BAYESIAN ANALYSIS OF MULTI-SPECIES DEMOGRAPHY: SYNCHRONY AND INTEGRATED POPULATION MODELS FOR A BREEDING COMMUNITY OF SEABIRDS

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A Thesis submitted for the degree of Doctor of

Philosophy in the subject of Statistics

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October 2012

ABSTRACT

In the study of wildlife populations, demographic data have traditionally been analysed independently for different species, even within communities. With environmental conditions changing rapidly, there is a need to move beyond single-species models and consider how communities respond to environmental drivers. This thesis proposes a modelling framework to study multi-species synchrony in demographic parameters, using random effects to partition year-to-year variation into synchronous and asynchronous components. The approach also allows us to quantify the contribution of environmental covariates as synchronising/desynchronising agents.

We apply the framework to long-term data from a breeding community of seabirds at the Isle of May, Scotland, studying synchrony in adult survival and parameters related to breeding success. We then combine demographic data with population counts and propose the first multi-species integrated population model (IPM), which estimates simultaneously the abundance of puffins, guillemots and razorbills and the demographic parameters that drive their fluctuations, while estimating synchrony in adult survival and productivity.

Most analyses are carried out within the Bayesian framework. Results indicate that for these three auk species the same climatic covariates act simultaneously as synchronising and desynchronising agents of a mostly synchronous adult survival, based on resighting data of ringed birds. They also reveal varying degrees of productivity synchrony in a set of five species, with the synchronous terms, a potential community-based indicator of local marine ecosystem health, indicating a decline in productivity during the study period.

The thesis also investigates options to optimise the monitoring of guillemot juveniles at the Isle of May. Using the historic data set, we show that ringing effort is adequate but that resighting effort could be substantially reduced while still being able to detect the dramatic variations in first-year survival and ecological relationships with individual-level covariates investigated. We finally explore the limitations of an IPM to compensate for the lack of direct juvenile data in the case of stopping the ringing of guillemot chicks.

Both synchrony models and the multi-species IPM are readily applicable to any species assemblage in any ecosystem, provided long-term data are available. They represent new steps towards more integrative approaches to modelling demographical parameters. The study of synchrony may facilitate the generation of further hypotheses about similarities and differences in species' ecology.

ACKNOWLEDGEMENTS

First and foremost, I would like to express my sincere gratitude to my PhD supervisors Professor Byron Morgan, Dr Stephen Freeman and Professor Sarah Wanless, as well as to Professor Mike Harris, for their continuous support. Their knowledge, patience, encouragement and enthusiasm have been invaluable for my research. To Byron, for the countless meeting hours that have shaped my view of statistical modelling as well as for being so supportive of me attending conferences; to Stephen, for always proposing interesting ideas and points of view that made me think; to Sarah and Mike, for sharing a piece of their tremendous knowledge and passion for seabirds. It has been a pleasure working with you!

Thanks as well to Dr Ruth King and Dr Diana Cole for examining my thesis. I would also like to acknowledge the Engineering and Physical Sciences Research Council (EPRSC), the National Centre for Statistical Ecology (NCSE) and the Centre for Ecology & Hydrology (CEH) for funding my work.

Thanks go to Mike Harris, Sarah Wanless, Francis Daunt, Mark Newell and Scottish Natural Heritage for collecting the Isle of May demographic data and population counts that are the motivation for this thesis, and for allowing me to use this fantastic data set. This research was only possible thanks to the many people who have helped through the years with ringing and looking for colour rings on the Isle of May. Part of their fieldwork was carried out with funding from the Joint Nature Conservation Committee's integrated Seabird Monitoring Programme. Scottish Natural Heritage allowed them to carry out these studies on the Isle of May National Nature Reserve. I am also grateful to Mike, Sarah, Francis and Mark for promptly answering my queries about data and seabirds; geographical distance has not been a problem! I would also like to thank them, as well as SNH and the Isle of May Bird Observatory, for the opportunity to stay at the Isle of May. These two visits allowed me to see data collection first-hand and spend a bit of time watching the study species, which helped me understand the system and data sets much better. I acknowledge the British Trust for Ornithology for providing ring-recovery data. The BTO Ringing Scheme is funded by a partnership of the BTO, the Joint Nature Conservation Committee (on behalf of: Council for Nature Conservation and the Countryside, the Countryside Council for Wales, Natural England and Scottish Natural Heritage), The National Parks and Wildlife Service (Ireland) and the ringers themselves.

Thanks also to Marc Kéry, Olivier Gimenez and several anonymous reviewers for helpful comments on two manuscripts, which improved chapters 2 and 3.

Finally, I could not forget to thank my family who, despite the distance, have always supported me; and my friends, especially all those in Canterbury, with whom I have shared beers and PhD worries. You are a great bunch!

Last but not least, to Guru, my love and companion, colleague and co-author, for sharing the highs and lows of PhD life. In the summer 2007, while still working as engineers in Finland, we visited the Hornøya seabird colony in northern Norway together. As in any seabird colony I have seen, the teeming life and continuous activity is a feast for the senses. I remember how we looked with envy at the ecologists staying at the lighthouse, studying the birds, and hoped we could ourselves someday do wildlife research.

Well, we made it!

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1 INTRODUCTION

The study of wildlife populations is of interest for several scientific and applied disciplines. The understanding of how populations change as well as the underlying demographic parameters that drive such fluctuations is first of all relevant in many areas within ecology, including evolutionary, population and community ecology (Begon, Townsend & Harper 2006). From the applied point of view, it is paramount for the correct management of populations (Williams, Nichols & Conroy 2002), for both harvested species (including fishery stocks) and species of conservation concern: it is by affecting demographic rates like survival and productivity that one can attempt to control population growth in order to, for instance, increase abundance of threatened species, reduce abundance of invasive species or manage harvested populations at a sustainable level (Caswell 2001, p.591). The need for this understanding is even more pressing as the growing human population continues increasing the strain on natural resources including harvested species, and we face an unprecedented biodiversity crisis, with species extinction rates estimated to be at least similar to those of previous mass extinctions (Barnosky *et al.* 2011). This situation is likely to be further aggravated by the impending global climate change (Thomas *et al.* 2004). Addressing this biodiversity crisis and reducing the rate of species extinctions have been recognized as international priorities (Millennium Ecosystem Assessment 2005).

Within the aforementioned disciplines, it is often of interest to monitor changes in the abundance of populations, which provides a feedback between implementation and management that is essential for decision-making (Possingham *et al.* 2001).

To understand population dynamics fully, it is also relevant to investigate how the different demographic processes like survival, migration and reproductive success, relate to changes in abundance, taking into account the specific ecology of a species of interest. Some species may act as indicators, with monitored changes in abundance or demographic rates providing early warnings of changing conditions in ecosystems that are difficult to study directly (Einoder 2009). Finally, the scientific and applied interest often lies in understanding what intrinsic or extrinsic factors drive the variations in the different demographic parameters.

To address these various issues, data collected in the field are analysed using statistical models matched to the type of data and the particular application or question to answer. It is within this context that this thesis is developed.

1.1 Thesis motivation: the multi-species perspective

The motivating example for this thesis is a long-term data set collected from an intensively-monitored seabird colony at the Isle of May, off the southeast coast of Scotland. This rich data set contains information about different aspects of demography for several species of seabirds that share physical space and resources during the breeding season. It also contains island-wide counts of the breeding populations, some of which have suffered drastic changes over the last 30 years.

