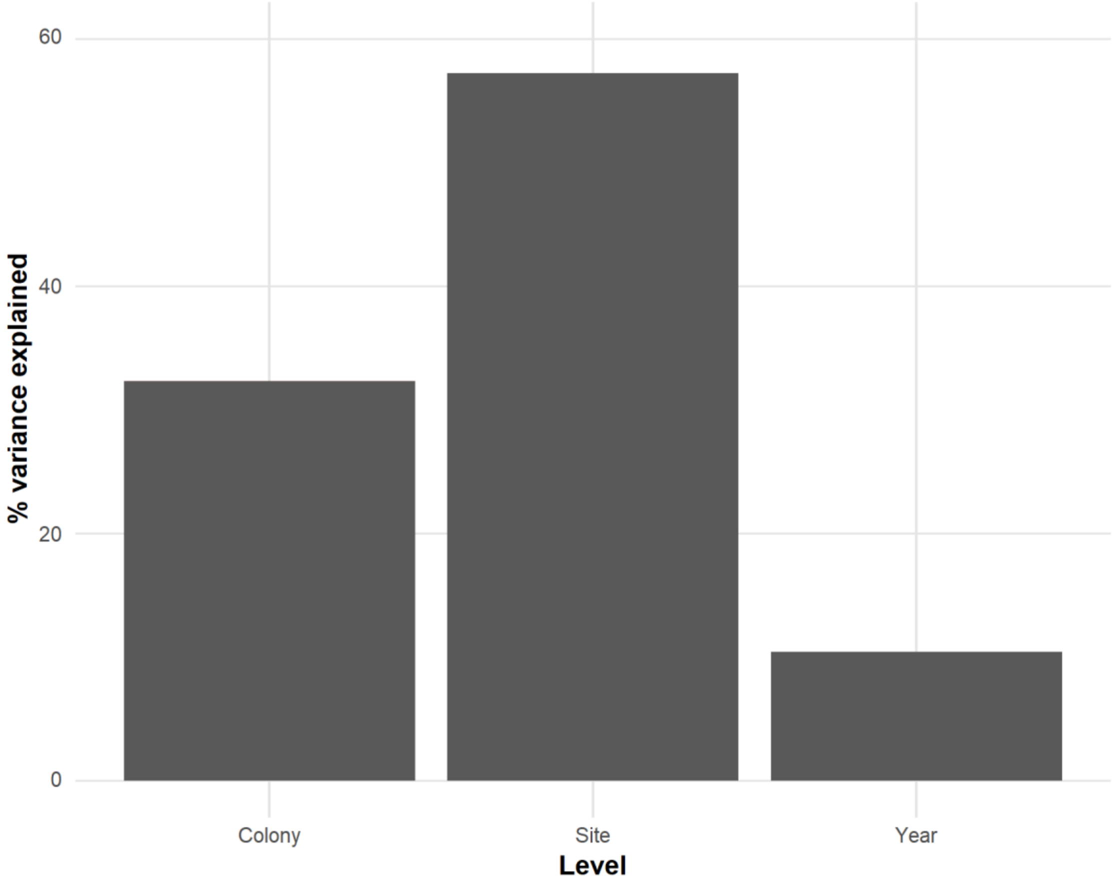


Figure 4.5: Hierarchical partitioning of variance reveals the influence of spatial and temporal heterogeneity in calculating fledgling survival, illustrating the effect upon explained variance in fledgling survival estimates when considered across colony (32.3%) and site level (57.3%), and across years (10.4%).

Effect of adult survival on population parameter estimates

Direct model

Population growth rates at the Skomer and Skokholm colonies were broadly the same, with only small variation between the one monitoring site on Skomer (Isthmus: $\lambda = 0.955$), and the three sites on Skokholm (Crab Bay: $\lambda = 0.957$, Lighthouse: $\lambda = 0.951$, Quarry: $\lambda = 0.955$), giving an estimate of $\lambda = 0.955$ at both colonies. Population trajectories were projected from matrices at each colony (Figure 4.6a) but given the similarity in population growth rate at each site there is very little distinction between these two trajectories.

Substitute model

The mean population growth rate estimated across all colonies and years, calculated from the transition matrix parameterised using the BTO RAS scheme estimate for adult survival in all cases, was 1.008, corresponding to an annual 0.8% increase in population size. Population growth rates calculated at the colony level indicated growth or near-stability at all colonies (range = 0.999 to 1.016, mean = 1.009, SE = 0.002, n = 5), equivalent to a mean 0.9% annual increase in population size. Lambda values at the site level varied to a lesser extent (range = 0.995 to 1.022, mean = 1.008, SE = 0.001, n = 24), corresponding to an annual mean 0.8% increase in population size. Estimates of overall population trajectory (Figure 4.6b), based on the three highest lambda values exhibited growth (mean λ = 1.020), while a marginal decline was visible for the population trajectory based on the three lowest site-level lambda values (mean λ = 0.998). Details of the sites included in the stochastic projections in Figure 4.6b are presented in Table 4.3.

Table 4.3. Monitoring sites with the three highest and three lowest population growth rates (λ), used for stochastic projection of transition matrices parameterised with substituted adult survival rates.

	Colony	Site	n years	Lambda
Lowest	Bardsey	Mountain North	5	0.995
	Skomer	Isthmus	29	0.999
	Bardsey	Traeth Ffynnon	6	1.001
Highest	Bardsey	Cristin	7	1.019
	Bardsey	Tŷ Pellaf	7	1.019
	Bardsey	Mountain South	4	1.022

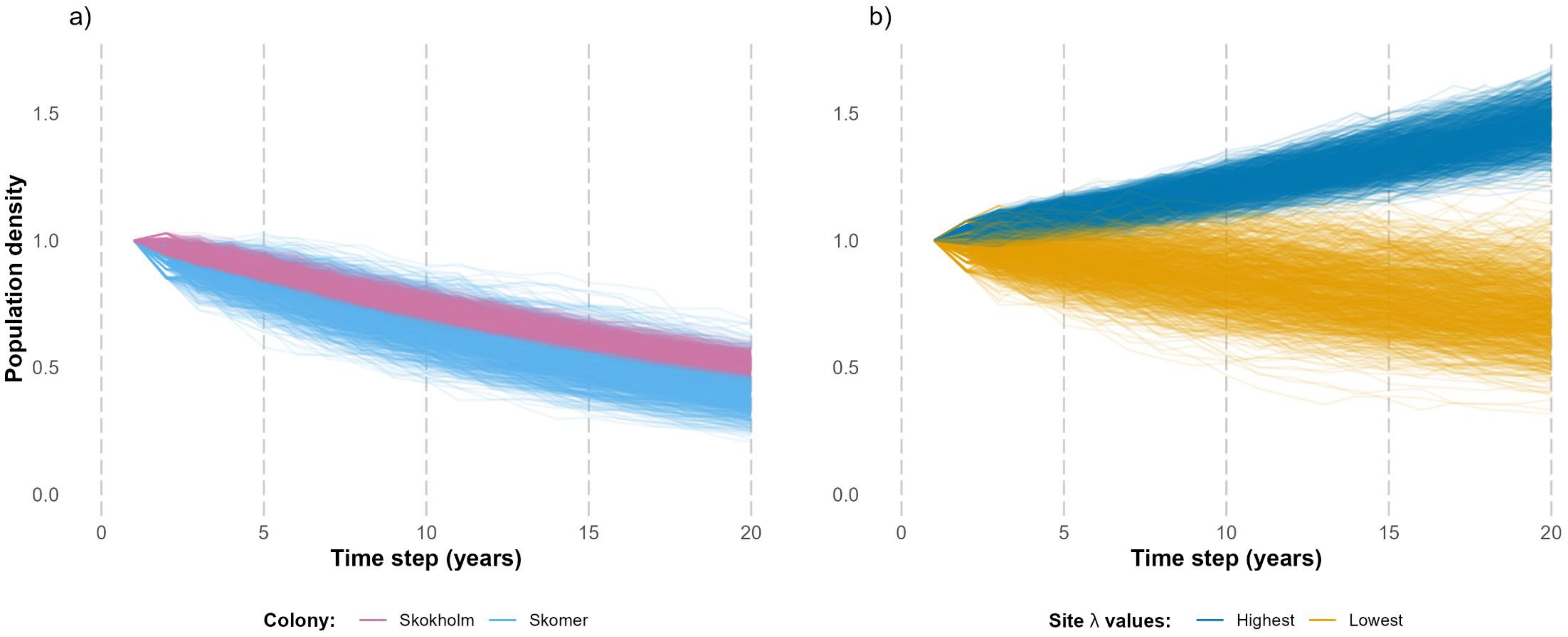


Figure 4.6. Stochastic projection of population trajectories estimated from observed fledgling and adult survival estimates at the Skomer and Skokholm colonies (a), compared with observed fledgling and substituted adult survival estimates (b).

Discussion

For species too scarce to monitor consistently, substitution of unknown demographic parameters when modelling population dynamics may be borne out of necessity. Conservation management decisions for scarce species may be informed, in part, by population models, and in the absence of empirical data, the only alternative may be to use data from a "similar" species. For less scarce species, substitution of demographic information may also be required, but the paucity of information is more likely to be due to logistical difficulties, rather than scarcity of individuals to monitor.

Estimates of annual fledgling and adult survival rates in Manx shearwater indicated an overall stable trend through time, with no significant change in vital rates at any of the colonies monitored. Fledgling survival estimates at the Skokholm colony did exhibit a small decline over the 2013-2019 period when monitoring overlapped with Skomer. However, this may be an artefact of the short period investigated (seven years) which may not have captured longer term variability, since inclusion of a single additional year (2020) in the regression negated any temporal effect. Continued monitoring at Skokholm will likely clarify long term trends here. Fledgling survival at Copeland did appear to display a sharp increase at the start of the monitoring period, followed shortly by a small decline, although no clear trend was discernible. Again, continued monitoring would clarify whether later observations at Copeland were the beginning of a decline in fledgling survival or simply a larger fluctuation in an otherwise stable long-term trend. Longer term monitoring, being more representative of local patterns, would also allow more credible comparisons between colonies.

Across all colonies, temporal effects accounted for 10% of variability in fledgling survival, with spatial effects accounting for the remainder: 32% between colonies, and 57% within colonies.

Not accounted for in this study, however, are environmental and intrinsic drivers such as age and sex (Oro et al., 2010; Sandvik et al., 2012, 2007) and individual behaviour, which may account for over 4% of variation in survival rates across taxa (Moiron et al., 2020). This is in contrast with observations from burrowing mammals, for which temporal variation has previously explained between 15% and 89% of survival in young animals (Ozgul et al., 2006). At sites where observations have more leverage over population-level estimates, removal of these observations may lead to under- or overestimation of fledgling survival rates by between 2.3% and 4.0%, respectively. Exclusion of all sites either above or below the mean survival estimate would change the overall fledgling survival estimate by up to 9.2% in either direction. It is important, therefore, that spatial variation of vital rates within the colony is incorporated into monitoring, so that colony-level estimates are representative and useful.

Results from these MPMs suggest that annual monitoring observations made at the Skomer and Skokholm colonies may not be reflective of overall population-level processes. Here, estimates of population growth rate and modelled population trajectories, derived from observations of annual fledgling and adult survival rates, suggest a long-term downward trend in population size, in contrast to the stable population observed from near-decadal censuses (Perrins et al., 2019, 2012; Smith et al., 2001). Given the stability of observed population size and annual survival estimates, compared with the population decline projected by these MPMs, it is possible that annual survival rates have been underestimated in either, or both, the fledgling and adult stages. When observed adult survival rates from Skomer and Skokholm (mean = 0.87) were supplemented with estimates from the literature to model the population across all colonies (the Substitute model), the mean adult survival rate across all colonies and years increased to 0.91, and the trajectory switched from long term decline to stability. This change represents just a 4% difference in adult survival rates but corresponds to a shift from a 4.6% annual population decline to a stable population. Unchanged, this projection would correspond to the population halving in size in approximately 15-20 years (Figure 4.6a), illustrating the significance of adult survival rates to overall population trends. Estimates of adult survival from additional colonies could improve the accuracy of these projections, and allow populations to be modelled more reliably at the multi-colony or regional scale.

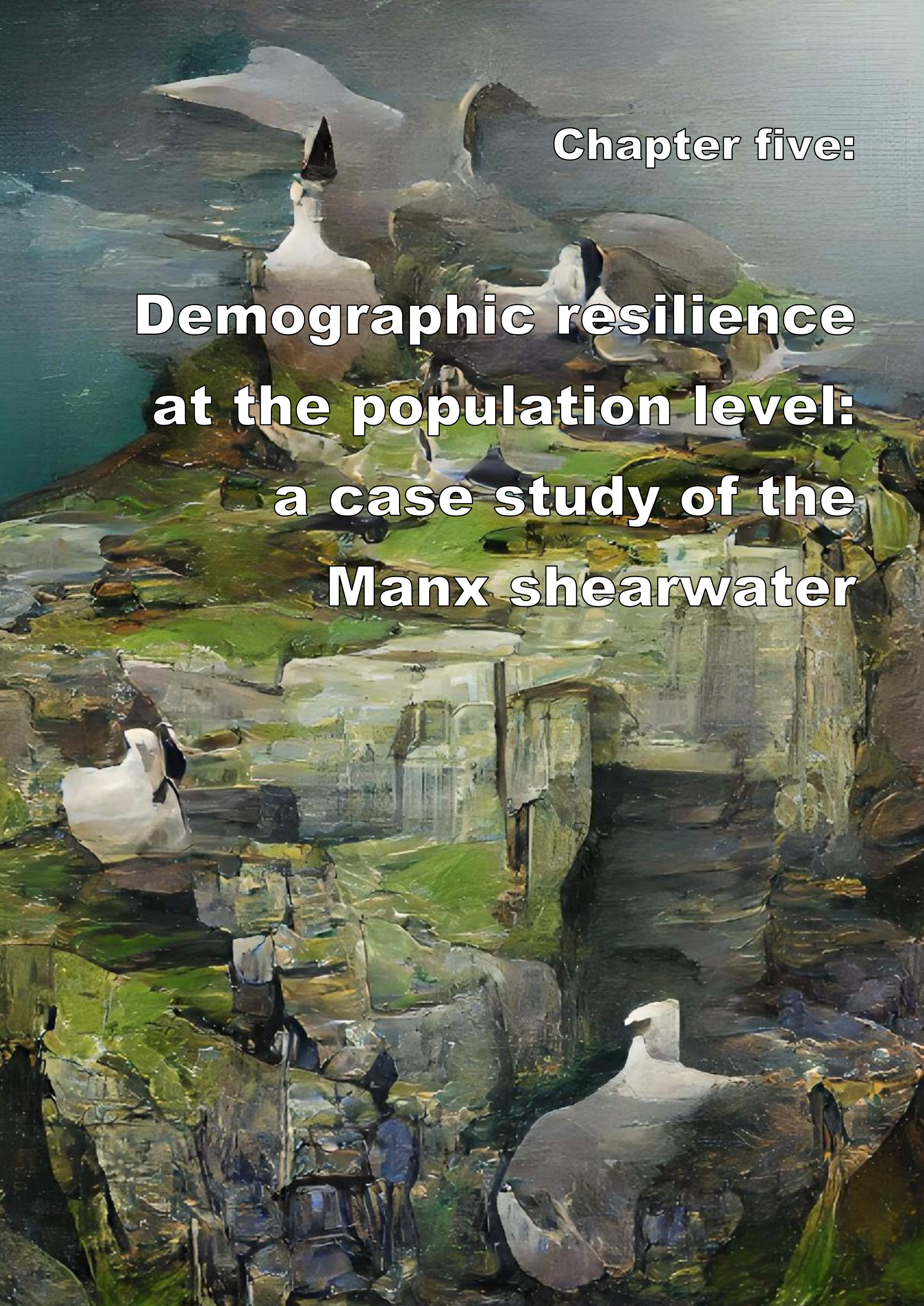
Although MPMs are a common tool for investigating population dynamics, their use can be limited by inappropriate parameterisation (Kendall et al., 2019) so accurate estimation of vital rates is critical to understanding, and reliably modelling, population trajectories (Abadi et al., 2010). Under-estimation of vital rates was previously identified as a potential issue in monitoring at Manx shearwater colonies (Robinson and Ratcliffe, 2010) where Integrated Population Modelling (IPM) was reviewed as a tool for monitoring of UK seabird populations. IPM allows demographic information to be modelled alongside census estimates to create a more (though not fully) comprehensive picture of population dynamics (Besbeas et al., 2002; Brooks et al., 2004; Schaub and Abadi, 2011). This approach may be of particular value when applied to species which are scarce or endangered, logistically difficult to monitor, or both (Oro et al., 2004; Schaub et al., 2007), or where the quality and completeness of data may be inconsistent (Ahrestani et al., 2017; Robinson et al., 2014). Even so, accurate and representative estimates of abundance and demographic rates are still required, whatever modelling approach is employed.

Monitoring sites with more or less favourable conditions for survival may inadvertently skew aggregated survival estimates (Engbo et al., 2020), so although variance appears above to be unaffected by the number of sampling locations, modelled projections may be refined by inclusion of observations across a greater spatial scale. However, increasing the spatial scale of demographic sampling could make modelling more complex, particularly when making projections at broader scales. In the most recent census of the Skomer and Skokholm colonies, ‘calibration’ surveys were undertaken in additional areas of the colony to improve the accuracy of the final population estimate (Perrins et al., 2019). This resulted in more uncertainty from higher variance in the additional observations: broader sampling may capture more information, but this doesn’t mean that results will be tidier.

Complexity aside, capturing within-colony observations over a greater spatial scale, particularly at the larger colonies (e.g. Skomer, Rum), could provide a more comprehensive overview of the population. This is evident from observations at the Bardsey colony, where fledgling survival was estimated at a total of 15 sites around the colony (albeit not all concurrently), which allowed patterns to be identified at a finer spatial scale, but appears to have introduced a greater degree of variability to the modelling. A greater range of sampling sites may also reduce the relative influence of any particular location upon colony- or population-wide estimates.

Procellariiforms (which includes the Manx shearwater) are noted for their high adult survival rates (Croxall and Rothery, 1991), and the estimates considered above are consistent with this. This also means that factors affecting adult survival may have a disproportionately large influence upon population dynamics (Croxall and Rothery, 1991; Doherty, Jr. et al., 2004), which is common amongst long-lived species and is observed across taxa, including bats (O’Shea et al., 2011), cetaceans (Arso Civil et al., 2019), pinnipeds (Thomas et al., 2019) and reptiles (Doak et al., 1994; Heppell, 1998). Monitoring is central to tracking change, but an understanding of demographic processes such as productivity and survival is important for interpreting past and current patterns, and for anticipating future dynamics (Robinson et al., 2014). Accuracy in estimating demographic rates is also critical (Abadi et al., 2010) for population trajectories to be modelled informatively. The results above highlight the fact that, while vital rates may usefully be substituted from elsewhere in a species' range, local variability in survival rates can skew the outputs of matrix population models. This is especially true when substituting estimates of survival for influential stages, and care should be taken in choosing appropriate replacements, or to select alternative methods which are able to accommodate limited data.