The monitoring of demographic parameters in wildlife populations is nowadays generating a wealth of valuable information for ecology and conservation and recent decades have seen a corresponding proliferation of statistical models, as we will see in section 1.4. However the potential to integrate different types of data has not been fully exploited, with the majority of these models targeted at analysing single demographic parameters for individual species (Lebreton *et al.* 1992; Williams, Nichols & Conroy 2002), although approaches such as integrated population modelling (Besbeas, Freeman & Morgan 2005), which we will see later, jointly estimate several parameters in a single-species analysis. Data from several species have recently been combined in models to study population trends (Sauer & Link 2002) or species richness (multispecies occupancy models, Russell *et al.* 2009) but demographic modelling has conventionally been carried out on a single-species basis with comparisons between different species being made a posteriori (e.g. Sandvik & Erikstad 2008; Cury *et al.* 2011). This is largely the case for the Isle of May monitoring program. During the several decades of data collection at the Isle of May, many scientific studies have been published on different aspects of the species' ecology (numerous references to such studies appear throughout the thesis), but most analyses have been carried out independently for different species (with the exception of Frederiksen, Mavor & Wanless 2007), and integrated population modelling has only been done for one of the species (Reynolds *et al.* 2009).

However, with environmental conditions changing rapidly, there is a need to move on from the 'single-species vacuum' (Sabo 2008; McCarthy 2011) and develop multi-species approaches that provide insights into how communities respond to environmental drivers. Species exist within the context of communities and ecosystems, and when populations of different species are sympatric they are exposed to biotic interactions and the same abiotic environment (Begon, Townsend & Harper 2006). Some species may react in a similar way to their common environment, showing synchrony in population trends or in the temporal variation of certain demographic parameters such as survival. The underlying cause of synchrony between species is usually not evident, with hypotheses suggesting shared stochastic effects, such as weather (Hawkins & Holyoak 1998) and the response to common predators (Raimondo *et al.* 2004). The study of a species in a community in isolation may lead to only a partial understanding of their ecology (McCarthy 2011).

Synchrony between sympatric populations of different species has received less attention compared to synchrony between allopatric populations of a single species (Raimondo *et al.* 2004). The relatively few multi-species examples to date typically address synchrony in abundance through the study of time-series of population size (Ranta, Lindström & Lindén 1995; Swanson & Johnson 1999; Raimondo *et al.* 2004; Mutshinda, O'Hara & Woiwod 2011) or are sometimes dedicated to understanding mechanistic predator-prey interactions (New 2009). In general, investigating the mechanisms underlying population change is a difficult task when studying time series of abundance alone, and the incorporation of demographic parameters such as survival, reproductive success and dispersal probabilities is often key in understanding such mechanisms (Loison *et al.* 2002).

The motivation for this thesis is to study the demography and population variations in a breeding community that consists of several species of seabirds, looking at multi-species synchrony in different demographic aspects and investigating when possible the role that climate-related parameters can play as synchronising and desynchronising agents. The ideas of multi-species synchrony and joint modelling of several species are therefore recurrent throughout the thesis, and culminate in a multi-species integrated population model, where all the available data are combined in a single model. Although all modelling revolves around the Isle of May seabird data set, we note from the start of the thesis that the framework and ideas discussed are equally valid for other species assemblages, although small adaptations of the models may obviously be required in some cases depending on the species' characteristics.

In the remainder of this chapter, we provide background on several topics relevant to the thesis. The following section introduces in more detail the Isle of May and the seabird species considered. We then give a general overview of environmental influences on seabird demography, existing statistical models to study animal populations and demography, and the Bayesian framework, the predominant form of inference in this thesis.

1.2 The Isle of May seabird colony

1.2.1 The seabird breeding community at the Isle of May

The Isle of May (Figure 1-1) is a small island located off the south-east coast of Scotland, in the outer Firth of Forth (56°11'N, 2°34'W). It is an important breeding site for grey seals and several species of seabirds, as well as stop-over for passerines during migration. The island is owned by Scottish Natural Heritage (SNH) and managed as a National Nature Reserve.

Figure 1-1 Aerial view of the Isle of May, looking north, showing the high cliffs in the western side, the lower-laying eastern shore and the grassy top of the island. Photo PA Macdonald/SNH.

Eleven species of seabirds regularly breed at the Isle of May. This thesis concentrates on five of them (Figure 1-2), including some of the most numerous. The species considered are

(i) three closely-related auk species (Family Alcidae): the Atlantic puffin *Fratercula arctica* (L.), the common guillemot *Uria aalge* (Pontoppidan) and the razorbill *Alca torda* L.;

(ii) a gull (family Laridae), the black-legged kittiwake *Rissa tridactyla* (L.), in many ecological aspects more similar to the three auks above than to its larger *Larus* relatives;

(iii) the European shag *Phalacrocorax aristotelis* (L.), a species of cormorant (family Phalacrocoracidae).

For simplicity, in the rest of the thesis we refer to these species as puffin, guillemot, razorbill, kittiwake and shag respectively. These species are selected for analysis because in each case long-term data sets are available for different demographic aspects, and because they share many traits of their life history and ecology.

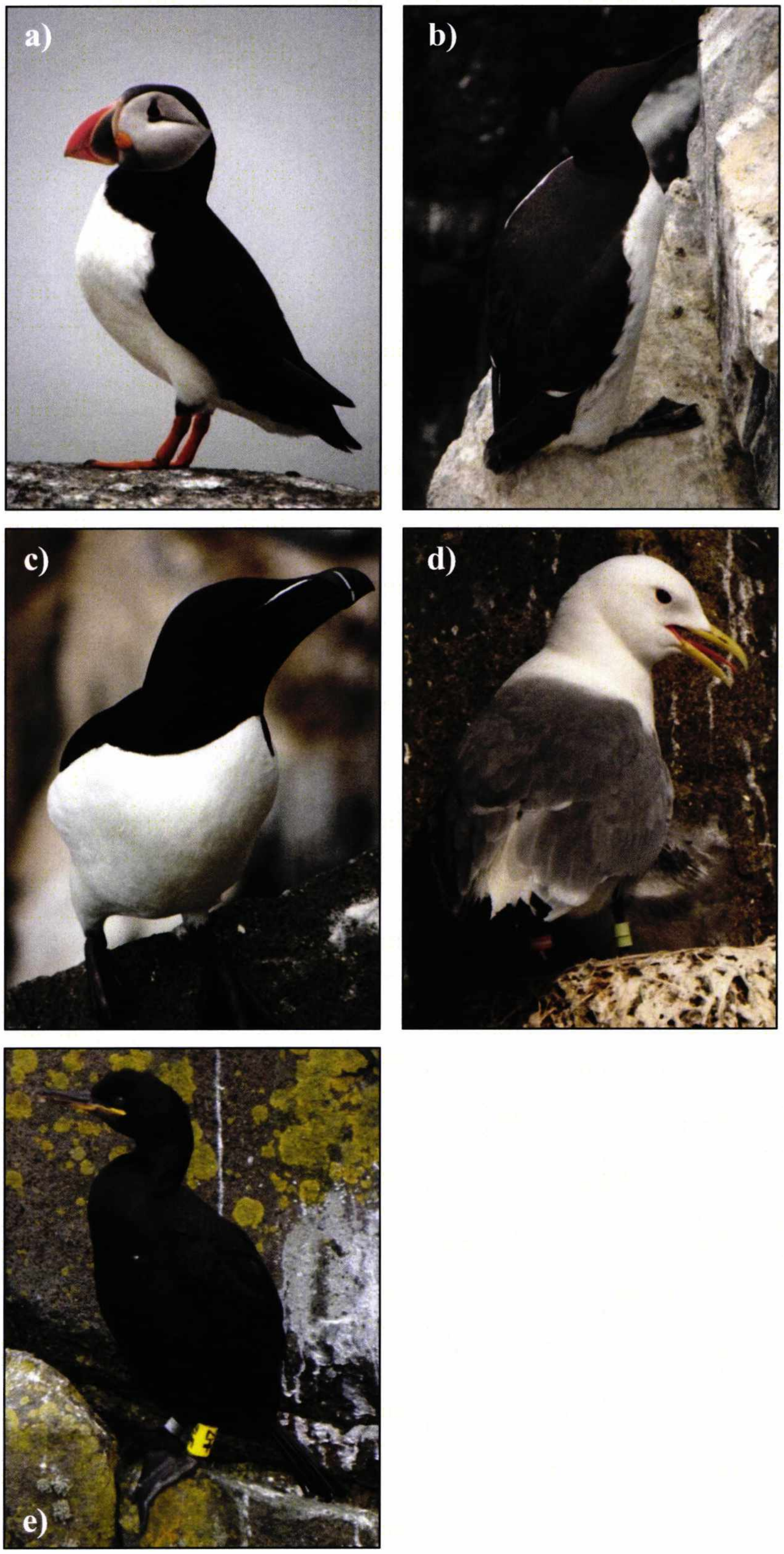

Figure 1-2 Pictures of puffin (a), guillemot (b), razorbill (c), kittiwake (d) and shag (e) at the Isle of May. Note the visible rings in the kittiwake and shag.

Other seabird species that breed at the Isle of May include common and arctic terns (*Sterna hirundo* and *S. paradisaea*; family Sternidae), northern fulmars *Fulmarus glacialis* (family Procellariidae), and three species of large gulls (family Laridae), herring gull *Larus argentatus*, lesser black-backed gull *L. fuscus* and great black-backed gull *L. marinus*. The latter three regularly predate on chicks of the other species; the last also kills adult and immature auks and kittiwakes.

Like many other seabirds, the five focal species have life-history traits characteristic of K-selected species (MacArthur & Wilson 1966): they are long-lived, with high adult survival, delayed recruitment, low productivity and typically invest great effort and time in the care of their young (Gaston & Jones 1998; Harris, Wanless & Rothery 2000; Parsons *et al.* 2008; Harris & Wanless 2011). They also show high colony fidelity once recruited into a breeding population but, although philopatry is high, some young reared on the island emigrate to breed elsewhere.

The five species also share a common prey base during the breeding season, which around the Isle of May consists mainly of small, lipid-rich, shoaling fish such as the lesser sandeel *Ammodytes marinus* and sprat *Sprattus sprattus* (Frederiksen *et al.* 2006; Daunt *et al.* 2008). The three closely related auk species in particular have broadly similar life histories and feeding ecologies (Gaston & Jones 1998). They all lay a single egg, are wing-propelled pursuit divers that feed on fish during the breeding season and transport food back to the chick in the bill. In contrast, kittiwakes and shags have multiple egg clutches, and also have different foraging strategies, with kittiwakes being surface-feeders while shags dive to the sea bottom propelled by their feet; both species feed their young by regurgitation (Frederiksen *et al.* 2006; Parsons *et al.* 2008). One aspect that sets the guillemot apart from the other two auk species is that only a single prey item is brought back per foraging trip. Razorbills and puffins bring back both single fish and multi-prey loads, with the puffin able to carry more than 50 items at a time (Harris & Wanless 2011).

Regarding the selection of breeding sites, there are marked differences among species. Puffins are the only species of the set that breeds in burrows, excavated in the grassy slopes on the top of the island (Harris & Wanless 2011). The other species are associated with the cliffs and rocky areas. However, while kittiwakes and shags build nests, guillemots and razorbills lay their egg directly on the ledge (Gaston & Jones 1998). There are also differences in breeding strategies such that guillemot and razorbill chicks only spend about three weeks at the colony, completing their development at sea (Harris, Webb & Tasker 1991), whereas the other species feed their chicks for much longer and the young are independent by the time that they leave the colony.

Outside the breeding season the species disperse to the open sea away from the breeding colonies, except for shags that remain largely coastal with some birds remaining close to the Isle of May (Daunt *et al.* 2006). Kittiwakes have the widest dispersal range, reaching as far as the Canadian arctic (Bogdanova *et al.* 2011). Regarding the adult auks, although traditionally thought to have largely overlapping overwintering distributions (Wernham *et al.* 2002), recent work with geolocation loggers at the Isle of May suggests a larger separation outside the breeding season, with puffins predominantly in the north-western North Sea (with some individuals making excursions into the Atlantic) and guillemots and razorbills showing a more southerly distribution, spending time in the southern North Sea, sometimes moving into the English Channel (M. P. Harris, *personal communication*).

Table 1-1 compares the five focal species, highlighting the similarities and differences between them.

1.2.2 Data collection at the Isle of May

The Isle of May is one of the four ‘Key Site’ seabird colonies in UK’s Seabird Monitoring Programme (together with Fair Isle in Shetland, Canna in north-west Scotland and Skomer in Wales), where detailed monitoring of abundance, breeding success and adult survival is carried out (Mavor *et al.* 2008). Fieldwork on the Isle of May is carried out by researchers from the Centre for Ecology & Hydrology (CEH) although most population counts are made by SNH staff.

Seabirds possess some characteristics that facilitate the monitoring of their abundance and demography. Although most species disperse over large areas during the winter, the majority are colonial during the breeding season so that the adult population is concentrated in a few well-known locations. They are then available for census, ringing and monitoring of breeding success and other aspects of their life history. Seabirds being long-lived species, the effort invested in marking (e.g. ringing) can provide information on individuals for many years, compared to most short-lived passerines.

Table 1-1 Comparison of some of the traits that characterise the five seabird species analysed in this thesis. 'Prey load' refers to the amount of fish that each individual can bring to the chicks in their bill.

<table>
<tr><th></th><th>Atlantic puffin</th><th>Common guillemot</th><th>Razorbill</th><th>Black-legged kittiwake</th><th>European shag</th></tr>
<tr><td>Family</td><td colspan="3">Alcidae (auks)</td><td>Laridae (gulls)</td><td>Phalacrocoracidae (cormorants)</td></tr>
<tr><td>Breeding sites</td><td>burrows</td><td colspan="4">cliff ledges</td></tr>
<tr><td>Nest</td><td>burrow</td><td colspan="2">no</td><td colspan="2">yes</td></tr>
<tr><td>Clutch size</td><td colspan="3">1 egg</td><td>up to 3 eggs</td><td>up to 4 eggs</td></tr>
<tr><td>Fishing style</td><td colspan="3">pursuit-diver</td><td>surface-feeder</td><td>bottom-diver</td></tr>
<tr><td>Underwater propulsion</td><td colspan="3">wing-propelled</td><td>--</td><td>foot-propelled</td></tr>
<tr><td>Prey load</td><td>multiple-prey loader (bill)</td><td>obligate single-prey loader (bill)</td><td>facultative multiple-prey loader (bill)</td><td colspan="2">multiple prey (in stomach)</td></tr>
<tr><td>Winter dispersal</td><td colspan="3">wide distribution</td><td>very wide distribution</td><td>mostly coastal</td></tr>
</table>

At the Isle of May, breeding adults of unknown age of all five focal species have been ringed, providing rich data sets of resightings that span over 20 years. Individuals of some of the species have also been ringed as chicks, especially a large number of guillemots; in this thesis we model their live-resightings and ring-recoveries. Breeding success has also been monitored at some plots within the island, as a representative sample of the complete population. A more detailed account of the data sets is given when these are used in the thesis.