The Manx shearwater is well-studied across its breeding range, particularly at the larger colonies of Rum, Copeland, Bardsey and Skomer, and long-term data on survival and productivity have been collected from multiple locations therein. While data are openly available from much of this monitoring, much remains inaccessible. Making data, and relevant metadata, accessible to investigators outside of the original research scope, particularly for less well-studied species, would greatly reduce the need for parameters to be estimated in the first place. Numerous facilities for the dissemination of ecological data already exist, and across taxa and ecosystems such openness would contribute to a greater understanding of the spatial and temporal variation in numerous species' population dynamics, and would undoubtedly enhance our broader understanding of the communities in which they occur.



Chapter five:

Demographic resilience at the population level: a case study of the Manx shearwater

Abstract

A species' response to perturbation is associated with that species' resilience and its ability to withstand disturbance. To measure, predict and manage changes within a population arising from perturbation, it is useful to quantify a species' resilience and the components or phases of its responses. Where perturbation affects population structure by driving change in survival at specific developmental stages, responses may depend upon the contribution of each stage to the population structure. Stages with higher survival or fertility may contribute more to population stability and growth, so disruption may have a greater effect on population size. The effect that disturbance may have on population-level processes can be estimated via perturbation analysis, which examines the response of future population dynamics to changes in vital rates or population structure.

The majority of research into resilience focuses on responses to perturbation at the ecosystem or community level. To address the paucity of knowledge of resilience at lower organisational levels I investigated the population-level responses of a species to perturbation at specific developmental stages. The Manx shearwater provides a good opportunity to investigate the effects of stage-specific perturbation upon population density because reliable demographic observations for specific developmental stages have been collected for over 30 years. I explored the effects of stage-specific perturbation by simulation of specific reductions in stage-specific survival rates for fledgling, juvenile and adult Manx shearwaters. From here I calculated indices of resilience to quantify the population-level response in the first time-step following perturbation, and the response over the longer term as the population returned to stability. My investigation suggested that reduction in stage-specific survival rates does elicit population-level responses to disturbance, with adult survival

exerting greater influence over population growth rate than survival rates at other stages. These responses were not uniform amongst indices, however, as the magnitude and direction of responses varied between stages. In the case of recovery, juvenile survival rates had a much greater impact on the time taken for the population to return to stability. These results also highlight the latency of population effects when disturbance to survival occurs to stages which make a smaller contribution (e.g. juveniles) to observed population dynamics.

Introduction

The concept of ‘ecological resilience’ (Holling, 1973) is based on the principle that multiple stable states can exist for any given system. Instead of focussing on the time taken to return to an ‘optimum’ state, ecological resilience considers the nature and magnitude of the disturbance and the response of the ecosystem, rather than how quickly the initial state is restored. To make sense of the processes involved in an ecosystem’s response to perturbation, and to be able to quantify, predict and manage subsequent changes, it may be useful to consider different components of resilience separately.

Previous attempts to establish a means for quantifying resilience have provided an overview of the topic, with descriptive accounts of some processes that may be measured (Angeler and Allen, 2016; Chuang et al., 2018). Others have made attempts to develop an applied framework, within which resilience metrics can be calculated, and subsequently compared between subjects (Baho et al., 2017; Capdevila et al., 2020; Stott et al., 2011). Exploration of resilience initially considered disturbance at a system-wide or landscape level (Holling, 1973; Lewontin, 1969). As the topic has developed, authors have investigated the concept at community and species level (Capdevila et al., 2021; Chuang et al., 2018; Donohue et al., 2016; Kordas et al., 2017; Wernberg et al., 2010) and the principle may also usefully be applied at the population, or demographic level (Capdevila et al., 2020; Stott et al., 2011; Sundstrom et al., 2012) to understand responses to disturbance within the community. Around these investigations, suggestions for a more focussed and simplified approach to quantifying resilience have been made, to simply determine the relative importance of two related processes: resistance and recovery (Hodgson et al., 2015).

Resistance

Resistance has been described as a component of ecological resilience rather than being truly analogous to it (Angeler and Allen, 2016; Walker et al., 2004), as resistance only considers a single equilibrium, rather than multiple scenarios that may be of similar value. As a means of measuring the capacity to tolerate disturbance, however, the two terms may be used largely interchangeably. Resistance can be quantified by estimating population density, ρ, following perturbation at time t_0, relative to an undisturbed system. The potential population density in the first time-step following perturbation (t_1) is described as the population's 'reactivity', and the 'inertia' of the population describes the return of stability in the long term (t_∞) (Stott et al., 2011). In this way, populations could either reduce in size, relative to the undisturbed system ('attenuation'), or may respond by increasing in size ('amplification'). Following perturbation, the 'transient period' describes the duration between the disturbance event and the return to stability.

Recovery

Recovery is concerned entirely with the return of the system to pre-disturbance conditions, and does not consider multiple equilibria. Given that any equilibrium is temporally discrete, recovery can be quantified as the time taken for a system to return to its previous state. This could be expressed as the rate at which oscillations in population size decay to stability (the 'damping ratio') or as an absolute measure of the time taken for stability to return ('convergence time').

Sensitivity and elasticity

Where perturbation affects developmental stages differently, responses may depend upon the relative contribution of each stage to the population structure. For instance, stages with higher survival or fertility rates may contribute more to population stability and growth than other stages, so disruption to survival in these stages may have a greater effect on post-perturbation population size. The effect that disturbance may have on population-level processes can be estimated via perturbation analysis, which expresses the relationship between each developmental stage and the population growth rate. Sensitivity is a measure of how much a process (such as growth rate) changes following a disturbance, and elasticity describes the effort required to drive a particular change (Benton and Grant, 1999; Caswell, 2001): for instance the magnitude of disturbance required to reduce population growth rate by a defined percentage.

Previous studies have investigated resilience at the species level (Capdevila et al., 2016; Reed et al., 2013), but in-depth exploration of population-level responses to disturbance are lacking. To explore resilience at the population level, I modelled the demographic structure of the Manx shearwater breeding colony at Skomer, and calculated indices from within the frameworks discussed by Stott et al. (2011) and Capdevila et al. (2020) to quantify features of resilience at specific magnitudes of disturbance. The Manx shearwater provides a good opportunity to investigate the effects of perturbation upon population density as the population is large and stable (Perrins et al., 2019, 2012), the structure of the population allows discrete developmental stages to be identified (Brooke, 1978b; Harris, 1966), the species' ecology is consistent and well-studied (Brooke, 2013), and reliable demographic observations have been collected for over 30 years (Newman et al., 2021; Wood et al., 2021).

The aim of this chapter is to demonstrate the continuation of the matrix population modelling methods described in Chapters three and four as an approach to estimate population responses to perturbation. This will be achieved by:

1) Constructing matrix population models with survival rates observed over long term monitoring to estimate population density and compare with census observations from the same time series.
2) Quantifying indices of resilience to describe population level responses through time, following simulated perturbation of stage-specific survival rates.
3) Test the hypothesis that perturbation of stage-specific survival rates is reflected in different population-level responses, and that these responses are consistent across demographic stages.

The majority of research into resilience in the field of ecology focuses on responses to perturbation at ecosystem and community level. By investigating population-level responses to changes in stage-specific annual survival rates, and by quantifying indices of resilience for these stages, I aim to address gaps in understanding of the indirect consequences of perturbation that may directly affect only a portion of a population.

Methods

Data collection

Stage-specific survival rates

Annual stage-specific survival rates were calculated for fledgling (year one) and adult (year six onwards) birds as described in **Chapter 4**, from monitoring observations at the Skomer Manx shearwater study site, between 1992 and 2019. Fledgling survival rates were available for every year of the study period, but reliable observations of adult survival were not available for the first and last years of this time series. To minimise the use of substituted values, which may have introduced uncertainty into the analysis models were parameterised using data collected between 1993 and 2018 only (n = 26). Juvenile survival rates were unavailable for the study period, but estimates have previously been calculated by Perrins et al. (1973) and Brooke (1977) wherein the overall mean survival rate for juvenile birds was given as 0.28 across the four-year period as a juvenile. This equated to an annual juvenile survival rate of $\sqrt[4]{0.28} = 0.73$ (Table 5.1).

Annual rates of adult fecundity was also unavailable for the duration of the study period so the per-pair estimate of 0.84 from Perrins et al. (1973) was halved to give an estimate of 0.42 for individual fecundity. Very few birds breed before the age of six, and estimated sub-adult fecundity rates are given from Harris (1966). These values should be interpreted with caution, however, since they originate from a single study with a very low sample size. Given the low value for juvenile fecundity (0.02) and small impact upon the outputs of the MPM these have been included for completeness.

Table 5.1. Stage specific vital rates used to parameterise baseline matrix

Developmental stage	**Year(s) of life**	**Survival rate**	**Fecundity rate***
Fledgling	1	0.65	-
Juvenile	2-5	0.73[†‡]	0.02[**]
Adult	6+	0.92	0.42[†]

* Individual fecundity taken as 50% of per-pair fecundity: 0.84/2 = 0.42
† Perrins *et al.,* 1973, ‡ Brooke, 1977, ** Harris, 1966

Data analysis

Matrix model construction

Following the methods for constructing matrix population models described in **Chapter four**, one transition matrix was generated for each year in which both fledgling and adult survival rates were available (i.e. 1993 to 2018: n = 26). Estimated rates of fecundity and juvenile survival were obtained from previous studies (Table 5.1) (Brooke, 1977; Harris, 1966; Perrins et al., 1973), and mean transition rates across all matrices were used to construct a single matrix, *A*. This provided a baseline characterisation of the colony across the study period, against which simulated perturbations and indices of resilience could be compared.

Simulation of population density

Population structure was estimated as the proportion of each developmental stage within the population each year, expressed as a numerical vector with a sum of 1. Population density (relative to a density set at 1 in the first year) was then estimated by multiplying each year's transition matrix by the vector representing the population structure in the preceding year. A sum of the resulting vector was then taken as an estimate of population density, relative to the preceding year.

Influence and perturbation of stage-specific vital rates

The influence of stage-specific survival rates upon population growth rate was investigated via recursive construction of transition matrices based upon the baseline matrix *A* described above. Theoretical adult and fledgling survival rates were set at between 0 and 1, with juvenile survival fixed at 0.73 (as per Table 5.1), and the resulting lambda values were plotted. Following this, mean adult and fledgling survival rates observed at Skomer were reduced by between 0% and 99.99%, and the resulting differences from the mean population growth rate were plotted. A 99.99% reduction in adult survival was assumed to represent a total loss of all adult birds, since the use of 100% introduced the potential for calculated results of infinity. Finally, stage-specific sensitivity and elasticity matrices were calculated using the ‘popdemo’ package (Stott et al., 2021) in R statistical software (R Core Team, 2022), based upon vital rates presented in Table 5.1.

Quantifying resistance and compensation

Calculation of resistance indices was conducted in R, either manually or using functions within the ‘popdemo’ R package, and a summary of these is presented in Table 5.2. Indices were calculated for each simulated reduction in stage-specific survival rates, for fledgling, juvenile and adult developmental stages, and the results plotted for each scenario.

Quantifying recovery: return to stability

As for resistance, recovery was quantified by calculation of indices derived from matrix *A* (the transition matrix)and the subsequent iterations following simulated reduction in survival rates, and was conducted using the ‘popdemo’ and ‘popbio’ (Stubben and Milligan, 2007) R packages. When calculating time to convergence the exponent of the ‘*accuracy*’ argument corresponds to the number of stages in the matrix model, i.e. the number of time steps between generations. In the Manx shearwater, although some breeding does occur from year 4, most birds breed from the 6th year (see Table 5.1 for disparity), so this was set to 10^{-6}. Calculation of recovery indices was followed by plotting of results for each stage and scenario, and indices are described in Table 5.3.

Table 5.2: Indices of resistance during the transient period, immediately following perturbation.

Metric	Description	Calculation	Calculation method
Reactivity	Corresponds to the potential population size in the first timestep following perturbation, relative to stable growth	Growth rate of the symmetric part of matrix **A** at t_1: $\lambda_1(H(\boldsymbol{A}))$ $(H(\boldsymbol{A}) = (\boldsymbol{A} + \boldsymbol{A}^T)/2)$.	*popdemo* “reac” function
Inertia	Population density following transient period, relative to pre-disturbance	When dominant eigenvectors ***w*** and ***v*** are scaled, the transpose of v for the standardised population vector at t_0: $v^T\hat{n}_0$	*popdemo* “inertia” function

Table 5.3: Indices of recovery during the transient period, as the population returns to stability.

Metric	Description	Calculation	Calculation method
Damping ratio	The rate at which oscillations in population density decay to stable growth. Dimensionless	Dominant eigenvalue divided by the second largest eigenvalue: λ_1/λ_2	*popbio* “damping.ratio” function
Time of convergence	Measure of time for convergence to stable growth	Time (t_x) required for λ_1 to become x times as great as λ_2.	*popdemo* “convt” function

Results

Simulation of population density

Estimates of annual survival rates for fledglings and adult birds, and relative population density estimates modelled from these observations, indicate that the population trajectory at the Skomer Manx shearwater colony appears to be relatively stable (Figure 5.1). Over the duration of these observations, fledgling survival appears to fluctuate to a greater degree than adult survival, and an overall slight downward trend in population density is apparent.

Influence and perturbation of stage-specific vital rates

Calculation of population growth rate following recursive modelling of, and changes to, stage specific survival rates indicated that adult survival has a greater influence on population growth rate than fledgling survival. Changes in cell darkness in Figure 5.2a are greater from left to right (increasing adult survival) than from top to bottom (increasing fledgling survival), and colour changes to a greater degree following reduction in adult survival than from reduction to fledgling survival (Figure 5.2b). Sensitivity to change and influence on population growth rate broadly correspond with the magnitude of vital rates: stages exhibiting higher survival/fecundity (i.e. adults) have a greater influence on population dynamics (Figure 5.2c and Figure 5.2d). All indices of resilience for all developmental stages are summarised in Table 5.4.

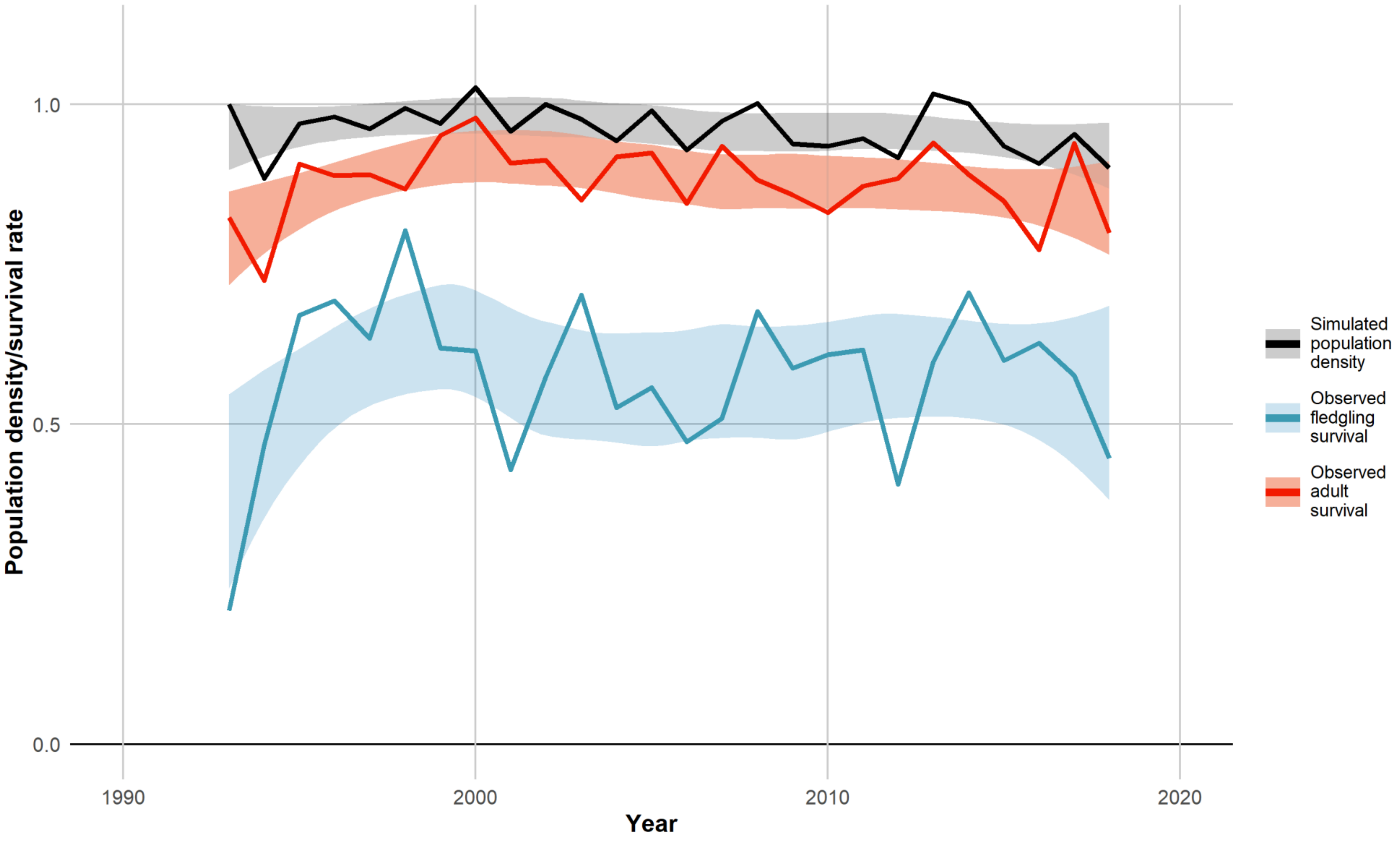


Figure 5.1. Modelled population density of the Skomer Manx shearwater colony, based upon estimates of annual survival in fledgling and adult birds, recorded between 1993 and 2018. Solid blue and red lines indicate annual variation in estimated fledgling and adult survival rates, respectively. Solid black line indicates estimated population density derived from matrix models parameterised with these survival rates. Shaded ribbons indicate 95% confidence intervals from generalised additive models, fitted simply as survival rate/density estimate against time (smoothed).