Abundance is monitored by counting the number of nests or breeding pairs, which is easier than attempting to count all individuals (Einoder 2009). Complete colony counts are carried out annually except for puffins (approximately every five years, within the time period modelled in this thesis). Puffin burrows are difficult to count, given the possibility of double entrances and the confusion with rabbit burrows; the protocol followed is described in Harris & Wanless (2011).

As already mentioned, many studies have been carried out at the Isle of May on different aspects of these species' ecology. Despite this wealth of information, to date data integration for different aspects of demography has only been performed for the common guillemot (Reynolds *et al.* 2009); in this thesis, we construct integrated population models for the first time for puffins and razorbills, as well as for the three auk species simultaneously (Chapter 5) which to our knowledge constitutes the first multi-species IPM of any kind.

1.3 Environmental influences on seabird demography

1.3.1 Climatic and oceanographic influences

Environmental covariates are known to influence demographic parameters in many species and have been shown in some cases to be responsible for inter-specific synchrony (Hawkins & Holyoak 1998). For North Atlantic seabirds, studies of survival often include covariates related to two oceanographic factors, the North Atlantic Oscillation (NAO) and the temperature at the sea surface (SST):

(i) The winter NAO index is a much-used indicator of climatic conditions over north-western Europe and has been shown to explain ecological processes (Stenseth *et al.* 2003), including survival of puffins, guillemots and razorbills (Harris *et al.* 2005; Sandvik *et al.* 2005; Grosbois *et al.* 2009). For this study, we used the Hurrell station-based extended winter (December to March) NAO index[1] ('wNAO').

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[1] wNAO values obtained at http://www.cgd.ucar.edu/cas/jhurrell/indices.html

(ii) Several different indices based on SST averaged over different areas and seasons have been used in relation to the species considered here (Harris *et al.* 1997; Harris *et al.* 2005; Sandvik *et al.* 2005; Grosbois *et al.* 2009). For this study, monthly SST values[2] were averaged for an area of 10 cells around the Isle of May, on a grid of 1°x1°. We used the average over January to May which corresponds to the spawning season and larval period of the sandeel, following Harris *et al.* (2005).

Some impacts of climate are direct (e.g. winter wrecks due to adverse weather, Frederiksen *et al.* 2008a), but for most species at the Isle of May the relationship appears to be indirect, probably operating through the food chain and thus affecting the distribution, phenology and abundance of prey species, particularly sandeel (Arnott & Ruxton 2002; Frederiksen *et al.* 2006). Such indirect effects often exhibit time-lags (Harris *et al.* 2005; Sandvik *et al.* 2005). To allow for potential indirect effects on demographic parameters, in the different analyses we also considered time-lagged versions of wNAO and SST, denoted by a subscript indicating the number of lag years (e.g., 'wNAO_1' indicates a 1-year lag; subscript 0 therefore indicates the direct effect of the covariate).

1.3.2 Fisheries

Seabirds and humans sometimes compete for the same resources and negative (and also positive) effects of fisheries on some seabird species have been documented (Newton 1998). The Isle of May seabird species that we consider in this thesis depend in large part on sandeels during the breeding season. Sandeels are used to produce fishmeal and a commercial sandeel fishery started to operate after 1990 in the Wee Bankie area, an important feeding ground for the Isle of May seabird community. Frederiksen *et al.* (2004) showed that the presence of the fishery had a negative impact on kittiwake breeding success at the Isle of May, although the exact link remains unclear and may include changes in behaviour of sandeels. No clear impact on productivity of the other species has been detected (Frederiksen *et al.* 2008b), perhaps because, unlike kittiwakes, the auks and shags are able to reach prey deeper in the water col-

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[2] SST values from http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.monthly/.sst.

umn: kittiwakes are thought to be more sensitive to variations in prey abundance than the other four species considered (Furness & Tasker 2000). The commercial fishery was closed in 2000 by the European Commission to avoid stock depletion and potential effects on marine top predators (Frederiksen *et al.* 2008b) and remains closed up to present (2012). As in previous studies, we used the presence of the sandeel fishery as an explanatory binary variable for productivity in our analysis.

1.3.3 Intrinsic effects: density-dependence

Both climate and fisheries are extrinsic effects, but intrinsic effects like density-dependence may exist, for example through competition for high quality breeding sites and/or food (not only intra-specifically but also between species with similar traits). For instance, some studies provide indication that density may affect different aspects of the guillemot life-history, e.g. recruitment at the Isle of May (Crespin *et al.* 2006) or the timing of egg-laying in Skomer Island, southwest Wales (Votier *et al.* 2009).

However, since a preliminary analysis conducted on productivity (the most likely candidate to exhibit density dependence among the demographic parameters for which we have data) did not show a clear indication of such effect, we do not model density-dependence. In Chapter 7 we discuss a possible extension of the multi-species integrated population model (proposed in Chapter 6) that provides a potential approach to modelling multi-species density-dependence in a statistically sound way.

1.4 Animal demography and population models

The development of statistical models to study animal abundance and demography has a long history that parallels the progress in general statistical methodology, and leads to the current variety and complexity of methods. We concentrate in this section on the different types of data (and related statistical models) that are used in this thesis. Recent technological advances have made possible the collection of many other data types (e.g. radio-tracking devices, geo-locators and bio-loggers to monitor physiology and behaviour; Ropert-Coudert & Wilson 2005), some of which have been used for the Isle of May studies (e.g. Bogdanova *et al.* 2011) but are not analysed here.

Unlike in many human demography studies, wild species are often notoriously difficult to find, follow and count. Imperfect detection is a recurrent concept in statistical models developed to study wildlife populations and demography, for example 'detection probability' in site-occupancy models (MacKenzie *et al.* 2006) based on unmarked individuals, 'recapture' and 'dead-recovery' probabilities for marked individuals, or 'observation error' in state-space models.

1.4.1 Marking animals to study survival

The identification of individuals within a population provides the possibility to study demographic parameters such as survival or emigration/immigration. The identification is commonly based on marks that distinguish individuals. These can be artificial marks fitted to the animals (e.g. ear-tags) or natural marks (e.g. the stripe pattern of tigers). In the case of birds, the most common type of mark used is rings (or 'bands'), either using unique colour combinations in several rings or by engraved individual alphanumeric codes; both types are used at the Isle of May. Early work with marked animals was oriented towards the estimation of abundance (Lincoln 1930, which actually did not require individual identification) but many models have been developed since then to study survival and related demographic parameters, relaxing the initial assumption of population closure. In such open-population mark-recapture ('MR') studies (also termed 'capture-mark-recapture', CMR), cohorts of individuals are marked and released at each time unit (e.g. year). Their fate is monitored over time, with attempts made to recapture or resight them at regular intervals; some individuals, although present, may be missed at some of these occasions. The data therefore consist of the identity of the individuals known to be alive and present at the study site at each recapture occasion. The classic Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965) estimates year-dependent survival and recapture probabilities. Many variations have been developed (e.g, age-specific parameters or the use of covariates), together with related methodological advances (e.g. goodness-of-fit tests); see reviews in Lebreton *et al.* (1992) and Williams, Nichols & Conroy (2002) for a more detailed account. As long as all data are collected at the study site, mortality and permanent emigration are confounded and the estimated survival actually represents 'apparent survival'. Several important extensions (e.g., robust design or multi-state MR models) have been developed, and are reviewed for example in Williams, Nichols & Conroy (2002), Royle & Dorazio (2008), King *et al.* (2009) and Kéry & Schaub (2012).

One particular type of model variation is relevant for the Isle of May data: in some cases, marks may be recovered when individuals die, creating a 'mark-recapture-recovery' (MRR) data set that contains both live recaptures and recoveries of marks from dead animals. MRR models include a 'recovery probability' to account for the fact that not all marks are recovered. The so-called dead-recoveries were initially modelled separately (details of history in Catchpole *et al.* 1998) until Burnham (1993) introduced a model which combined them with live recaptures. This scheme was based on cohorts and thus did not allow e.g. for age-specific effects to be modelled. Catchpole *et al.* (1998) approached the combined modelling of live recaptures and ring-recoveries from the recapture histories, presenting a more general framework that had full flexibility in cohort and age structures. They describe a cohort-based model using sufficient statistics consisting of four matrices; the equivalent age-based model was presented in a Bayesian framework shortly afterwards (King & Brooks 2002). Catchpole *et al.* (1998) did not separate survival from permanent emigration; King & Brooks (2003) expanded the approach for the more general multi-site (or multi-state) case, introducing sufficient statistics now consisting of three matrices, for time-and-cohort as well as age-and-cohort models. A further case, with time-and-age structure, was described recently (McCrea 2012). Under the assumption of permanent emigration, multi-state models allow defining an 'outside the study' state so that fidelity can be estimated if ring-recovery data is collected from that state.

In the analyses of the Isle of May data, we use both the Cormack-Jolly-Seber MR model and the McCrea (2012) multi-state MRR model; a more detailed account of these models will be given in the respective sections (2.3.1 and 5.4.2).

1.4.2 Productivity

Productivity (also termed breeding success or reproductive success), another important demographic parameter, is generally defined as the number of offspring produced by a female per breeding attempt. Early work on nest success (Mayfield 1961) based on detailed frequent nest observations was directed at accounting for the fact that monitored nests are typically found after incubation has started and that the date of nest failure cannot usually be determined exactly; models for this type of detailed data have been refined since then (Heisey & Nordheim 1995).

In the case of the Isle of May, this sort of bias is not an issue as the fate of the monitored clutches is known from laying until fledging. However, clutch and brood data for shag and kittiwake are limited to particular seasons when more intensive studies have been carried out, so the analysis of overall productivity in Chapter 3 uses total counts of chicks that fledge. Such data are available for all species and years analysed in the thesis, for a number of monitored nests which constitute a small percentage of the total breeding populations. We also use a more detailed data set that includes the total number of eggs laid, for guillemots and razorbills. Finally, kittiwake and shag clutch sizes have been recorded in some years and we look at changes in their distribution over time.

1.4.3 Abundance and integrated population models

At the Isle of May, abundance data consist of island-wide counts of breeding pairs. As population counts are not usually without some degree of error, they are often modelled using a state-space approach (Buckland *et al.* 2004; King *et al.* 2009, p.307) that separates the system process (the true underlying abundance) from the observation process (our imperfect counts, conditional on the true state). Population models can be directly defined as a function of growth rates and fitted to count data. A more insightful way to project year-to-year changes in abundance is to relate these to the demographic processes and age-structure of the population, acknowledging that the fluctuation of population abundance over time is ultimately controlled by mortality, birth and migration, so that, in an open population, abundance at time $t + 1$ (N_{t+1}) can be related to abundance at time t through the number of deaths D, births B, emigrated E and immigrated I individuals at that time

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

Such a population model can be represented by a matrix that relates the population abundance for the different age-classes from one time step to the next one (e.g. a Leslie matrix, Caswell 2001) and the appropriate stochastic structure.

When abundance of a population is modelled over time for a given species as a function of such demographic processes, demographic parameters such as survival, productivity and migration rates appear in the population model. The values for these parameters may be obtained in an ad hoc manner from the literature or previous analyses. But if data are also collected to study specific demographic parameters (e.g. mark-recapture data for survival), the likelihood functions for the respective models share parameters with the likelihood of the population model. This is the basic idea behind 'integrated population modelling' (IPM), a concept that has been developed in the last decade (Besbeas *et al.* 2002) and which consists of the joint modelling of abundance and demographic parameters. In an IPM, the likelihoods of the different data sets and the population model are multiplied to form a joint likelihood. That is, the demographic parameters have to explain their specific data sets (e.g. adult survival and the MR data) but also the abundance variations observed in the population, together with the rest of the demographic parameters (e.g. breeding success). We note that when the likelihood for the IPM is constructed as the product of the likelihoods of the different data sets, we are implicitly assuming independence between the data sets; the impact of violating this assumption depends on the relative amounts of information contained in the different components of the model (Besbeas, Borysiewicz & Morgan 2009; Abadi *et al.* 2010a; Cave, King & Freeman 2010).

As stated above, an IPM has to reconcile the estimates of demographic parameters with the population counts, obtained with observation error. If, as expected, the different sources of data do not contain contradicting information, this joint modelling may provide a more precise estimation of the shared demographic parameters. This point is one of the main motivations of the IPM approach, the other one being that in some cases, depending on model structure and data availability, parameters can be estimated that could not be obtained from independent analyses of the different data sets (Besbeas *et al.* 2002).

IPMs have been analysed in both the frequentist (Besbeas *et al.* 2002; McCrea *et al.* 2010) and the Bayesian (Brooks, King & Morgan 2004; King *et al.* 2008; Abadi *et al.* 2010b) frameworks. Since the publication of the first IPM, such models have grown in complexity, incorporating different data types, and have been applied in ecological and conservation studies; Schaub & Abadi (2011) provide a comprehensive review of the published literature and discussion about future research directions.

1.5 The Bayesian framework

Most of the analyses conducted in this thesis use the Bayesian framework for inference. The next sections provide background and explain the reasons why this choice was made.

1.5.1 The Bayesian and frequentist approaches

Bayesian statistics are based on Bayes' Theorem (Bayes 1763) which states that, given an observed data set $\boldsymbol{d}$ and a statistical model $\Pr(\boldsymbol{d}|\boldsymbol{\theta})$ that describes the probability of $\boldsymbol{d}$ as a function of a series of model parameters $\boldsymbol{\theta}$, we have

$$\pi(\boldsymbol{\theta}|\boldsymbol{d}) = \frac{\Pr(\boldsymbol{d}|\boldsymbol{\theta})\,\pi(\boldsymbol{\theta})}{\Pr(\boldsymbol{d})}. \tag{1.1}$$

The prior distribution $\pi(\boldsymbol{\theta})$ represents our prior belief about the parameters. This belief is updated with the new data $\boldsymbol{d}$ to form the joint posterior distribution $\pi(\boldsymbol{\theta}|\boldsymbol{d})$, the probability of the model parameters conditional on the observed data. In Bayesian statistics the $\Pr(\boldsymbol{d}|\boldsymbol{\theta})$ term is often called the 'likelihood' by analogy with the likelihood function $\mathrm{L}(\boldsymbol{\theta}|\boldsymbol{d})$ from which inference is carried out in the frequentist framework; although mathematically equivalent, their interpretations are different. The normalising constant $\Pr(\boldsymbol{d})$ in (1.1) is often omitted as it does not involve the model parameters; the posterior is then proportional to $\Pr(\boldsymbol{d}|\boldsymbol{\theta})\,\pi(\boldsymbol{\theta})$.

The construction of the joint posterior distribution (up to proportionality) is mathematically trivial, but direct inference about the marginal posterior distributions $\pi(\theta_i|\boldsymbol{d})$ of each of the parameters of interest θ_i is most often not possible as the other parameters must be integrated out, which is in general a mathematically intractable problem; this was the historical reason for the dominance of frequentist statistics over much of the XXth century (King *et al.* 2009).