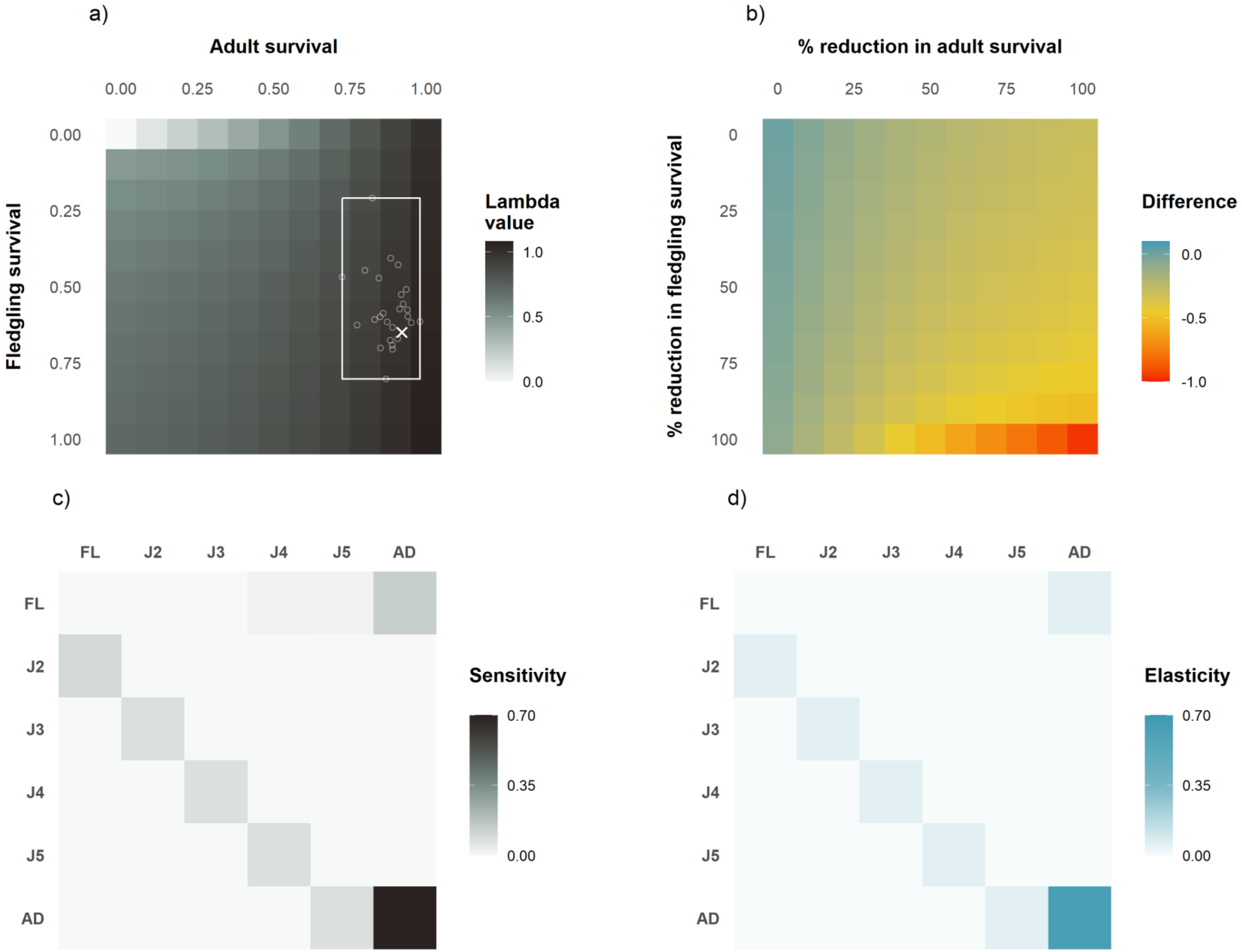


Figure 5.2. Influence of fledgling and adult survival rates upon population growth rate (a), change to population growth rate relative to mean observed rates, following reduction to stage specific survival rates (b) and sensitivity and elasticity of population growth rate to perturbations in stage-specific survival and fecundity rates (c and d). In (a), ‘x’ indicates mean observed lambda value, ‘o’ indicates all observed lambda values, box indicates range of observations

Quantifying resistance and compensation

Reactivity and inertia appeared to have a direct relationship with adult survival rate (Figure 5.3). The greater the reduction in adult survival at t_0, the lower the population density at t_1 (reactivity), and the lower the population density over the long term (t_∞). For instance, a 10% reduction in adult survival at t_0 corresponded with a population density of 0.96 at t_1, whereas a 99.99% reduction at t_0 led to a density of 0.87 at t_1. In contrast, population density may increase rapidly following a reduction in fledgling or juvenile survival, with long-term density trending upwards with greater declines in fledgling survival. Here a 10% reduction in fledgling survival at t_0 may increase population density slightly to 1.01 at t_1, while a reduction of 99.99%, may result in a population density of 1.10: a 10% increase in population density in the year following near extinction of all fledglings.

Quantifying recovery: return to stability

Changes to juvenile survival rates had a much greater impact upon the return to stability (damping ratio) following perturbation than either fledgling or adult survival, ranging from a magnitude of 1.75 when survival at t_0 was reduced by 10%, to 313.78 when survival was reduced by 99.99% (Figure 5.4a). Since higher damping ratios correspond with a quicker return to stable population structure, this suggests that a reduction in juvenile survival may, counterintuitively, enhance stability. This is also reflected in the time taken to reach population stability (Figure 5.4b).

Here, decreasing juvenile survival appears to correspond with shorter convergence times (ten years to four years, for reductions of 10% and 99.99%, respectively), increased disruption to adult survival tends to increase these times (20 years to 943 years), and the degree of disruption to fledgling survival appears to have a consistent population-level response

(11 years from 10% to 90% reduced survival, and six years at 99.99%). This contrasts with other indices of resilience for which adult survival tends to have the greatest influence on population-level processes. Details of the resilience indices corresponding to perturbation of survival rates at each developmental stage are summarised in Table 5.4.

Table 5.4: Summary of resilience indices. Ranges correspond to index at 10% and 99.99% reduction in survival for respective stages. Values in parentheses are minima/maxima where a trend changes direction (e.g. trajectory falls then rises). Arrows indicate overall direction of trend.

Index	**Fledgling**	**Juvenile**	**Adult**
Sensitivity	0.10	0.08	0.70
Elasticity	0.06	0.06	0.64
Reactivity	1.01 - 1.10 (↑)	1.00 - 1.04 (↑)	0.96 - 0.87 (↓)
Inertia	1.01 - 1.12 (↑)	1.00 - 1.01 (0.99) (↓↑)	0.98 - 0.90 (↓)
Damping ratio	1.57 - 9.24 (↑)	1.75 - 313.78 (↑)	1.32 - 1.01 (↓)
Time of convergence	11 – 6 (↓)	10 – 4 (↓)	20 – 943 (↑)

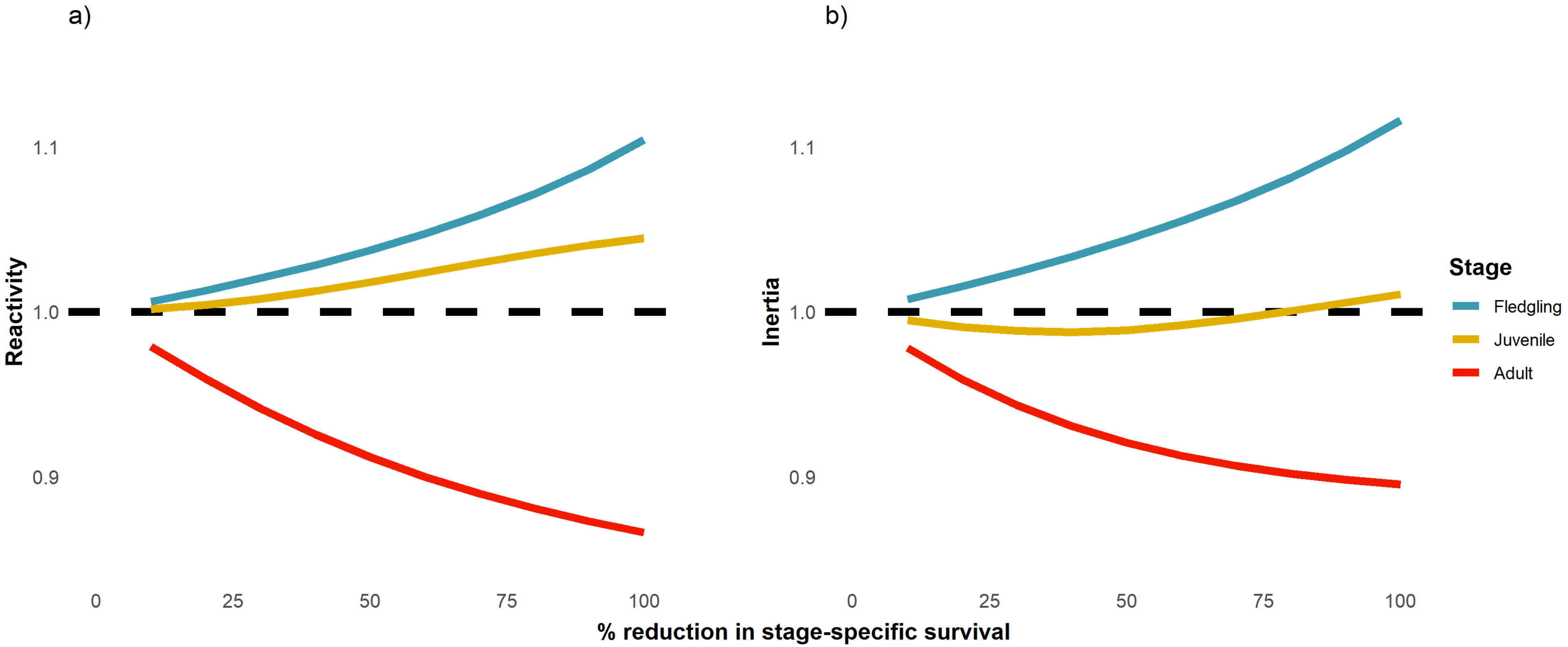


Figure 5.3: The effect of stepwise experimental reduction in stage-specific survival upon indices of resistance at the population level, illustrating a) reactivity (the potential population density in the first time-step following perturbation) and b) inertia (the return of stability in the long term). Stage-specific effects upon population dynamics are similar across these two indices of resistance, with disruption to fledgling survival being less influential than juvenile survival, which in turn was less influential than adult survival.

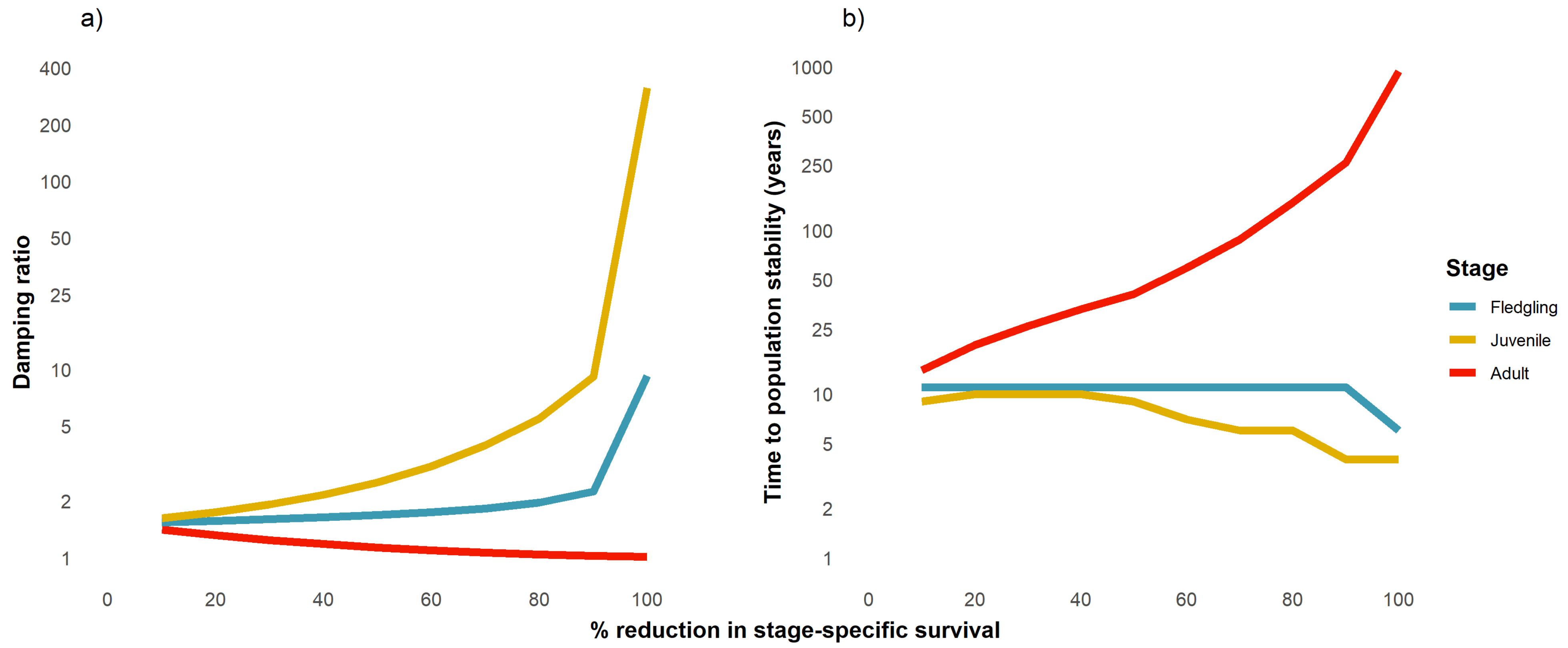


Figure 5.4. The effect of simulated reduction in stage-specific survival upon indices of recovery at the population level, illustrating a) the damping ratio (the rate at which oscillations in population size decay to stability) and b) time of convergence (the absolute measure of the time taken for the population to return to a stable structure). Stage-specific effects upon population-level recovery are different across these two indices of recovery. Reduction in juvenile survival appears to increase the rate at which oscillations in population size decay towards stability (a) while disruption to fledgling and adult survival have a far milder effect. Disruption to adult survival has a marked effect upon the time for the population to return to stable structure (b), whereas juvenile and fledgling survival appear substantially less influential.

Discussion

Much existing research on ecological resilience focuses on responses to perturbation at the ecosystem or community level, with less attention paid to responses at lower organisational levels like population and demography. Likewise, the indirect effects of disturbance at lower levels (e.g. demographic stages) to higher level dynamics (e.g. at the population level) is not well documented. I therefore sought to investigate how demographic perturbation may be reflected in population-level dynamics, and how responses to perturbation may be quantified, applying this approach to a well-studied seabird species: the Manx shearwater. The investigation of matrix population model-based resilience indices presented above suggests that perturbation to survival rates at different developmental stages in the Manx shearwater does elicit stage-specific effects upon population-level responses to disturbance. These responses are not uniform amongst indices, however, as the magnitude and direction of responses varies between stages. The stable population trajectory (Figure 5.1) that was estimated from observed survival rates in fledgling and adult birds between 1993 and 2018 is consistent with the most recent censuses of the Skomer Manx shearwater colony, carried out in 1997-98, 2011 and 2018 (Perrins et al., 2019, 2012; Smith et al., 2001). Abundance estimates from these studies indicated that the population at this colony has maintained a stable size of between 300,000 and 350,000 breeding pairs, at least since 1997.

Population growth rate in these simulations changes more following modification of adult survival rates than by changes to fledgling or juvenile survival, which aligns with the consensus in the field (Arso Civil et al., 2019; Croxall and Rothery, 1991; Oli and Dobson, 2003; Sæther and Bakke, 2000). A sensitivity index of 0.70 was obtained from the baseline matrix (**as described above**), compared to 0.10 for fledglings and 0.08 for juveniles. Adult survival would also require a greater magnitude of disturbance for that disturbance to be reflected as a change in survival rate, with an elasticity index of 0.64, compared to 0.06 for both fledgling and juvenile birds. These results indicate that population growth rate is influenced to a greater degree by adult survival, but that adult survival is more difficult to change: its resistance is greater.

Associated with this, reduced adult survival had the greatest effect upon potential population density in the time step following perturbation: t_1 (reactivity). When adult survival was reduced further, reactivity also reduced, whereas reduced fledgling survival tended to *increase* the potential population density at t_1, and this disparity between stages was mirrored over the longer term, in calculations of inertia. Following the transient period, adult survival also had the greatest size of effect upon the time taken for the population to recover to stable growth, but the dimensionless measure of the decay of oscillations in population size, the damping ratio, appeared to be affected much more by disruption to juvenile survival.

The unexpectedly large effect of juvenile survival upon damping ratio that was observed here is not reflected in the literature, and may simply be an anomaly connected to a single developmental stage being represented by consecutive transitions in the baseline matrix. Rather than a single matrix element being perturbed by a reduction in survival probability, four elements were affected simultaneously. This may have fostered an internal feedback loop, within the model, enhancing the effect of the perturbation (Weinans et al., 2021). The influence of one reduced element upon the next reduced element, and so on, may be negating the decay in oscillations to stable population growth which the damping ratio measures. Nonetheless, this highlights the potential effect of a long-term reduction in juvenile survival upon the stability of the population. Although population growth rate is not sensitive to juvenile survival (see Figure 5.2c and Table 5.4), juvenile survival does appear to be less resistant to perturbation (i.e. has lower elasticity: Figure 5.2d and Table 5.4). Any reduction in juvenile survival would not be immediately apparent in the population, largely as these birds would be absent from the colony during a census, but would instead be reflected in a lower rate of replacement of adults (Morris et al., 1999). The adult contribution to population growth rate would still be high (assuming only juvenile survival was reduced), but the latent reduction in adult replacement may be reflected in a slower return to stable growth.

After the post-fledge migration, juvenile birds may take up to four years to return to the natal colony (Wynn et al., 2022), during which time these birds may experience a different suite of stressors than adult birds. The spatial segregation of birds at different developmental stages may influence population dynamics if real-world stage-specific perturbations were to mirror the perturbations simulated here. Interactions between juvenile Manx shearwaters and South American fisheries (Brooke, 2013) may reduce foraging resources in lean years, or increase the incidence of this stage as bycatch, or both. Regional stochastic events may also increase mortality risk in seabirds (Baduini et al., 2001; Blake, 1984; Clairbaux et al., 2021; Morley et al., 2016; Van Hemert et al., 2021), and a spatial overlap between these events and the distribution of juvenile birds could reduce their survival.

There can be weaknesses with the use of matrix population models when certain elements are unknown (Kendall et al., 2019), and the approach taken here of estimating survival rates for birds that are away from land (and therefore very difficult to reliably monitor) for up to four years may produce unpredictable results. Juvenile birds of different ages may have different levels of experience that could influence their fitness and ability to deal with perturbation. One set of estimated survival probabilities for juveniles is, however, as arbitrary as any other, so empirical observations of annual survival between departing the natal colony and returning to breed, is required. In situations when data are limited, matrix methods do still provide a useful method of conducting Population Viability Analysis (PVA). This approach is less reliant on simple counts of individuals, which may not be possible for species which are scarce, and allows demographic rates to be used to forecast population trajectories, either under existing conditions or under a given scenario, and the relative influence of survival in specific classes (Morris et al., 1999; Searle et al., 2019). Similarly manipulation of demographic rates (similar to that conducted here) can simulate the effects of management options for species of conservation concern to inform decision making and target resources (Morris et al., 1999; Zambrano et al., 2007), but detailed outputs on possible stage-specific responses to perturbation (such as the indices of resilience discussed above) are lacking.

Manx shearwaters are long-lived, produce few offspring annually, exhibit high parental investment in young, and spread their reproductive output across multiple years. Like other K-selected species, adult survival is a critical life history parameter (Arso Civil et al., 2019; Oli and Dobson, 2003). The Yelkouan (*Puffinus yelkouan*) and Balearic (*Puffinus mauretanicus*) shearwaters are Mediterranean relatives of the Manx shearwater and share these traits, but are at risk as fisheries bycatch, from illegal hunting and predation pressure (Oppel et al., 2011). Adult survival rates in these species is subsequently low, and has been suggested as a driver of population declines. Where fulmar (*Fulmarus glacialis*) and kittiwake (*Rissa tridactyla*) share their distribution with the Manx shearwater, these species are subject to similar resources and conditions, but are also experiencing declines as a result of climate change (Frederiksen et al., 2007; Grosbois and Thompson, 2005), prey availability (Cordes et al., 2015; Frederiksen et al., 2005) interactions with fisheries (Frederiksen et al., 2004; Phillips et al., 1999) and trophic mismatch (Shultz et al., 2009) while the Manx shearwater population appears to be stable. Whereas conditions may be comparable, intrinsic traits such as diet, foraging method, behavioural traits and the ability to adapt to pressures may reduce the ability of individuals or a cohort to resist change.

The patterns in population responses to demographic disturbance illustrated above broadly align with our understanding of population dynamics in relation to demographic structure and species' life history. Individuals (or stages) with greater life expectancy make a greater contribution to the population by their survival to reproductive age, and their survival to reproduce again. Survival rates at these stages therefore have a greater effect upon population dynamics than other vital rates. Indices of resilience are not consistent across developmental stages, however, and our understanding of how stage-specific survival relates to the nuances of population dynamics is ultimately determined by the accuracy of our models, and the parameters used to construct them. Future research that incorporates an investigation of species' population dynamics would be enhanced by consideration of within-population processes, including the contribution of specific developmental stages to the overall population trajectory. In doing so, however, it is important that researchers maintain an open mind, since the contribution of developmental stages to population trajectory may not be intuitive.

Chapter six:

General discussion

The limitation of resources drives competition within and between species, and the observation that the distribution of resources in space and time is uneven has led to the development of some of the fundamental ideas in ecology. The concept of the ecological niche (Chase and Leibold, 2003), the competitive exclusion principle (Hardin, 1960), the Lotka-Volterra models and subsequent extensions (Berryman, 1992) and the theory of natural selection (Wallace, 1858) are all based on the notion that resources are limited, and that organisms must adapt to these limitations to fulfil fundamental life processes like development, survival and reproduction. These processes were the basis of investigation for this thesis, which aimed to address gaps in our understanding of how populations respond to environmental heterogeneity. To do so, this thesis explored spatial heterogeneity in the distribution of breeding colonies, spatial and temporal heterogeneity in reproductive phenology, spatial and temporal heterogeneity in stage-specific survival rates and temporal heterogeneity in the distribution of environmental conditions. Alongside this, it has also considered spatial and temporal heterogeneity in data collection methods and spatial and temporal heterogeneity in data availability, and the effect of these upon the analysis and modelling of demographic processes and population dynamics.

The investigations presented above found that pupping phenology in the Irish Sea grey seal population may be influenced by seasonal and inter-annual heterogeneity in sea surface temperature, but that responses were not predictable or consistent across the four colonies investigated. Grey seal pup survival rates exhibited spatial and temporal heterogeneity within and between colonies in south-west Wales, while pups at the Calf of Man exhibited consistently higher survival probability. Temporal heterogeneity of within-colony survival was greater than heterogeneity of between-colony survival, and some evidence of density dependency was evident at the Ramsey colony, where focused research would be encouraged.

For Manx shearwater, the results above suggest that, although vital rates may be substituted from elsewhere in a species' range, local variability in survival rates can skew the outputs of matrix population models, especially when substituting parameters for influential stages, such as adults. Perturbation to stage-specific survival rates resulted in measurable changes at the population level, and responses to disturbance were not consistent amongst indices, as the magnitude and direction varied depending on which stage was affected.

Heterogeneity in the marine environment

The study sites discussed in this thesis are mostly located within the Irish Sea, with the exception of Rum, in the Inner Hebrides, and cover a latitudinal range of 5.2°, equivalent to approximately 600 km from north to south, and a range of altitudes between 0 m (i.e. sea level) and 821 m (the summit of Askival, Rum). The potential range of conditions at these sites – low and high altitudes, the latitudinal gradient, exposure and shelter from the direct influence of the Atlantic – and the potential for climate change to affect marine fauna in other regions of the UK (Cordes and Thompson, 2013), and globally (Weimerskirch et al., 2003), had led me to expect that some influence of this spatial and environmental heterogeneity may be detectable in this study.

In **Chapter two** I investigated the influence of temporal heterogeneity in SST upon the timing of the grey seal pupping season at five of the study sites (Calf of Man, Bardsey, Ramsey, Skomer and the Marloes Peninsula), with a range of 2.3° (~260 km) from the Calf of Man to the Marloes Peninsula. Although very highly correlated between grid-squares ($r = 0.988$, $p < 0.001$, $df = 322$), seasonal SST was only found to influence the timing of the pupping season at two sites, Skomer and Ramsey, located approximately 15 km from each other, but no effect was observed at Marloes (less than 1 km east of Skomer) or the Calf of Man, 260 km north. Likewise, in **Chapter three** I found that survival of grey seal pups, and population growth rate, at these four colonies was explained more by differences between individual pupping sites (68% of explained variance) than by differences between colonies (25%), or by region (i.e. Pembrokeshire versus the Calf of Man: 5%). Although I didn't investigate the influence of meteorological or marine conditions, the fine spatial scale of these differences suggests that climate and SST would not have been direct drivers. Instead, these patterns may have been influenced more by topographical heterogeneity, exposure, density-dependent processes, food availability and maternal behavioural (Engbo et al., 2020; Hall et al., 2001; Smout et al., 2011; Thomas et al., 2019; Twiss et al., 2012, 2003). Given the number of sites that were included, and the range of sizes and aspects of these beaches (and caves), the first three of these are likely to have had the greatest effect on patterns of pup survival.

The full geographical range of the study sites was included in **Chapter four**, as Manx shearwater populations from Skokholm at the south, to Rum in the north. Rum, Skokholm and Skomer are subject to prevailing south-westerly winds blowing from the Atlantic, but the difference in latitudes between Pembrokeshire and Rum mean that temperatures may be very different. Similarly, the lowland habitats in which shearwater burrows occur at the Skokholm, Skomer and Copeland colonies, compared to the upland habitat of Rum, and the combination of both on Bardsey, led me to expect that survival rates of fledglings may have been lower at more exposed or hostile colonies. Again, within-colony differences explained the majority of the variance in fledgling survival (57%), with differences between the colonies accounting for just over 32% of the variance. Although the number of monitoring sites did not affect variance significantly, the higher number of sites on Bardsey (n = 15) makes it easier to visualise within-colony heterogeneity in survival rates.

Overall, the temporal heterogeneity in SST that was investigated directly, and the subsequent temporal heterogeneity in environmental conditions that can be inferred at the colony level, did not have a significant effect on the survival of young animals at the grey seal and Manx shearwater breeding colonies. Conditions that were not measured (see above, re: Chapter three, and others), may have a tangible and detectable effect upon pup and fledgling survival, and these warrant further investigation.

Heterogeneity of data

Data collection methods

Data collection methods are largely dependent upon logistical factors and resource availability, and these vary between species and between monitoring site. As well as these long-term considerations, more proximal influences such as daily weather or recorder availability and experience can affect how data are collected. At three of the grey seal breeding colonies (Calf of Man, Ramsey, Skomer) monitoring of pup production is conducted during discrete periods (July/August to November) as these islands are largely uninhabited between December and March. Ad-hoc observations of pupping outside of the main recording period are made at the Marloes colony, and this is largely a result of being attached to the mainland, but the remoteness of the site means that these observations are few. Bardsey is inhabited or visited throughout the year, so observations may be recorded at any time, but despite this, structured monitoring is not conducted here, and observations appear to be more sporadic. For instance, in 2007 monitoring was conducted for 13 consecutive days in September, but nothing was recorded outside of this time. In other years, monitoring intervals vary between daily and weekly or greater, although focussed monitoring has previously occurred here (Westcott and Stringell, 2003). Although logistic modelling of pup production can smooth out some of the irregularity in these observations (see **Chapter two**), it is not possible to accurately estimate the abundance or timing of pupping from such short or infrequent observational windows.

At pupping locations where regular, structured monitoring is undertaken, beach access may influence the accuracy of estimates. On Skomer and Marloes, access to beaches is possible and on Skomer individual seal pups are dye-marked to assist with identification and reduce double-counting. At Marloes, pups are not marked, but observations are compared between visits and survival between developmental stages is estimated. Furthermore, beaches where more pups are born are monitored more frequently. At the Ramsey and Calf of Man colonies, all observations are made from cliff-top vantage points, with particular care taken to avoid disturbing the animals. Pups located out of sight may not, therefore, be counted, and distance sampling may increase the likelihood of double counting, so on Ramsey a correction factor is applied. Four monitoring protocols are in use across these four breeding colonies, so the analyses in **Chapters two** and **three** will therefore contain inherent biases associated with these different approaches. However, sensitivity analysis in **Chapter three** allowed the relative influence of each pupping site upon overall estimates of survival to be investigated. Similarly, the number of observations required to make an accurate estimate of overall mean pup survival was explored, and determined for each colony. As long as heterogeneity in collection methods is considered in subsequent analyses, as discussed above, these data are still of high quality, and the resulting estimates of pupping phenology and population dynamics can still be of great use.

The method of monitoring Manx shearwaters also differs between colonies, with fledglings at four of the five colonies (Rum, Copeland, Skomer and Skokholm) being observed in artificial or semi-artificial burrows. Here, it may be easier to track the breeding success of birds between years, since pairs show strong site-fidelity and return to breed in the same burrow, but focussing on these burrows alone may mean that birds in natural burrows are not monitored, and subsequent estimates of survival may not be entirely representative of the whole colony. Monitoring on Bardsey is more comprehensive, with burrows being first investigated to determine residency, and those where a bird or pair is present are subsequently visited through the season. The burrows visited may not be the same between years, however, making direct comparison difficult, and since some burrows are too deep to allow monitoring, there still remains the likelihood that estimates from the accessible selection of burrows may not be entirely representative of the colony. Again, the expertise of those conducting nest monitoring at all colonies illustrates that although collection methods vary, the reported data are still of high quality. To this end, in **Chapter four** I used these data to parameterise MPMs to investigate population dynamics and the potential effect of substituting missing data (on data gaps, see below). At the Skomer and Skokholm colonies where survival estimates for fledgling and adult birds is available, it was possible to reconstruct a deterministic estimate of population trajectory. This indicated a stable population trend, and aligned with census observations made at these colonies since 1997 (Perrins et al., 2019, 2012; Smith et al., 2001). The long (29 years) and consistent data collected at Skomer also allowed me to extend the use of MPMs in **Chapter five** by using these methods to estimate indices of resilience, and to simulate perturbations to stage-specific survival rates. Juvenile survival is often excluded from population estimates since this stage does not contribute through breeding, but the results of Chapter five highlight the fact that juveniles replace adults in the population, and a perturbation to this stage simply delays the detection of the effect (Morris et al., 1999). The greatest difficulty in simulating perturbations to juvenile survival in Manx shearwater, and in accurately estimating population dynamics in the grey seal, however, was that estimates of juvenile and sub-adult survival rates were largely absent.

Data collection gaps

Both the grey seal and Manx shearwater are mobile and often cryptic species which can be logistically challenging to monitor, so estimates of their population size are reliant upon observations made solely at breeding colonies. Of greater relevance to this thesis is the difficulty in estimating vital rates at all developmental stages, from limited temporal observations of abundance. Thomas et al. (2019) conducted a detailed and comprehensive modelling exercise of the size and dynamics of the grey seal population around the UK, and the resulting estimates of stage-specific survival were used to parameterise the MPMs in **Chapter three**. Although these provided a suitable baseline on which to build MPMs for the Irish Sea, regional and within-stage (i.e. the specific age of breeding adults) differences in survival rates are known to exist (SCOS, 2022). Outputs of these MPMs were useful and informative, but may lack the accuracy of models parameterised with annual estimates for every stage. However, the resources required for this would be prohibitively expensive, logistically improbable and disruptive, and would likely constitute a monitoring programme so comprehensive that the modelling itself would be unnecessary.

Estimating adult survival in Manx shearwaters requires birds to be re-trapped relatively consistently between years. This either needs a high level of effort to maximise the probability of repeatedly encountering free-ranging individuals, or for measures to be taken to allow access to birds in a secure and predictable location. On Skomer and Skokholm, burrow density is sufficiently high that birds have little choice but to use the artificial nests which allow researchers direct access to the birds. At the other colonies, however, artificial nests are either too few, or too seldom used by breeding pairs to facilitate calculation of adult survival estimates. In **Chapter four** I looked into the effects of substituting these missing data with estimates from other locations and sources. I found that, although this is a reasonable approach to take and may be better than having no data (and therefore no population model), inaccurate data can lead to population dynamics being over- or under-estimated, particularly when missing data represent critical life stages. The adult survival rate from the RAS programme was estimated as 0.92 (BTO, 2015), compared with a mean of 0.88 on Skomer (Newman et al., 2021) and 0.86 on Skokholm (Brown and Eagle, 2021). In extreme cases an inaccurate substitution could lead to expensive management programmes being initiated for species or populations that don’t actually require intervention, or to a vulnerable species or population declining since modelled projections indicated a stable population. In reality I would hope that any organisation with the resources to consider making these interventions would not base decisions solely upon substituted vital rates, but this does highlight the theoretical consequences of inaccurately parameterised population models.

Given the three-to-four year period during which juvenile Manx shearwaters remain at sea, and well out of range of curious biologists, this gap in stage-specific survival data also presents challenges to modelling. During the process of developing the MPMs in Chapter four I investigated options for estimating annual juvenile survival based upon whole-stage estimates calculated by Perrins (1973) and Brooke (1977). These options were to:

a) hold annual juvenile survival constant as the n^{th} root of the estimate for the duration of the stage (i.e. four years): $\sqrt[4]{0.28} = 0.73$; or
b) estimate annual productivity on the assumption that survival would increase with age/experience, such that the product would equal the published estimate, 0.28.

I opted for the former, since the difference between population growth rate, stable structure and stage-specific reproductive value for the two approaches was small, and any estimate I made would have essentially been a guess.

For consistency I took the same approach in estimating juvenile survival to parameterise MPMs when I investigated indices of resilience in Chapter five. My method of systematic reduction of stage-specific transition probabilities within the baseline matrix, and deterministic projection of these using the resulting (perturbed) stable structure, worked as expected for the fledgling and adult stages. When applied to the juvenile stage, however, I was curious whether reducing survival rates for the whole stage, across four consecutive transitions, may have caused the anomalous result when calculating the damping ratio (Figure 5.4). However, given that results throughout the rest of this analysis did not appear unusual for the juvenile stage, I am inclined to believe that the effect is genuine. I would very much like to have investigated this further, but as with any time-constrained project, a line must be drawn and I was unable to explore this avenue.

Environmental heterogeneity and marine predator ecology

Future air and sea temperatures are predicted to continue to rise as global climate change proceeds (IPCC, 2015). The effect of temperature upon the phenology of ecological processes is well established across taxa and organisational levels (de Bettignies et al., 2018; Ficetola and Maiorano, 2016; Poloczanska et al., 2016; Sydeman et al., 2015), although phenological responses to temperature change are not universal. Earlier breeding is associated with more successful weaning and greater survival probability (Bowen et al., 2015; Maniscalco and Parker, 2018; Pomeroy et al., 1999), so where disparities exist between colonies the timing of births may become more aligned. For colonies which may already have a competitive advantage, this advantage may become reduced if pupping at nearby colonies coincides more closely. If the pupping season diverges between colonies, then a competitive advantage may increase, but only if phenological change is synchronous with greater resource availability.

If environmental variability does influence colony-level pupping phenology, the mixed results discussed in **Chapter two** still obscure the potential response to drivers at the individual level. Where colonies differ, the assumption may be that phenological change occurs across the whole population of breeding females, but this does not account for individual age or experience. Amongst pinniped and other mammal species, younger or less experienced females tend to breed later, and with lower rates of success (Boltnev and York, 2001; Bowen et al., 2006; Maniscalco and Parker, 2018; Peláez et al., 2017; Wolcott et al., 2015). Moreover, since older females tend to breed earlier, rather than a wholesale shift in the pupping season, the apparent temperature-mediated advance in pupping season may simply be driven by an increased likelihood for older females to breed, altering the age structure of the population

(Bull et al., 2021). For this reason future research should consider incorporating information on demographic traits when modelling phenological responses.

Seabirds appear to be phenologically unresponsive to sea temperature change (Keogan et al., 2018), but anecdotal observations suggest that in recent years the timing of egg-laying at the Skomer Manx shearwater colony may have begun to shift (M. Wood, 2020, pers. comm.). Given the consistent-quality demographic data available for fledglings and adults here, this would seem to be an excellent opportunity to incorporate demographic information into phenological modelling of Manx shearwater populations, and explore patterns of reproductive phenology across two very different species breeding at the same location. Frustratingly, however, despite monitoring of Manx shearwater productivity and chick survival having been conducted on Skomer since the mid-1970s (Newman et al., 2021), throughout this period no records have been made on the estimated date of laying. If a shift in laying date has been suspected here, given that this contrasts with broad-scale observations of seabird breeding phenology (Keogan et al., 2018), and this colony is believed to represent more than half of the global breeding population of this species (Perrins et al., 2019), then a research focus to quantify trends in laying date and explore drivers behind potential fluctuations is strongly encouraged.

Environmental heterogeneity and population modelling

Understanding the effect of heterogeneity of environmental characteristics and monitoring protocol upon calculated estimates of pup survival is key to ensuring that biases are minimised and that modelling can provide accurate estimates of population trajectory. Likewise, as discussed in **Chapters three** and **four**, spatial heterogeneity must be considered when parameterising models from spatially aggregated data as location-specific variability is likely to influence summary estimates of demographic rates. The spatial heterogeneity in year-one survival rates that is illustrated in **Chapter three** at four grey seal colonies and in **Chapter four** at five Manx shearwater colonies in the Irish Sea is reflected in estimates from other monitoring locations not included in these investigations. Grey seal sub-populations around Scotland and the English North Sea coast, which represent the majority of the UK population estimate, vary in their size, demography and trajectory (SCOS, 2022). Similarly, monitoring at additional Manx shearwater colonies in Scotland highlights the effect of colony collapse and early recovery on survival estimates. Breeding collapsed on Canna and Sanday likely due to the presence of brown rats (Newton et al., 2004), such that no nests were detected between 1998 and 2008 (Swann, 2016, 2013, 2000). Limited recovery has occurred here since an eradication programme was implemented (2006-2008) but the number of eggs laid annually remains below five, which has resulted in some extreme estimated survival rates of one and zero.

While population density and rates of pup and fledgling survival vary across the species' ranges, the magnitude, direction and spatial distribution of such variation is not uniform. Sensitivity analysis in **Chapters three** and **four** indicated that estimates of mean pup and fledgling survival can be affected by the inclusion or omission of certain sites, and within-site heterogeneity accounted for 68% (grey seal) and 57% (Manx shearwater) of variance in survival rates. Other drivers such as temporal and spatial heterogeneity of environmental conditions, and intrinsic characteristics such as age, sex and individual behaviour may also drive variation in survival probability (Moiron et al., 2020; Oro et al., 2010; Sandvik et al., 2012, 2007).

When site was excluded from analysis in **Chapter three**, the small effect of pup population size upon sensitivity suggested that survival estimates from high-output beaches and less populated beaches may be assumed to be similarly representative. However, when estimated at the colony level, the effect of pup population size upon sensitivity became apparent, with clear separation between Ramsey and the Calf of Man. This again highlights the need to account for site-specific differences in population with a suitable weighting incorporated into colony-wide survival estimates. The results of **Chapters three** and **four** also indicate that projections could over- or under-estimate population trajectories if models are parameterised with estimates from sites where survival rates are substituted for published values, or are either more consistent or more variable, than broad-scale estimates. This location-specific sensitivity may also explain why the sample size required to achieve an accurate estimate of pup and fledgling survival varied between colonies of both species. Perhaps more importantly, the population growth rate calculated from 25 years of monitoring at the Skomer colony suggested an annual decline here of approximately 4.5%, in contrast to census estimates indicating a steady increase in population size over this period (Perrins et al., 2019, 2012; Smith et al., 2001).