The breakthrough arrived with the invention of Markov chain Monte Carlo (MCMC) (Metropolis *et al.* 1953). The increasing availability of computational power was then coupled with the development of several seminal MCMC methods (especially the Metropolis-Hastings algorithm (Hastings 1970) and Gibbs sampling (Geman & Geman 1984)), but it was only after Gelfand & Smith (1990) that the existence and utility of MCMC was recognised by the wider Bayesian community. Details of the methods can be found in general references like Gelman *et al.* (2004), King *et al.* (2009) or Brooks *et al.* (2011).

The Markov chains in the MCMC simulate samples that are representative of the joint posterior distribution. Inference can be carried out by calculating summary statistics for any model parameter of interest from a sufficiently large number of samples from the MCMC chains so that the marginal posterior distribution is properly characterised. Usually point estimates are obtained using the mean or median of the samples, with 'Credible Intervals' (the Bayesian equivalent to Confidence Intervals, although with different interpretation) being derived as measures of uncertainty around the point estimates. From the different alternatives available, we use medians and symmetric 95% Credible Intervals (defined as limited by quantiles 2.5% and 97.5%; King *et al.* 2009, p.86) when reporting our results.

It is important to ensure that the Markov chains have converged to the stationary distribution before using the MCMC samples to characterize the posterior. In practice this is achieved by discarding samples from the initial part of the chains, the so-called 'burn-in' (King *et al.* 2009, p.102). In order to establish the length of the burn-in period, trace plots of the MCMC samples can be explored visually, comparing several replications initialised at different over-dispersed starting values. A more robust approach uses the Brooks-Gelman-Rubin diagnostic (Brooks & Gelman 1998), which is based on an analysis of variance to detect differences between replications with different starting values; several implementations have been proposed, as well as other convergence diagnostic tools (King *et al.* 2009, pp.125-128).

The Bayesian framework provides some clear advantages. Unlike in frequentist inference, model parameters have distributions, which often provide a more natural interpretation in terms of probabilities. The propagation of uncertainty to derived parameters is straightforward and does not rest on asymptotic assumptions as in the frequentist approach (Kéry 2010). It is also an intuitive framework for hierarchical models (including state-space models) to be developed. Finally, the Bayesian approach is more flexible for handling missing data and random effects than the frequentist framework (Barry *et al.* 2003): in MCMC sampling, missing and random terms are seen as auxiliary variables which are simply updated with the rest of the MCMC chains of the model parameters (King 2012).

These advantages do not come without a cost. MCMC methods are computationally intensive and often require long analyses to ensure convergence of the chains and a proper exploration of the parameter space. Prior specification can also be tedious, even when vague priors are desired. Convergence of the MCMC chains has to be assessed formally. Also, model selection is not as well developed and tested as in the frequentist approach: although different methods exist in the literature (e.g. DIC, Bayes Factors or reversible jump MCMC; see King *et al.* 2009 for details), they may not be robust for all models (particularly hierarchical models with random effects) and are often sensitive to the choice of priors. Equally, although some approaches exist (e.g. Bayesian p-values; see section 2.3.8), goodness-of-fit methodology is still in development.

1.5.2 Bayesian inference in ecology

Bayesian statistics are progressively seeing a more widespread use in ecology, as reflected in the increasing number of publications that use this framework for inference as well as a recent series of general manuals specific to its application in this field (e.g. McCarthy 2007; King *et al.* 2009; Kéry 2010; Kéry & Schaub 2012). Such broader acceptance has been at least partly motivated by the interest in hierarchical models, which separate the sampling process from the ecological process of interest, and the use of random effects in ecology (McCarthy 2011). In contrast, the possibility of incorporating prior knowledge in the form of priors is rarely used, although there are of course many exceptions (see e.g. Péron, Nicolai & Koons 2012 for a recent example in an integrated population model). In our analyses, we use uninformative/vague priors, letting the inference be strongly based on the data through the likelihood.

The fact that most models in this thesis have random effects is one of the main reasons why we have chosen to do Bayesian inference in most cases. The second main reason is related to the use of integrated population models. In the originally proposed frequentist form, the construction of the likelihood for the population model is based on a Kalman filter (Kalman 1960), which requires certain assumptions of linearity and normality in the system and observation processes (King *et al.* 2009, p.312). Although multivariate normal approximations have been proposed when the sample sizes are large (Besbeas, Lebreton & Morgan 2003), one of the advantages of the Bayesian approach is that the population model is fitted without the need of a Kalman filter, relaxing the aforementioned assumptions. It is then also straightforward to obtain confidence intervals for the abundance of the different age classes (Brooks, King & Morgan 2004).

We started using program WinBUGS (Spiegelhalter *et al.* 2003), for the analyses in Chapter 2, but then switched to program JAGS v2.2.0 (Plummer 2003) for the modelling in the later chapters. Although both programs are largely based on the same MCMC methods and can run the same code with (in most cases) minimal or no changes, we found that in our application JAGS was substantially faster than WinBUGS, at least when analysing large models like the IPMs, for which there is an appreciable amount of data (an example is given in section 5.4.3). We acknowledge that programming the MCMC algorithms as bespoke code (e.g. in MATLAB or C) may provide faster processing, but we believe that programs like WinBUGS and JAGS provide an excellent flexible platform for testing different variations in model structure.

Finally, we note that some of the analyses in Chapter 6 (sections 6.1 and 6.2) with MRR data were performed in the maximum-likelihood framework using program MARK (White & Burnham 1999). The main reason for this choice was the higher speed to fit a large number of model variations (for a standard model structure, available in MARK) and the possibility to do model selection based on Akaike Information Criterion.

1.6 Thesis structure

This thesis consists of five core chapters, apart from this introductory Chapter 1 and the concluding Chapter 7.

Chapter 2 discusses the different uses of the concept of synchrony in ecology and the modelling approaches associated with its study (section 2.1). We then describe a framework for the estimation of multi-species synchrony in demographic parameters (section 2.2) and we apply it to the study of synchrony in the year-to-year variations in adult survival in the three auk species that breed at the Isle of May (section 2.3), based on mark-recapture data.

In Chapter 3 we turn to another important demographic parameter: productivity. We start by quantifying synchrony in overall productivity for the set of five seabird species at the Isle of May (section 3.1), based on annual counts of the total number of chicks that fledge from a number of monitored breeding pairs. In the modelling of such data, we deal with the added complication that some of these species lay multiple-egg clutches. We demonstrate then how the framework is equally valid for studying components of productivity when more detailed data are collected (section 3.2), using both simulations and data from guillemots and razorbills. In the last section (3.3), we model the distribution of clutch sizes over time for kittiwakes and shags, the two species that lay more than one egg. Clutch sizes are typically underdispersed compared to a Poisson distribution, and we quantify synchrony in the degree of underdispersion exhibited by these two species at the Isle of May.

In both Chapters 2 and 3 we look at the role that environmental covariates play in generating synchrony and asynchrony in different aspects of the demography of the species considered.

Chapter 4 explores in more detail the properties and performance of the multi-species synchrony framework, under different scenarios that may typically be encountered in ecological studies (section 4.1). The aim is to clarify the concept of multi-species synchrony as defined in this thesis, and offer guidance for its use. Several extensions are also proposed (section 4.2) to address different questions or to apply the framework beyond the multi-species situation.

Chapters 2 and 3 apply the multi-species synchrony framework to a single demographic parameter. In Chapter 5 we integrate in a single model data not only for several species but also for several demographic parameters, together with population counts. We start by describing the structure of independent integrated population models for each of the three auk species at the Isle of May (sections 5.2, 5.3 and 5.4). The three species are then modelled jointly (section 5.5), estimating multi-species synchrony in adult survival and overall productivity, in addition to population abundance and demographic parameters, in what to our knowledge constitutes the first 'multi-species integrated population model'.