These findings illustrate how heterogeneity in the collection and aggregation of demographic information can affect subsequent inferences of population-level trends. In these cases, spatial heterogeneity affected estimates of survival probability in grey seal pups and fledgling and adult Manx shearwaters (which in the latter conflicted with robust census estimates) and similar consideration would need to be given to other species (Dobson and Jouventin, 2010; Harris et al., 2005; Kilduff et al., 2015; Paradis et al., 2000; Schaub et al., 2005). My observations highlight the importance of maximising the range of monitoring sites where logistics and resources allow, to ensure that estimates are representative of the spatial variation in survival probabilities and the diversity of site characteristics.

Environmental heterogeneity and resilience

Many of the results from the calculation of resilience indices in **Chapter five** were in line with expected patterns: adult and fledgling survival had the largest effect upon population growth rate, with adult survival having the greatest sensitivity and elasticity estimates. Similarly, reduction in adult survival caused the predicted population-level recovery from perturbation to be longer than reductions in fledgling or juvenile survival. The effect of reductions in juvenile survival upon damping ratio that was observed here was unexpectedly large, and this trend is not reflected in the literature. As discussed above, this may simply be due to a single stage being represented by four consecutive transitions, but the small effect of juvenile survival with other indices (as expected) suggests that this effect may well be genuine.

Although population growth rate is not as sensitive to perturbations in the survival rate of juvenile birds as it is to other stages, juvenile survival does appear to be less resistant to disturbance. After fledging, Manx shearwaters may take up to four years to return to the natal colony, during which time they may experience different pressures than adults. For instance, interactions between juvenile Manx shearwaters and South American fisheries (Brooke, 2013) may reduce prey availability, or increase the incidence of bycatch. Regional stochastic events may also increase mortality risk in seabirds (Baduini et al., 2001; Blake, 1984; Clairbaux et al., 2021; Morley et al., 2016; Van Hemert et al., 2021), so juvenile birds in the vicinity of these events could reduce survival of this cohort. For other species where spatial segregation of subadults and juveniles occurs, for instance in sea turtles, sharks and cetaceans, similar effects may be expected (Fujinami et al., 2022; Hartman et al., 2014; Pillans et al., 2022), and an increase in biologging studies and the application of machine learning techniques is now more able to elucidate the 'lost years' of juvenile animals (Mansfield et al., 2014; Péron and Grémillet, 2013).

Reduced juvenile survival may not be immediately apparent in studies of population size, but lower juvenile survival would result in a lower rate of replacement of adults (Morris et al., 1999). The adult contribution to population growth rate would still be high (in the theoretical scenario when only immature individuals are affected), but the latent reduction in adult replacement may drive lagged effects upon population growth rate. Indices of resilience are not consistent across developmental stages, so our future understanding of the relative effect of stage-specific survival upon population dynamics is reliant upon accurate and direct observations of all stages to inform analytical methods. Greater research focus on ecological resilience at the demographic and population level is advocated, given the paucity of studies relative to those investigating resilience at ecosystem and community level. The use of MPMs is intuitive and uncomplicated compared to other methods, and in light of accelerating biodiversity loss, estimates of potential responses of species to climate-linked perturbations is greatly needed.

Final remarks

Heterogeneity in the marine environment occurs through temporal and spatial variation in natural processes such as atmospheric conditions, biogeochemical and physical cycling, and changes in the distribution of resources. Increasingly, anthropogenic pressures interact to amplify or dampen the magnitude of natural processes, and the consequences of these interactions are the focus of countless avenues of research. This thesis has sought to investigate some of these avenues.

Phenological responses to modified temperature regimes are well-documented, and are used as intuitive and tangible examples of responses to anthropogenic climate change. The investigation in **Chapter two** suggests that while temporal heterogeneity in sea surface temperature may influence reproductive phenology, responses to this environmental change also exhibit temporal and spatial heterogeneity. Demographic modelling of population dynamics offers an accessible means of using simple abundance data across temporal and spatial scales to inform management decisions. However, **Chapters three** and **four** serve as a clear warning on the importance of considering the inherent heterogeneity within data sets when planning, conducting and interpreting analyses. **Chapter five** illustrates that less-studied sections of a population or community are not necessarily less-studied because we already know enough about them. Moreover, when those sections appear to make a relatively small contribution to broader trends, remembering that this contribution may simply be delayed is critical to robust forecasting of a species' population trajectory, and to the understanding of its resilience to future perturbations.

Overall, the investigations above highlight the need for future research to consider the intrinsic characteristics and inherent spatial and temporal heterogeneity of the study subjects, as well as mindful collection, management and analysis of data, when exploring the role of heterogeneity in the population ecology and resilience of marine predator species.

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Appendices

Appendix one

Environmental drivers of grey seal pupping phenology

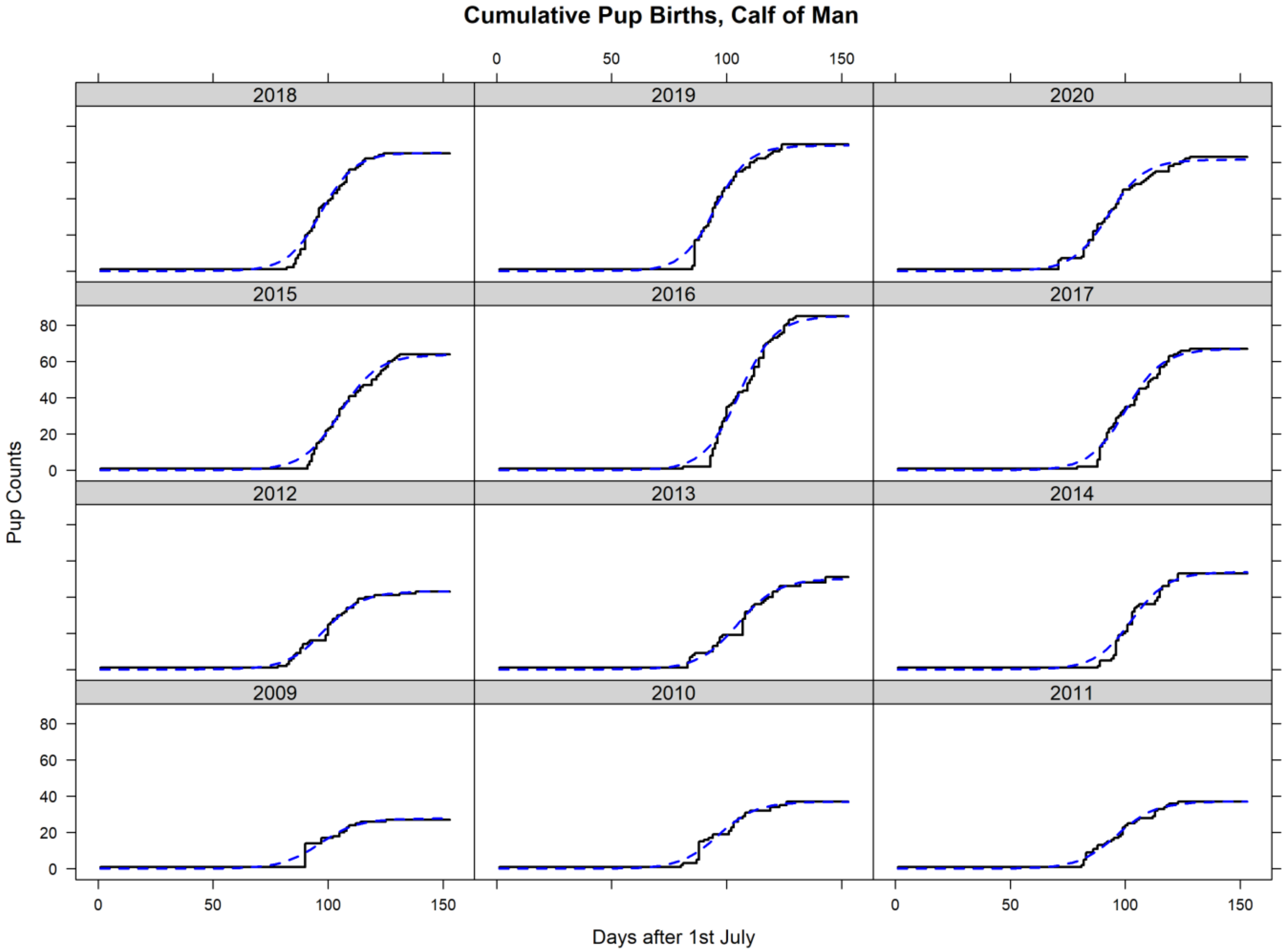

Figure A1. Cumulative distribution function of grey seal pup births at the Calf of Man colony, 2009-2020

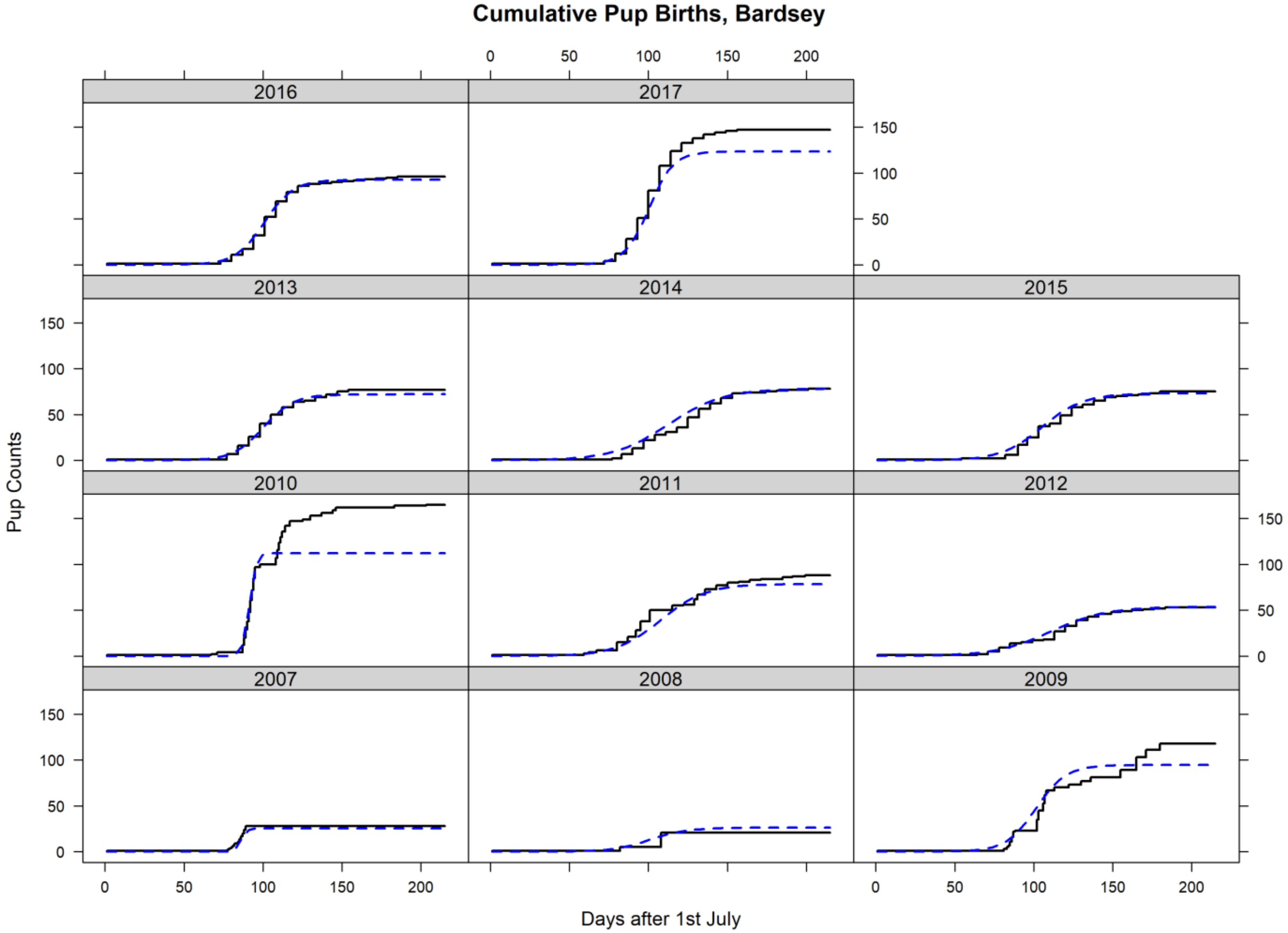

Figure A2. Cumulative distribution function of grey seal pup births at the Bardsey colony, 2007-2017

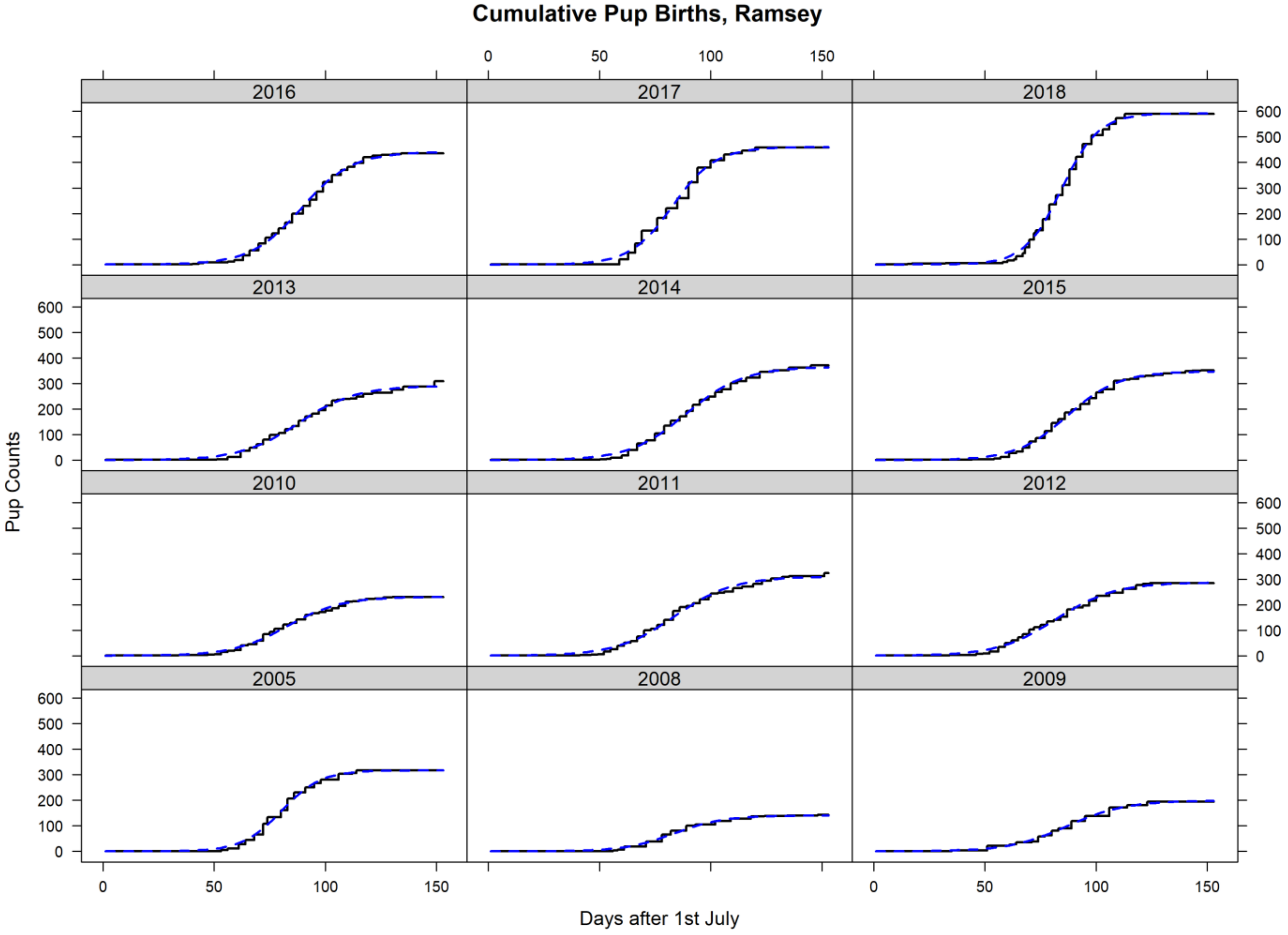

Figure A3. Cumulative distribution function of grey seal pup births at the Ramsey colony, 2005 and 2008-2018

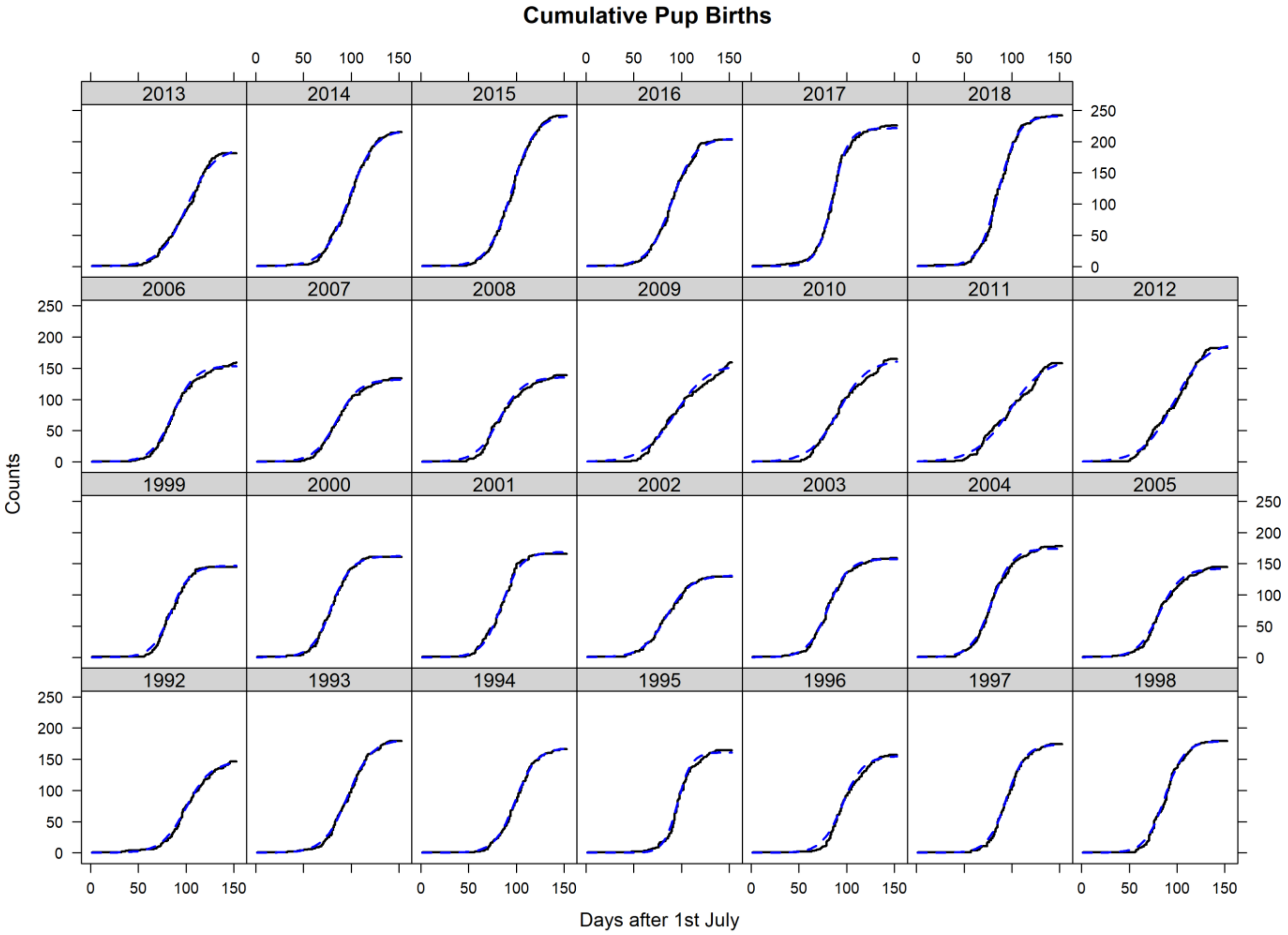

Figure A4. Cumulative distribution function of grey seal pup births at the Skomer colony, 1992-2018