Chapter 6 departs from the multi-species theme that underlies the majority of the thesis, to consider an important issue of study design, with the aim of optimising the use of resources to monitor the guillemot population breeding at the Isle of May, which involves a substantial time investment to ring birds and resight ringed individuals. After analysing the mark-resight-recovery data set collected from guillemots ringed as chicks and investigating the effect of two individual-level covariates in first-year survival (section 6.1), we explore the effect of reducing fieldwork effort (either ringing or resighting) on our ability to detect variations in first-year survival and make ecological inferences about this parameter with respect to the aforementioned covariates (section 6.2). Finally we investigate in section 6.3 the effect of stopping completely the marking of guillemot chicks. In this context, we test the ability of a guillemot integrated population model to compensate for the lack of direct immature-related data, and the impact that the lack of such data would have on the estimation of abundance and adult-related demographic rates.

All chapters conclude with a Discussion section, and we end the thesis with a general discussion and overview of future research in Chapter 7.

The analysis in Chapter 2 has been published in Methods in Ecology and Evolution (Lahoz-Monfort *et al.* 2011) and we recorded a short video at the Isle of May (Figure 1-3), which is available at the journal's website[3]. Part of the productivity synchrony analyses (sections 3.1 and 3.2) has been accepted for publication in Ecology (Lahoz-Monfort *et al.* in press). Two manuscripts are under preparation based on chapters 5 and 6.

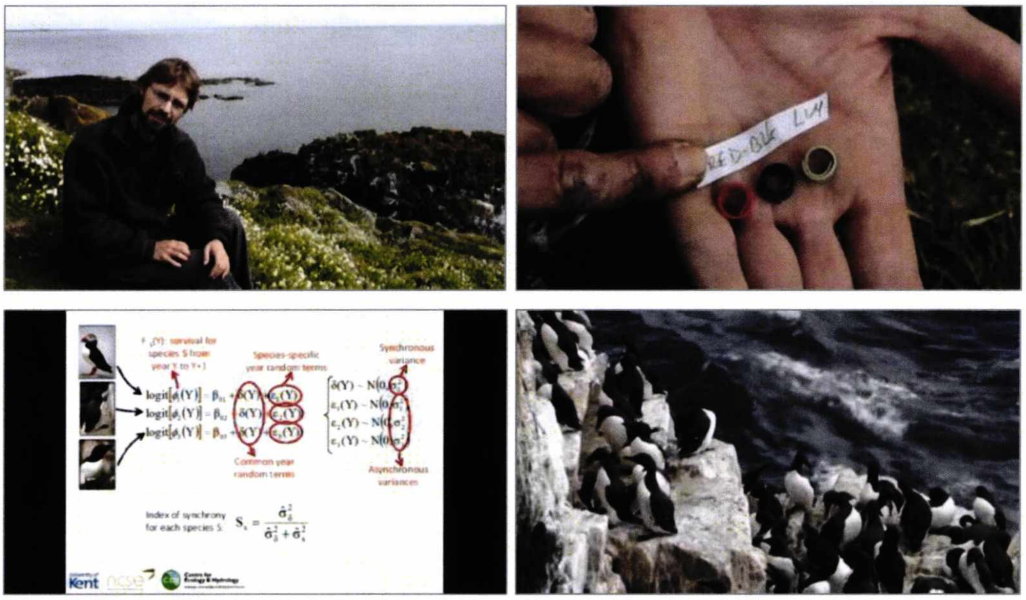

Figure 1-3 Stills from the video produced for Methods in Ecology and Evolution. Clockwise from top-left: the author at the Isle of May; combination of colours in three rings about to be fitted to an adult puffin; a slide explaining the use of random effects in the synchrony models; a group of adult guillemots on low-laying ledges.

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[3] http://www.methodsinecologyandevolution.org/view/0/VideoPodcastArchive.html

2 MULTI-SPECIES SYNCHRONY IN ADULT SURVIVAL

2.1 The concept of synchrony in ecology

2.1.1 A wide range of meanings

The term 'synchrony' has been applied in a wide variety of contexts in ecology. Broadly speaking, it conveys the idea that 'a set of parameters vary over time in a similar way' (Vik *et al.* 2004). This is obviously a rather vague concept, as 'in a similar way' may encompass different aspects, and it can be applied to very different types of parameters.

In the context of the study of wildlife populations, most studies of synchrony in the value of a parameter refer to spatial synchrony of population abundance (or growth rates) at different locations (also termed spatial autocorrelation; Koenig 1999), where data consist of time series of abundance, usually for a single species (e.g. Buonaccorsi *et al.* 2001) although sometimes several sympatric species are considered (e.g. Ranta, Lindström & Lindén 1995; Raimondo *et al.* 2004). Often the interest is in quantifying the spatial structure of synchrony, looking at how it varies with the distance between populations (Bjørnstad, Ims & Lambin 1999). Fewer studies are dedicated to the study of synchrony in demographic parameters (e.g. Tavecchia *et al.* 2008).

Synchrony can be considered in other aspects of models. Without being exhaustive, we mention here two important possibilities found in the literature. Firstly, synchrony can be defined by the simultaneous occurrence of particular features of a parameter, such as peaks or troughs. This would happen for example when abundance fluctuations only match for particularly good (peaks of abundance) or bad years (troughs), which may happen in highly non-linear systems (Cattadori, Haydon & Hudson 2005). Synchrony may also refer to the timing of cyclic oscillations, indicating that the cycles tend to oscillate over time simultaneously, i.e. with the same pace of rising and falling. This 'cyclic' or 'phase' synchrony is often measured in terms of the parameter values, as in the coupled oscillations of prey-predator density (e.g., the classic case of snowshoe hare and Canadian lynx; Elton & Nicholson 1942), with new statistical methods developed recently for analysing such cases (e.g., Cazelles & Stone 2003). 'Phase synchrony' can also be defined purely in the timing of events, without consideration of amplitudes (e.g., degree of overlap of a part of the ovarian cycle of individual females in Tobler, Pledger & Linklater 2010), or even in the phase state in irregularly fluctuating parameters (e.g., state of the parameter trajectory: either 'increase', 'decrease', 'peak' or 'trough'; Haydon *et al.* 2003). The quantification of 'phase synchrony' and non-linear synchrony induced by extreme years requires specific statistical techniques and will not be discussed further in this thesis. We concentrate in the next section on the case of synchrony in the temporal variation of a parameter value, which is the closest to the cases discussed in this thesis.

2.1.2 The study of synchrony in variations over time

Although synchrony is an interesting issue in ecology, limited attention has been dedicated to the development of statistical techniques for quantifying it. Buonaccorsi *et al.* (2001) summarise a range of options available in the context of spatial synchrony of population density over time, for one species. For comparing two time series, these include

(i) Correlation among series values, which is often calculated from data or point estimates (e.g., population densities, Buonaccorsi *et al.* 2001), although process correlation can also be modelled (Reynolds *et al.* 2011). Pairwise cross-correlation, which can cope with time-lags between time series, has been used to explore synchrony between populations (Ranta, Lindström & Lindén 1995);

(ii) Correlation in residuals (e.g. after fitting an autoregressive model). This option has also been applied after 'detrending' (accounting for a linear trend) or removing periodic oscillations;

(iii) Measures based on changes, with several possibilities for quantifying how the series move in the same direction ('up' and 'down'). These link also with 'phase synchrony', where more sophisticated modelling has been proposed (e.g., using a Markov model to characterise moves between phase states of the system; Haydon *et al.* 2003);

(iv) Coincidence of peaks in the time series.