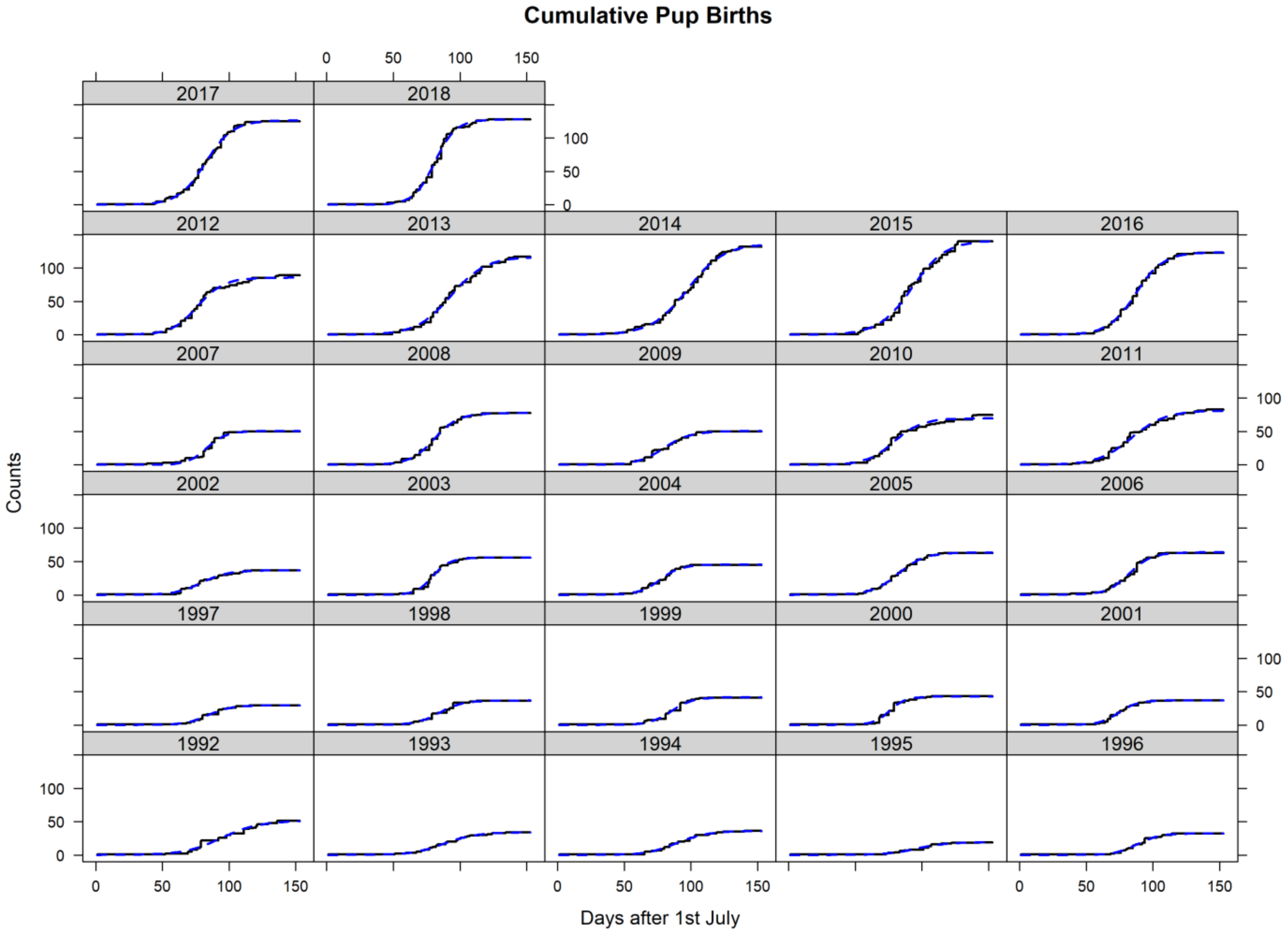

Figure A5. Cumulative distribution function of grey seal pup births at the Marloes colony, 1992-2018

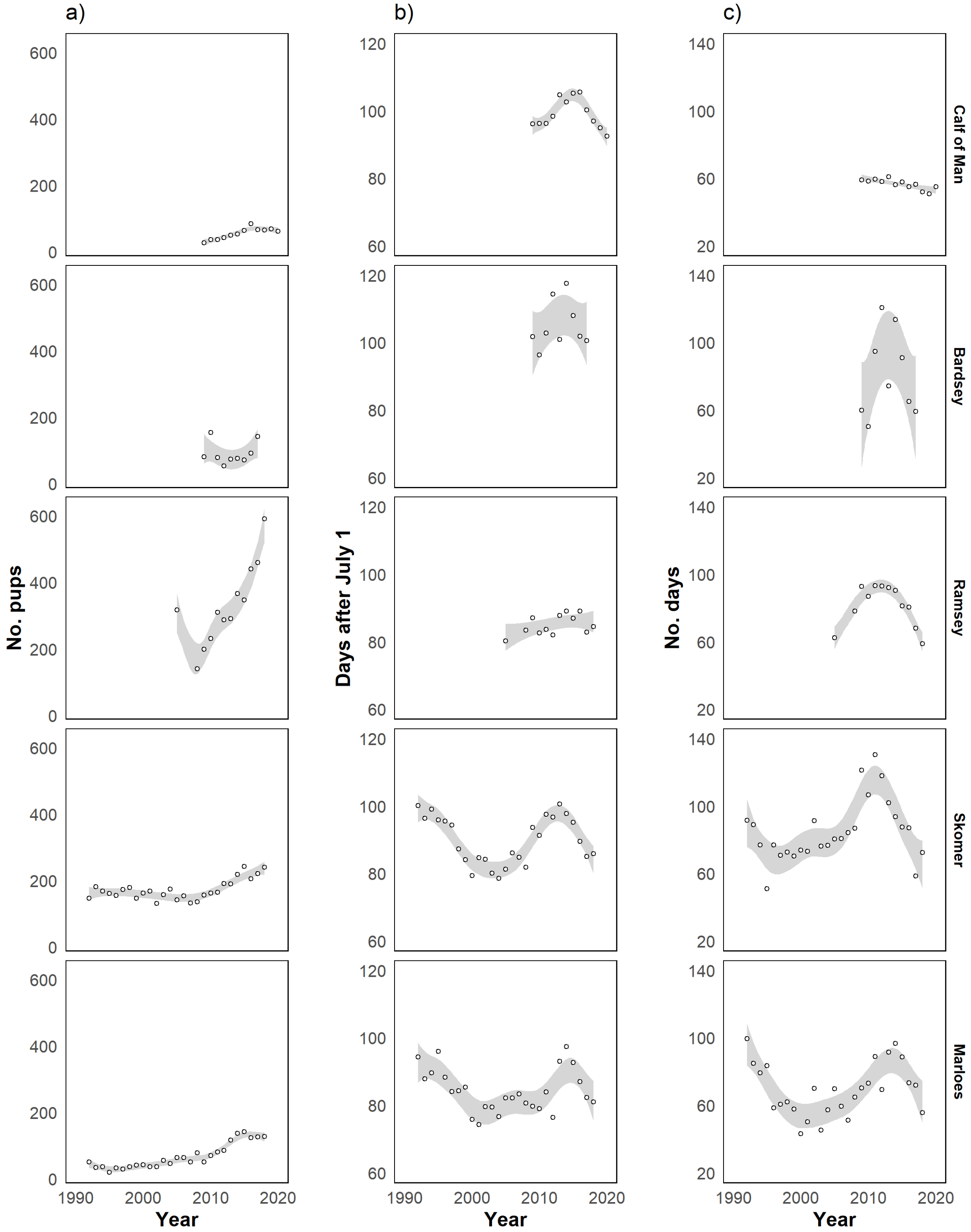

Figure A6. Parameter estimates from logistic population models, derived from colony-specific cumulative distribution functions.

Appendix two:

Effects of spatial and temporal data aggregation upon estimates of grey seal population dynamics

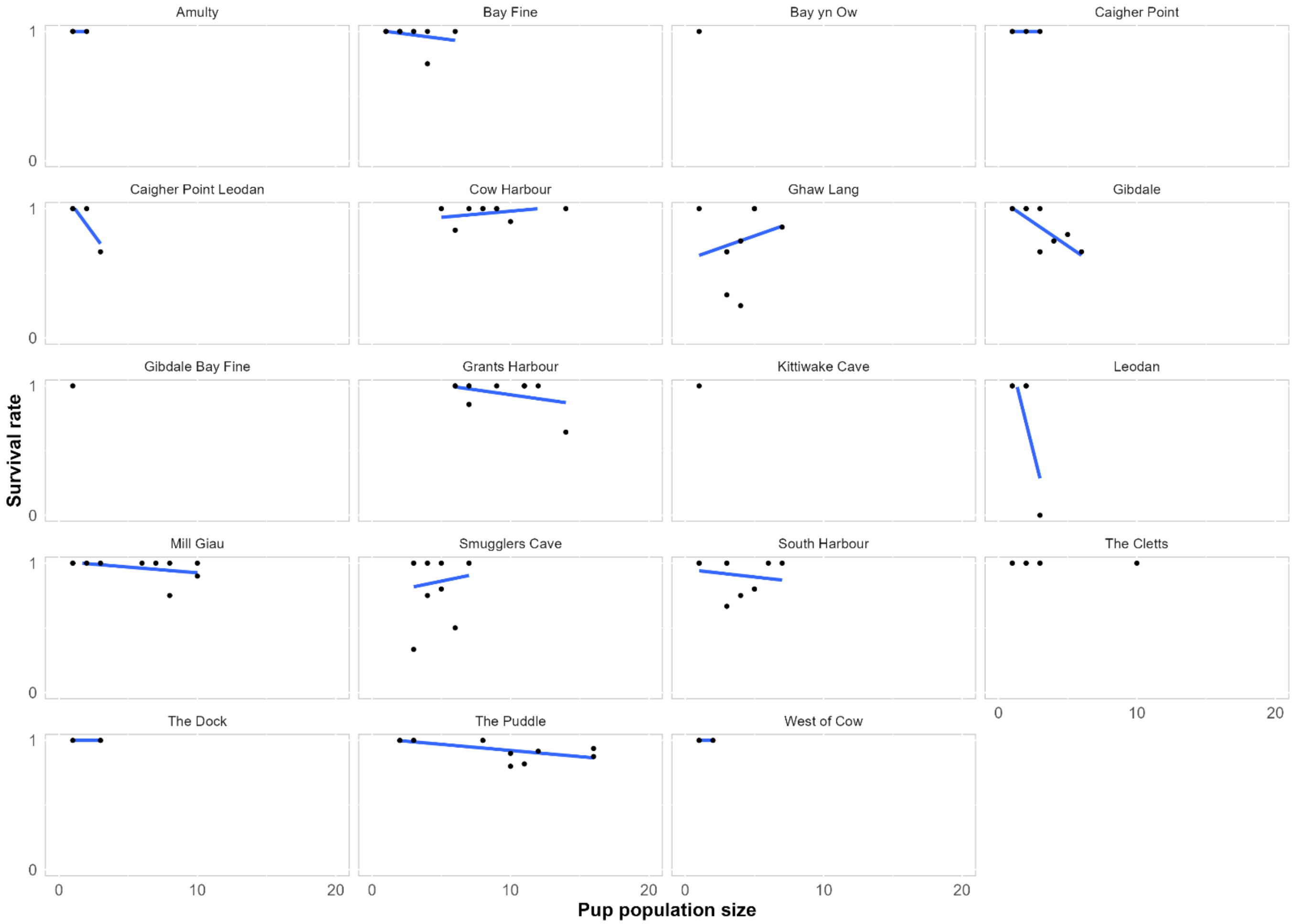

Figure A7. Density-dependent effects upon pup survival estimates at the Calf of Man colony

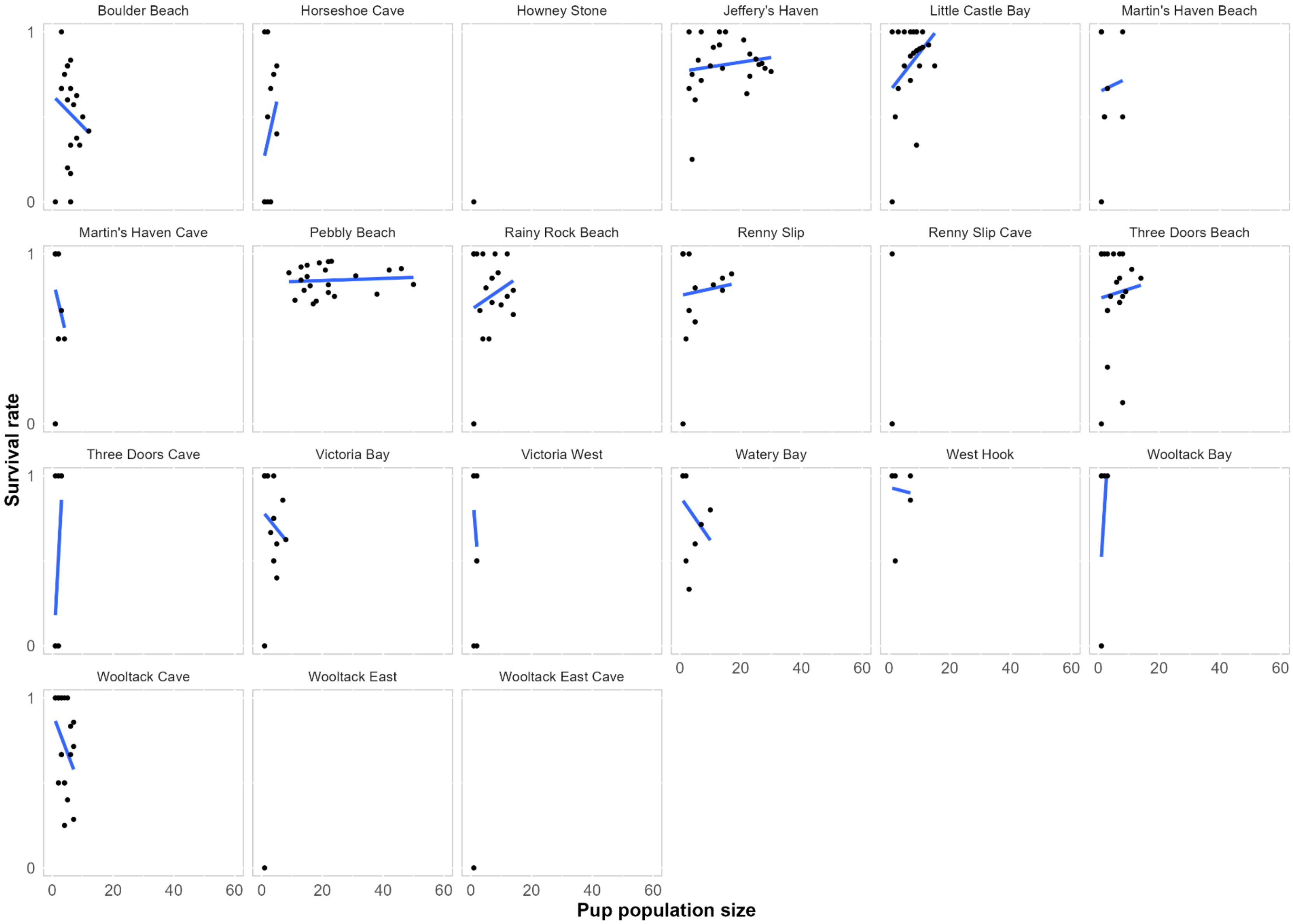

Figure A8. Density-dependent effects upon pup survival estimates at the Marloes colony

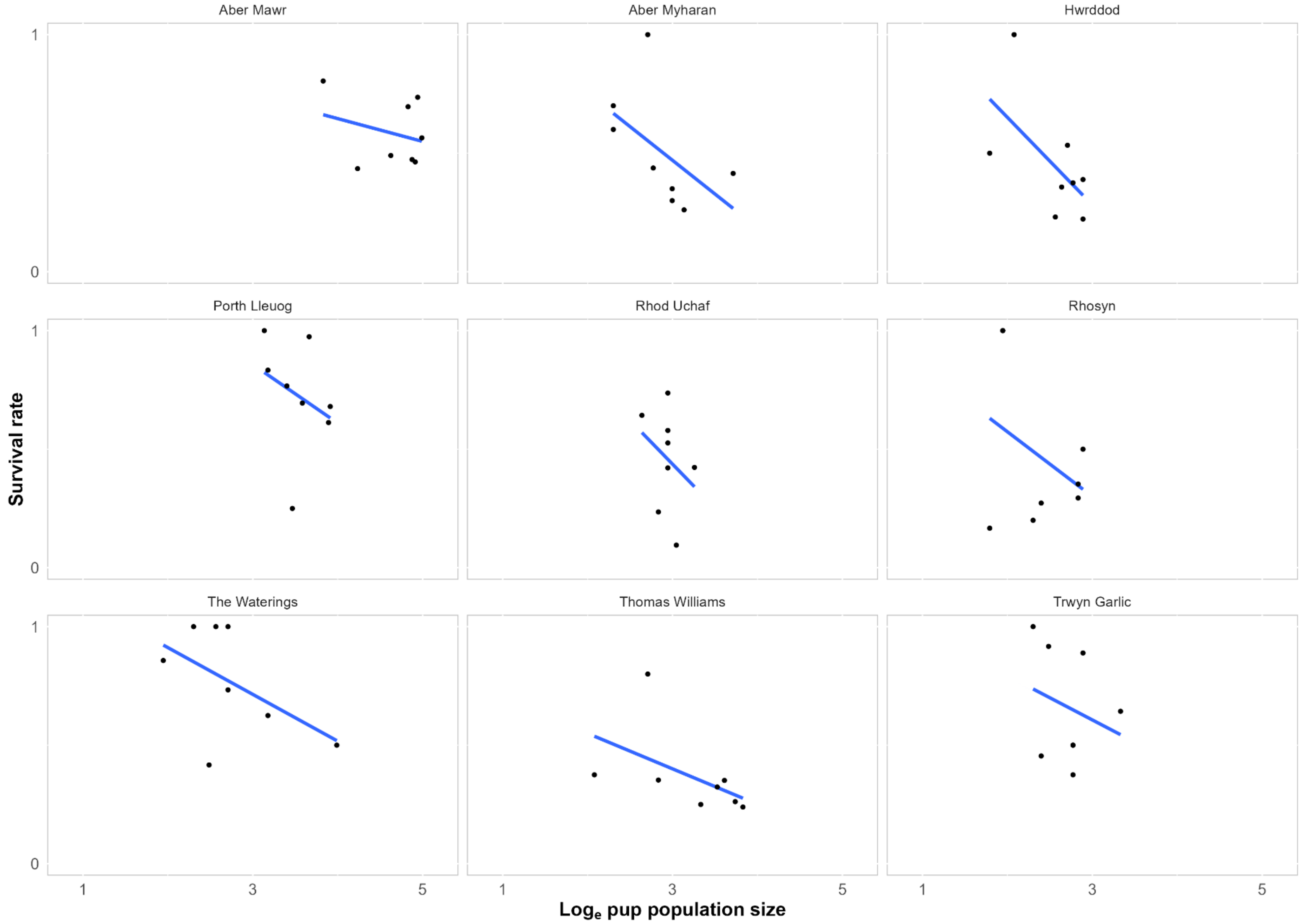

Figure A9. Density-dependent effects upon pup survival estimates at the Ramsey colony

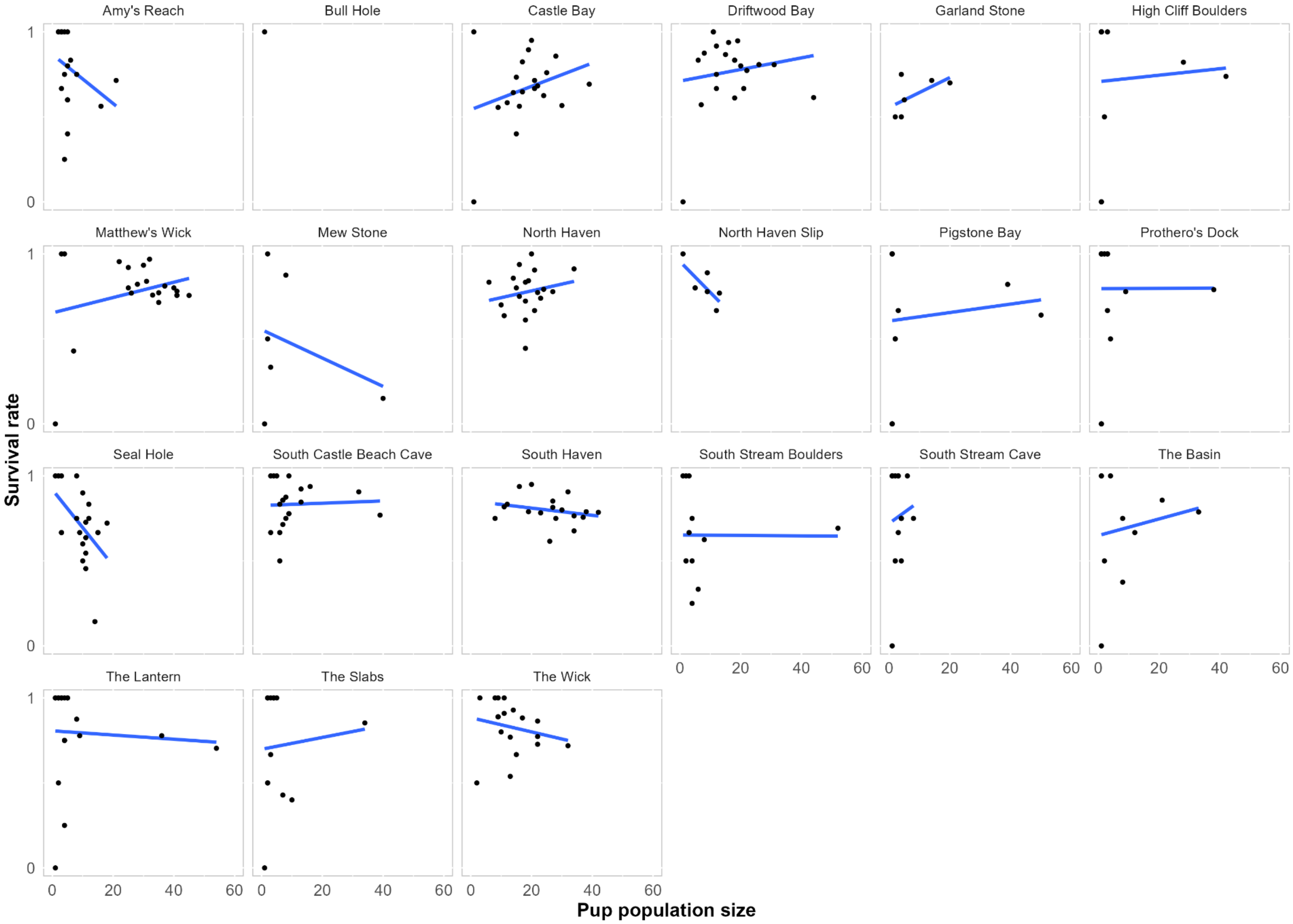

Figure A10. Density-dependent effects upon pup survival estimates at the Skomer colony

Appendix three

Consequences of parameter substitution in modelling spatially heterogeneous populations

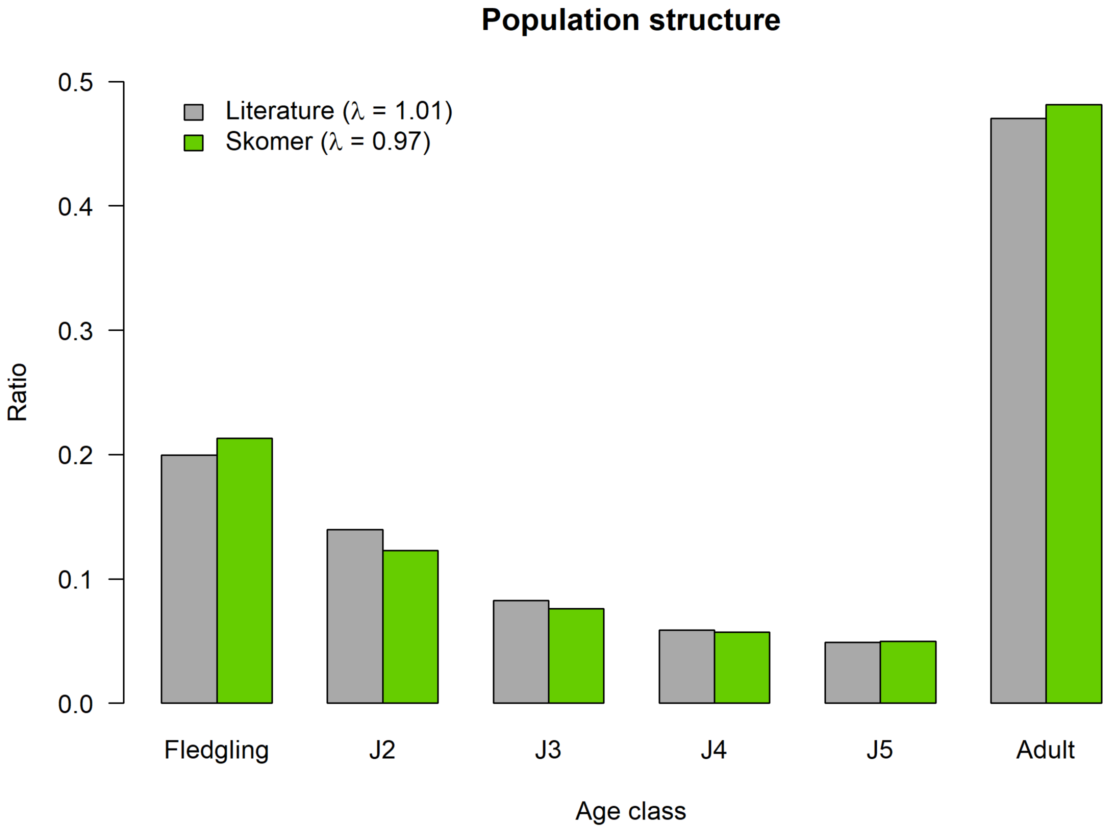

Figure A11. Comparison of population stable structure from observed adult survival estimates (Skomer) and estimates substituted from the literature (BTO RAS scheme)

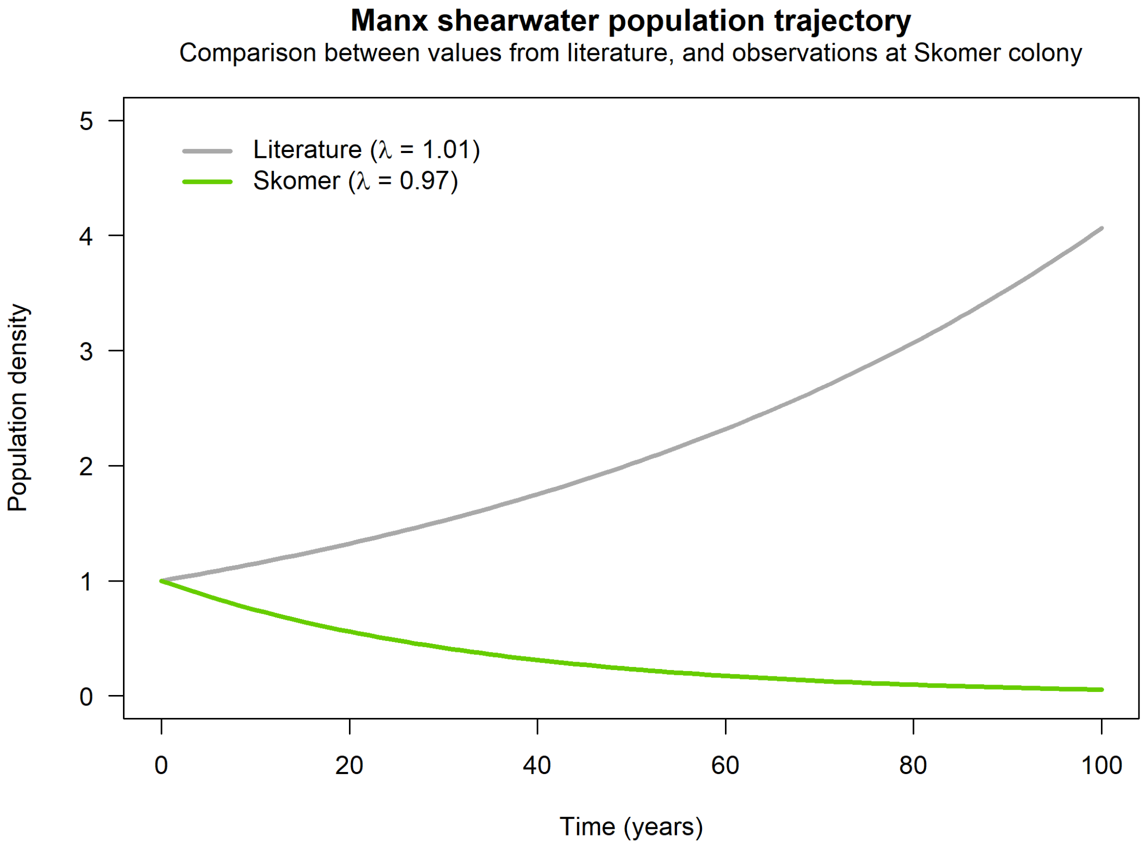

Figure A12. Simple deterministic projection of Manx shearwater population trajectory, from adult survival estimates calculated from Skomer, and those substituted from the BTO RAS scheme.

Appendix four

Demographic resilience at the population level: a case study of the Manx shearwater

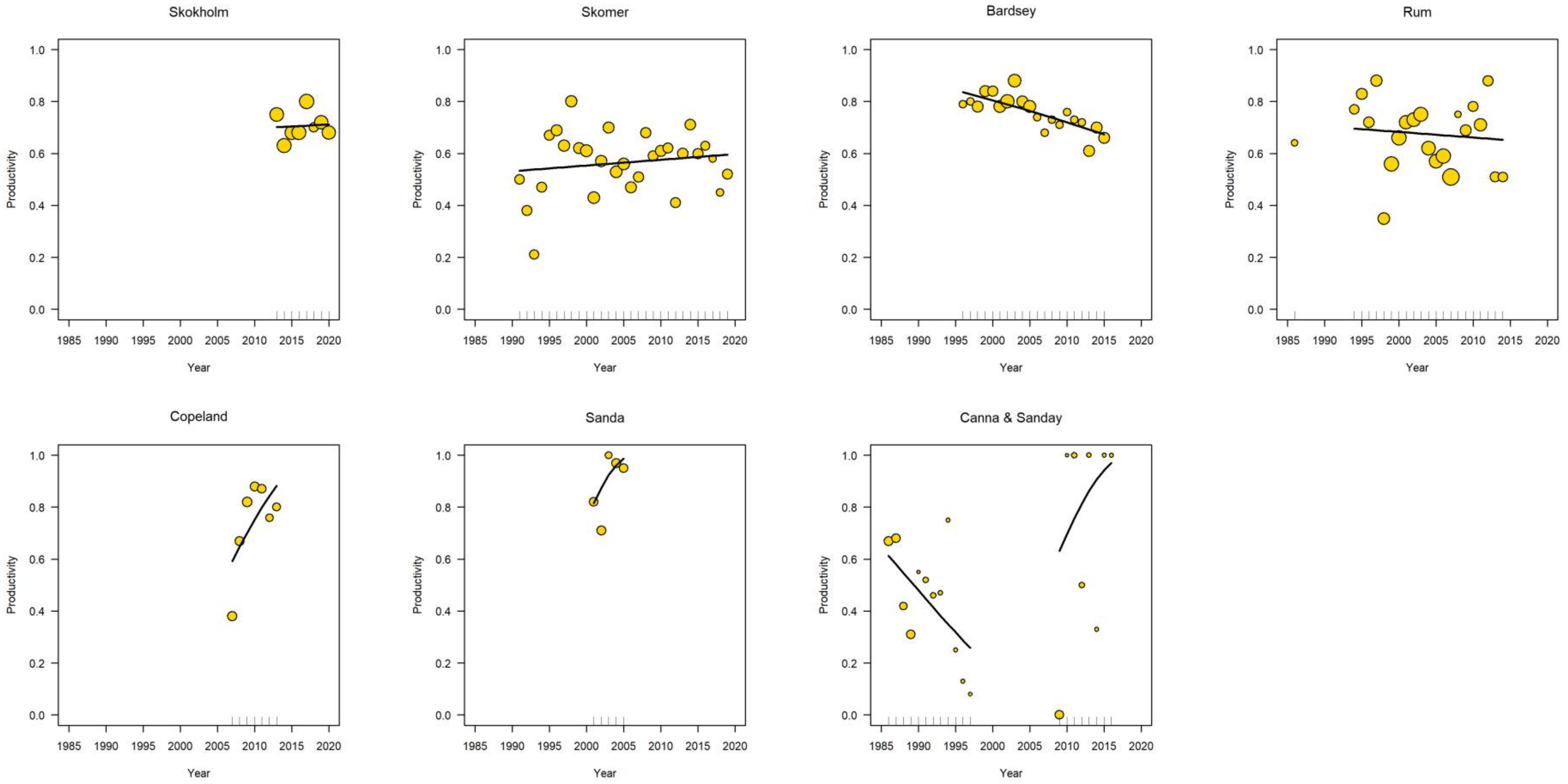

Figure A13. Estimates of survival (productivity) from all available Manx shearwater colonies. Point size indicates number of nests sampled. Note collapse of Canna colony and subsequent recovery marked by extreme estimates of zero and one

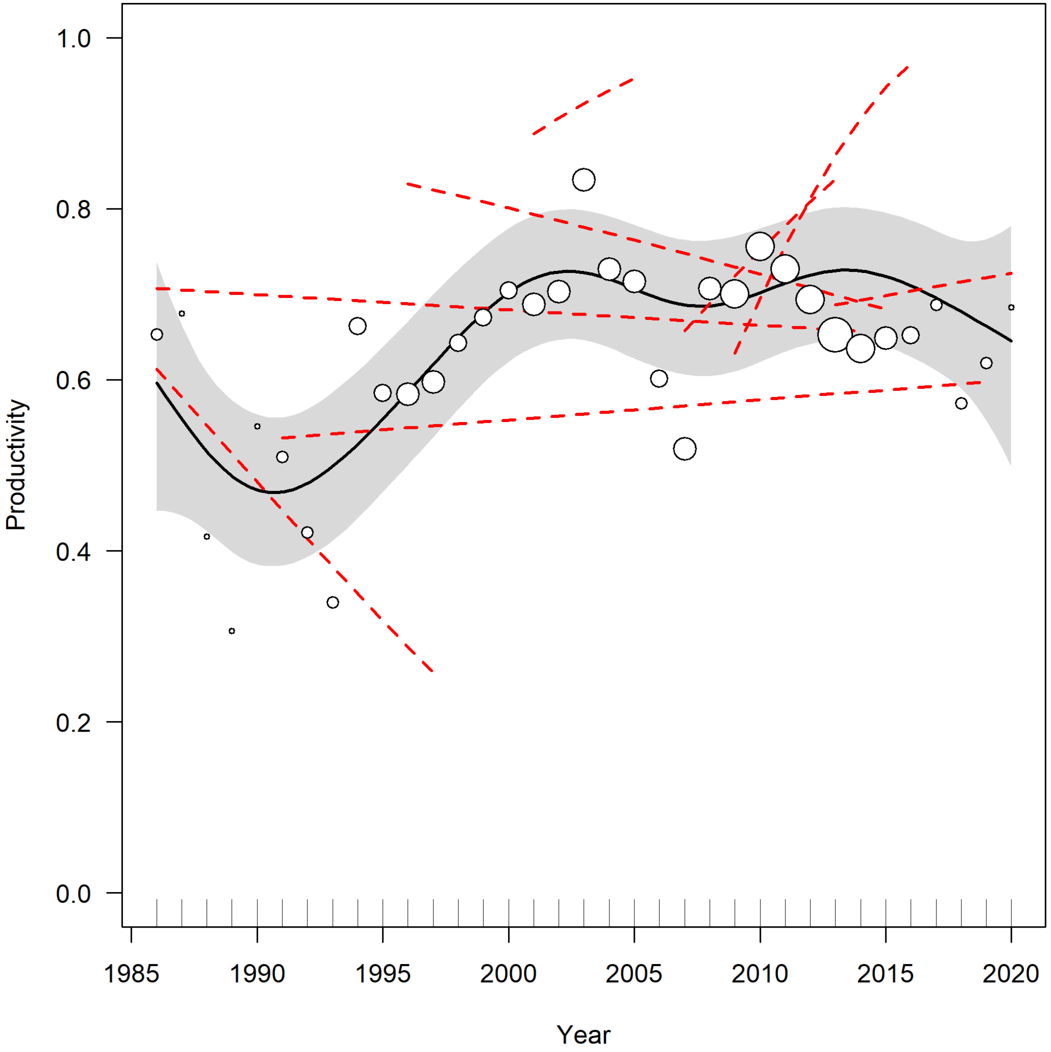

Figure A14. GAM estimate of mean fledgling survival (productivity) across all sampled sites (Figure A13). Note the initial decline, when monitoring was only being conducted at Canna

Appendix five

Exploring Manx shearwater trophic and spatial ecology via Stable Isotope Analysis (SIA)

Introduction

Seabirds are a useful indicator of the health of marine ecosystems, and an understanding of their trophic and spatial ecology can highlight changes in marine foodwebs that may otherwise be difficult to detect. Understanding how diet may vary during different life stages, how birds are distributed while away from the breeding colonies, and the degree to which these patterns change between years, may also serve to understand broader shifts within seabird populations. Studies of seabird trophic and spatial ecology usually rely upon direct observation of feeding behaviour and analysis of stomach contents, and upon data loggers attached to the birds. These methods can be invasive and logistically challenging, and are prone to gaps in observations. Stable isotope analysis offers the opportunity to gather information without the need for invasive methods or expensive field equipment. Isotopes are chemical elements that exist in a number of forms, and their ratio varies depending on geographic location and ecosystem processes. By analysing isotope ratios in body tissue it is possible to investigate patterns of diet and spatial distribution from when these tissues were grown. Feathers are particularly suitable as they are inert, so they retain their unique isotope ratio indefinitely, and when moult patterns are well understood, feathers can provide a reliable source of information.

The Manx shearwater breeds in burrows at offshore colonies in the northeast Atlantic during the spring and summer, before migrating to the east coast of South America for the (boreal) autumn and winter. Birds return to the same colony to breed year after year, but it is not well understood how this species disperses after the breeding season Do birds from different colonies interact with each other or do they tend to segregate according to colony. Does this vary during the season and between years? Adult Manx shearwaters replace their primary flight feathers while at the wintering grounds, and moult is completed before return migration to the breeding grounds. Analysis of new-growth feathers can therefore provide information about their diet and distribution during the non-breeding season. By analysing feathers from birds breeding at different colonies it may be possible to determine whether these birds spent the preceding autumn and winter together as one ‘population’, or in separate regions of the southwest Atlantic. Investigating how colonies interact may help to understand the potential for immigration of birds to colonies that are recovering from historical population declines, such as that on the Calf of Man.

Proportions of ^{15}N to ^{14}N are expressed as $\delta^{15}N$ and give an indication of trophic level. Higher delta values correspond to higher trophic levels, and a greater range of values within the sample corresponds to a more generalist diet. Carbon ratios $\delta^{13}C$ describe the relative proportions of ^{13}C and ^{12}C, and give an indication of the source of nutrition (benthic vs pelagic food webs), and an indication of the latitude at which feeding occurred (more negative $\delta^{13}C$ values correspond to higher latitudes (i.e. distance from equator)).

Stable isotope analysis of feathers cannot provide detailed information on dietary composition, but it can be used to estimate trophic position, i.e. the level in the food web that birds are feeding. Flight feathers can provide this information for the non-breeding season, but analysis of body feathers can be used to investigate trophic ecology during the breeding season, since adults replace these feathers while at the breeding colony, before migration to the wintering grounds. Similarly, fledglings will have grown their body and flight feathers while at the colony, so analysis of these can allow comparison of trophic ecology between chicks and adults.

Methods

Collection of feathers

Contour feathers were collected from birds at the Calf of Man colony during the 2019, 2020 and 2021 field seasons. Adults were sampled in June, during the chick-provisioning period, and 3-5 feathers were cut from the flank of each bird during routine night-time ringing activities. Fledglings were sampled in the same way in late August and early September, when adults had already departed. Primary flight feathers were collected from adult carcasses only, at the Skomer, Calf of Man and Rum colonies between June and August of the 2019 and 2020 field seasons.

Processing and isotope analysis of feathers

Each sample of body feathers was washed in a solution of 0.25M NaOH, before rinsing with distilled water and drying at 50°C for 48 hours. Mass varied between samples, so dried feathers were homogenised to ensure that analysis was conducted across the whole sample, and transferred to 1.5ml microtubes. Flight feathers were washed and dried in a similar way, and the top 4cm of the sixth and ninth primaries was sampled. Feather barbs were cut from the shaft to ease homogenisation, and transferred to microtubes. Samples were analysed via mass spectroscopy, and the ratios of carbon and nitrogen isotopes recorded. A summary of feather samples and results of stable isotope analysis is presented in Table 5.

Data analysis

Isotope ratios for body and flight feathers were investigated separately. As this pilot study analysed too few samples for full Bayesian analysis of trophic width, preliminary results are presented visually to indicate patterns in the observations. Adult body feathers grew in the season preceding collection (i.e., feathers collected in 2019 were grown in 2018), whereas fledgling feathers were grown in the year of collection. To ensure clarity in the comparisons, the years described below refer to the year in which feathers were grown/moulted. Given the lack of formal statistical analysis, care should be taken with the interpretation of patterns.

Results

Trophic ecology and foraging/provisioning strategy during the breeding season

Preliminary results suggest that birds in 2020 may have been provisioned from a lower trophic level relative to birds in 2019 and 2021, as indicated by the separation of data points in the first pane of Figure A15a. Similarly, it appears that adults may have been feeding themselves at a higher trophic level. The range of fledgling and adult $\delta^{15}N$ values also suggests that adults may favour a more generalist strategy when feeding (larger $\delta^{15}N$ range), compared with a narrower range of prey when provisioning young (narrower within-year $\delta^{15}N$ ranges). The geographical source of provisioning also suggests some separation between years, but there is much greater overlap in the $\delta^{13}C$ values of fledgling feathers (Figure A15b). Any difference here may simply be an artefact of annual fluctuation in isotope ratios at the source, rather than representing actual changes in foraging range, and would require comparison against isotope ratios from environmental and/or prey sources to verify this. The broad range of $\delta^{13}C$ values in adult feathers (Range = -15.7‰, -18.2‰; mean = -16.7‰) suggests that individuals may exhibit individual preferences in where they forage, with some preferring to forage further from land than others.

Figure A15c presents $\delta^{15}N$ and $\delta^{13}C$ ratios together, for each year of sampling, illustrating the difference between trophic level and source of prey for adults and fledglings. The solid lines and filled points indicate the year in which observations coincide for both adults and fledglings. The smaller ellipses and more closely distributed points for fledglings suggest provisioning from sources which may be trophically and spatially restricted sources, particularly in 2019 and 2021 where a greater overlap is visible. Since each point represents an individual bird, these The elongated ellipse from 2020 suggests that birds may have been provisioned from a spatially restricted source that was more diverse in its trophic composition. The broad ellipse and sparsely distributed adult points may indicate a more generalist foraging strategy spread across a relatively wide geographical area.

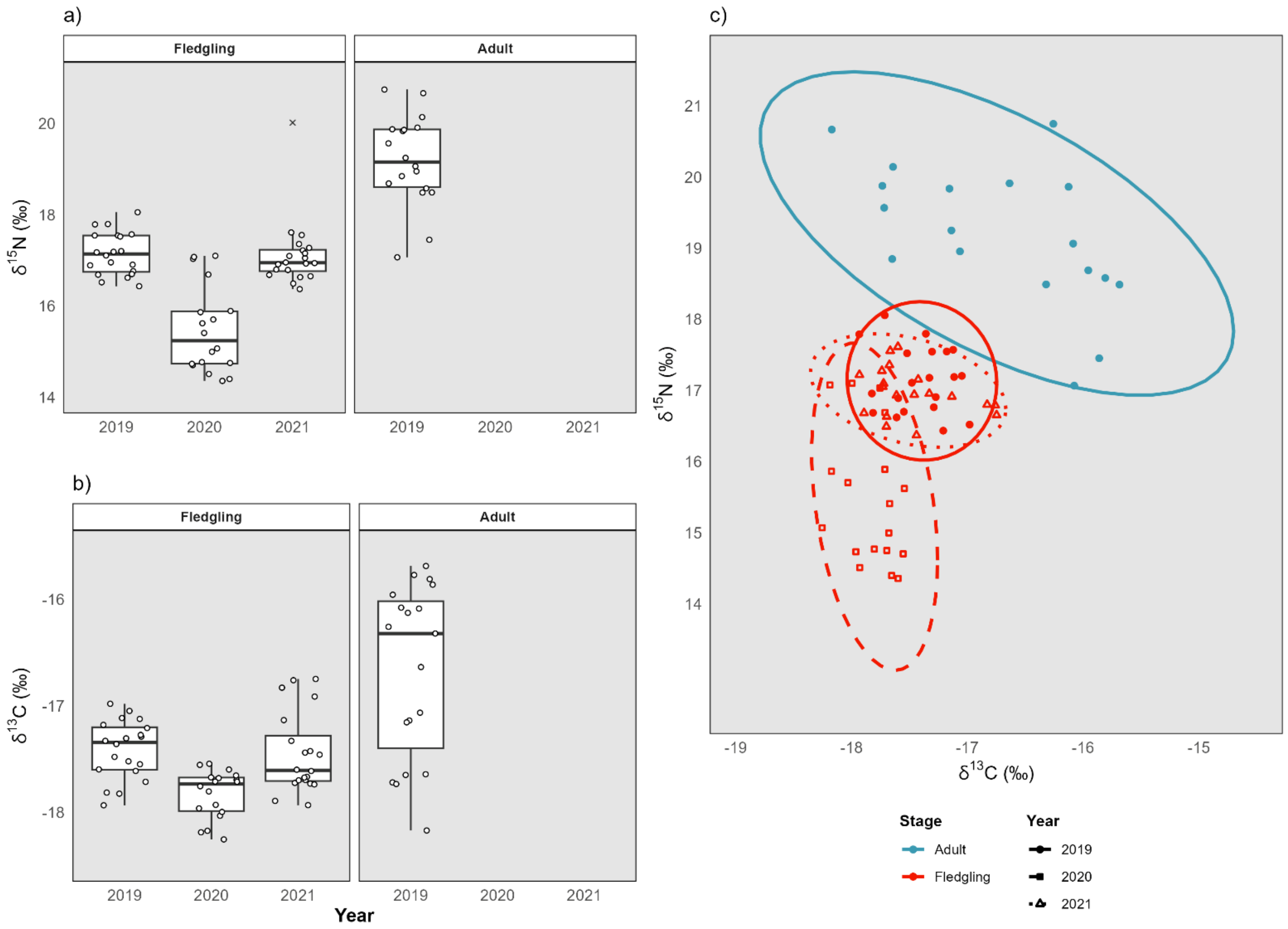

Figure A15. Nitrogen and carbon isotope ratios of contour feathers sampled from fledgling (2019-2021) and adult (2020: grown in year preceding sampling) Manx shearwaters at the Calf of Man colony. Outliers indicated by ‘x’, and ellipses indicate 95% confidence intervals.

Trophic ecology and spatial distribution of adults during the non-breeding season

The range of $\delta^{15}N$ values in primary flight feathers moulted during the non-breeding season appear the suggest little differentiation between colonies (Figure A16a). Birds from the Calf of Man and Skomer colonies do not appear to exhibit foraging specialism, as no clustering of individual values is apparent. Although the $\delta^{15}N$ value from Rum suggests a lower trophic level than birds from the other two colonies, only one bird was available for sampling here, so this should not be considered representative of the colony, and has simply been included for completeness. Carbon isotope ratios during the 2018 non-breeding season indicate very little difference in north-south distribution for birds breeding at the Skomer and Calf of Man colonies, but that birds from the Rum colony may have migrated further south (Figure A16b). Comparison between years for birds from Skomer suggests some consistency in the latitude of migration at this point on the moult cycle, although closer inspection reveals one individual that may have ventured further south in 2019.

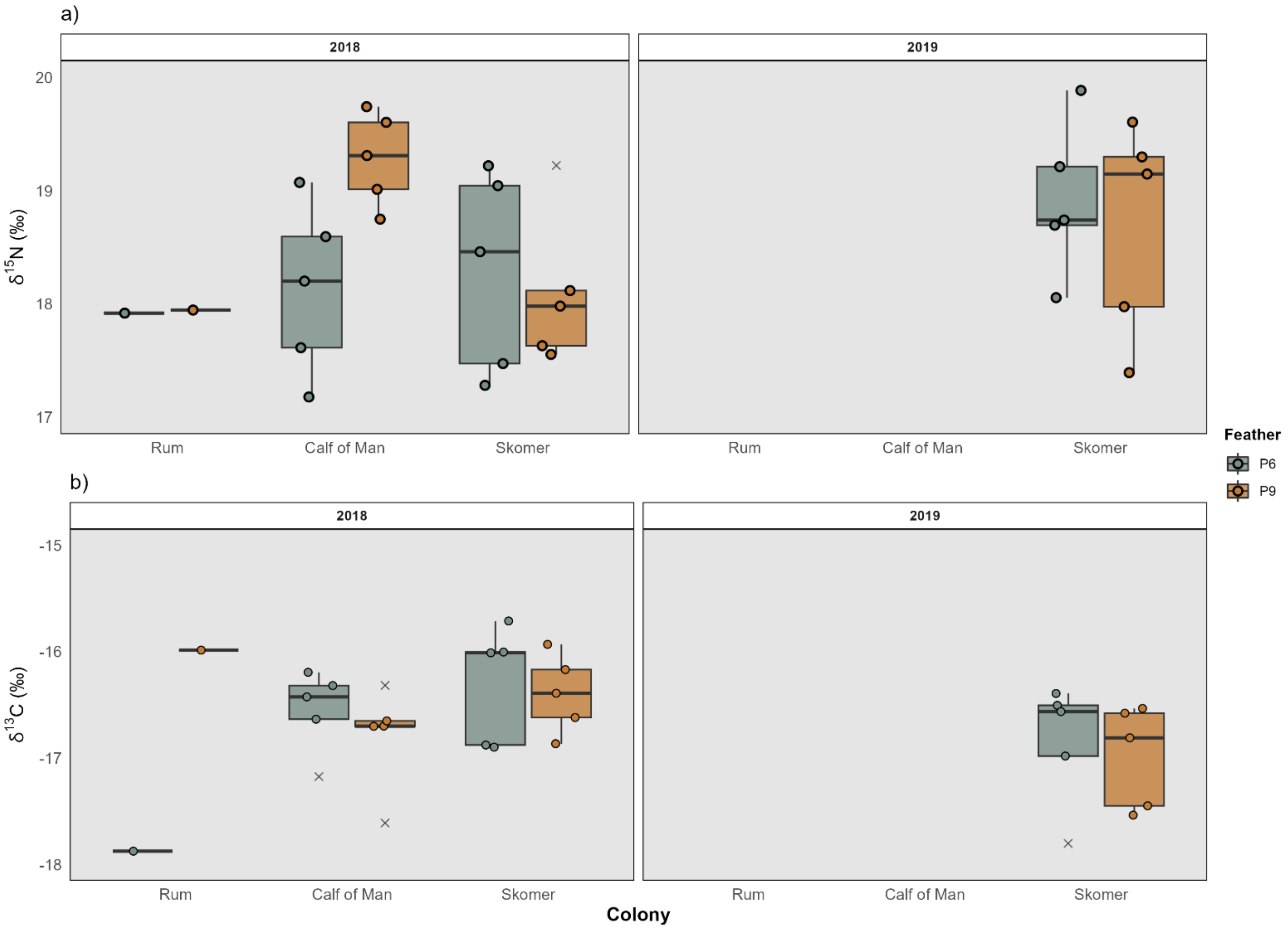

Figure A16. Nitrogen and carbon isotope ratios of P6 and P9 primary flight feathers sampled from adult Manx shearwaters at the Rum (2018), Calf of Man (2018) and Skomer colonies (2018-2019). Outliers indicated by ‘x’.

Table 5. Summary of feather stable isotope analysis samples.

Year	Colony	Feather	Stage	Count	Mean δ^{13}C	sd δ^{13}C	Mean δ^{15}N	sd δ^{15}N
2019	Calf of Man	Contour	Fledgling	20	-17.41	0.28	17.15	0.47
2020	Calf of Man	Contour	Fledgling	18	-17.83	0.23	15.48	0.95
2021	Calf of Man	Contour	Fledgling	20	-17.45	0.38	17.13	0.76
2019	Calf of Man	Contour	Adult	19	-16.68	0.82	18.63	2.64
2018	Calf of Man	P6	Adult	5	-16.55	0.38	18.13	0.76
2018	Calf of Man	P9	Adult	5	-16.80	0.48	19.28	0.41
2018	Rum	P6	Adult	1	-17.87	-	17.92	-
2018	Rum	P9	Adult	1	-15.99	-	17.95	-
2018	Skomer	P6	Adult	5	-16.30	0.55	18.30	0.89
2018	Skomer	P9	Adult	5	-16.39	0.37	18.10	0.67
2019	Skomer	P6	Adult	5	-16.85	0.58	18.92	0.68
2019	Skomer	P9	Adult	5	-16.98	0.48	18.68	0.95

Discussion

The investigation above offers a preliminary account on the use of stable isotope analysis to study the trophic ecology and spatial distribution of the Manx shearwater. No intra-colony patterns in foraging strategy emerged amongst adult birds, and between-colony differences were lacking. Differentiation between adult self-feeding and chick-provisioning strategies was apparent, however, as differences in the trophic level of adult birds and fledglings were identified. Results also suggested between-year variation in the trophic level of fledglings. Similarly, at colonies where multiple samples were collected, no clear patterns emerged in the spatial distribution of adult birds during the non-breeding season. Birds from the Rum colony ostensibly distributed further south in the migratory region than birds from the Calf of Man and Skomer colonies. However, closer inspection revealed that this result was from a single bird, and that the $\delta^{13}C$ ratio of this bird was similar to that of a bird from Skomer in the following year. Without data from additional individuals to give information on the wider colony, it is not possible to confidently conclude that this observation is genuine.

Although it is believed that adults replace their contour feathers at the breeding colony (Baker, 2016), it is not clear whether all feathers are replaced in one season. If the moult of contour feathers is not completed within one breeding season, then some feathers may retain isotope ratios assimilated during previous seasons, or away from the colony, potentially confounding the results of this analysis. Ongoing stable isotope analysis of prey species within the breeding season foraging range would provide an environmental baseline against which within- and between-colony patterns could be compared, both within and between years. Correlation-based analysis of stable isotope ratios and sea surface temperature can provide the basis for determining spatial distribution (MacKenzie et al., 2011), and simultaneous biologging of individual movements could allow to be ground-truthed (Cherel et al., 2016). These complementary techniques could facilitate further study of spatial ecology in Manx shearwaters, which would be required before robust conclusions can be drawn.

Collecting primaries from carcasses may also have introduced bias into these results. The cause of mortality for these individuals was unknown, so if individual fitness or nutritional status were contributing factors, then the intake of prey and subsequent tissue isotope ratios may have been affected. Similarly, if the sampled carcasses had been those of prospecting sub-adults then isotope ratios would not have reflected the trophic and spatial ecology of adult birds. After departing the colony in its first year, a juvenile Manx shearwater will spend the next two to three years in the southwest Atlantic, before travelling northwards to the east coast of North America. Following this, birds return to the natal colony so if these individuals account for carcasses sampled here, then isotope ratios are likely to be very different to birds engaged in the adult migratory cycle.

Known-fate, live birds. Will also give opportunity for repeated measures to identify within-individual patterns between years. Current approach only allows snapshot of spatial distribution for individuals, and no insight into previous and subsequent migratory destination.