Different measures of synchrony applied to the same data set will give numerically different results that may even be conflicting (Buonaccorsi *et al.* 2001) as they may have different interpretations. With regard to measuring synchrony in more than two series, the typical way to proceed has been to average the corresponding values of the chosen pairwise measure of synchrony.

Increasingly sophisticated statistical models to study 'synchrony' have been published in recent years, using random effects to obtain a model-based estimation of covariances. In the multi-species context, Mutshinda, O'Hara & Woiwod (2011) study abundance in a community of moths, using fixed effects for modelling inter-specific density-dependence and species-specific random effects with cross-species covariances for the unmodelled stochasticity. Related to this concept but in a rather different context, Cam *et al.* (2002) and Wintrebert *et al.* (2005) use individual-level random effects ('frailty') to estimate covariance between two demographic parameters (adult survival and breeding propensity) at the individual level; we will return to the issue of multi-parameter synchrony in section 4.2.6. Although none of the studies mentioned in this paragraph present their models in terms of 'synchrony' explicitly, we note that pairwise covariances can be seen as a form of 'synchrony' (Buonaccorsi *et al.* 2001). We nevertheless emphasize that in all these cases the study of 'synchrony' has been limited to pairwise relationships, compared to the approach used in this thesis and presented in next section, where the concept of 'synchrony' is based on a comparison with the common signal to all species in the community. Both approaches represent different ways of addressing the issue of 'synchrony' and provide different insights which may be useful depending on the particular aspect of interest in a study.

2.2 Multi-species synchrony framework

We propose a statistical framework for studying synchrony in the year-to-year variations of a demographic parameter at a multi-species level, through the use of random effects. Between-year variance in the demographic parameter is divided into a 'synchronous' component, that represents the common response of all species considered, and 'asynchronous' components, specific to each species. We also estimate the contribution of environmental covariates to each of these components. We note that the framework can be readily applied to more than two species, which sets it apart from other multi-species classic methods of synchrony that rely on pairwise species comparisons. The framework is based on that presented by Grosbois *et al.* (2009) for studying synchrony in adult survival for a single species at a multi-population scale. The multi-species framework is conceptually different from the multi-population model in its interpretation (in the later, synchronous and asynchronous components may be related to factors acting at large- and local geographical scales respectively). Furthermore, we relax the variance structure in the model to accommodate differences among species.

2.2.1 Synchrony model and derived parameters

Given a demographic parameter $\theta_s(t)$ (e.g. adult survival or productivity) for species s and year t, we define a structure with two levels of normally-distributed annual random effects: a year effect $\delta(t)$, common to all species considered, and 'species-specific' effects $\varepsilon_s(t)$ that represent an interaction between species and year. The random terms are conveniently defined on a transformed domain which, in the common case of demographic parameters that are probabilities, can be a logit link function

$$\mathrm{logit}(\theta_s(t)) = \log\left(\frac{\theta_s(t)}{1-\theta_s(t)}\right) = \beta_{0s} + \delta(t) + \varepsilon_s(t). \tag{2.1}$$

Other demographic parameters may require different link functions (e.g. log for 'mean number of fledged chicks per nest' in section 3.1.2). The β_{0s} terms are species-specific intercepts on the logistic scale that account for possible differences in the baseline value of θ for the different species. The random terms are assumed independent of each other and of the other random effects. All are normally-distributed with zero mean

$$\delta(t) \sim \mathrm{N}\left(0, \sigma_\delta^2\right), \quad \varepsilon_s(t) \sim \mathrm{N}(0, \sigma_s^2). \tag{2.2}$$

This structure of random effects allows us to partition the overall variance of each species into a component that is common to all the species in the set analysed ('common' or 'synchronous') and components that are specific to each species ('species-specific' or 'asynchronous'). In the proposed model, the parts of the likelihood that relate to each species share the common random terms $\delta(t)$. The model is fitted to the multi-species data and the random effect variances σ_δ^2 and σ_s^2 are estimated, together with the other model parameters. An index of synchrony $I_s \in [0,1]$ can then be defined for each species s in the set based on the estimated variances (as done in Grosbois *et al.* 2009 in a single-species multi-population framework)

$$I_s = \frac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2}. \tag{2.3}$$

These indices represent the synchrony of species s with the rest of the species, that is, the proportion of the year-to-year variation in $\boldsymbol{\theta}_s$ that is synchronous to all species in the set. When $\hat{\sigma}_\delta^2$ is large compared to $\hat{\sigma}_s^2$, then I_s is large and the between-year variation for that species is then mostly synchronous with the other species.

Covariates can be introduced for each species s on the logistic regression of the parameter of interest $\boldsymbol{\theta}$, resulting in a mixed-effect model

$$\mathrm{logit}\left(\theta_s(t)\right) = \beta_{0s} + f_s\left(c_{s1}(t), \ldots, c_{sn}(t)\right) + \delta(t) + \varepsilon_s(t). \tag{2.4}$$

The species-specific function $f_s(.)$ specifies the relationship with the covariates $\{c_{si}\}$. It can for example be a linear regression (as used in this thesis) or a nonparametric relationship (e.g. splines, Gimenez *et al.* 2006). When covariates have explanatory power for a species s, we expect a reduction in either or both variances (σ_δ^2 and σ_s^2), depending whether the covariate explains part of the variation of the common or/and species-specific terms. We define as 'total variances' ($\hat{\sigma}_\delta^2(\text{tot})$ and $\hat{\sigma}_s^2(\text{tot})$) those estimated from the model without covariates, and 'residual variances' ($\hat{\sigma}_\delta^2(\text{res})$ and $\hat{\sigma}_s^2(\text{res})$) those estimated from the model with covariates. A new set of indices of synchrony can be defined as in (2.3) based on the residual variances from the model with covariates, which now represent the proportion of the synchronous/asynchronous variation in $\boldsymbol{\theta}$ not accounted for by the covariates that is common/specific to each species in the set. Finally, in order to evaluate the effect of the environmental covariates in generating synchrony and asynchrony in $\boldsymbol{\theta}$, we use the residual and total variances estimated independently from models with and without the covariates respectively, following the method in Loison *et al.* (2002) and Grosbois *et al.* (2009)

$$C_\delta = 1 - \frac{\hat{\sigma}_\delta^2(\text{res})}{\hat{\sigma}_\delta^2(\text{tot})}, \qquad C_s = 1 - \frac{\hat{\sigma}_s^2(\text{res})}{\hat{\sigma}_s^2(\text{tot})}. \tag{2.5}$$

These coefficients represent the contribution of the environmental covariates to the inter-specific synchronous $\delta(t)$ and asynchronous $\varepsilon_s(t)$ components respectively, that is, to synchronising and desynchronising the year-to-year variations in parameter $\boldsymbol{\theta}$ in the set of species.

2.2.2 Synchrony aspects not considered by the framework

It is worth clarifying what the definition of synchrony implied in this framework does not mean. First of all, synchrony is defined in terms of the year-to-year variation so that even in a highly synchronous set of species, the demographic parameter of interest (on the probability scale) would not necessarily be the same for all species over time, as these may have different baselines (intercepts β_{0s}). We note also that, since the random terms are defined on the logistic scale, the actual magnitude of the year-to-year variations may appear quite different once they are transformed to the probability scale, for species with different intercepts β_{0s}. In relation to this, we note that $\bar{\theta}_s$, the average value of the parameter θ_s (on the probability scale) is in general not equal to the inverse logit of β_{0s}, i.e. $\bar{\theta}_{\beta_{0s}} = \left(1 + e^{-\beta_{0s}}\right)^{-1}$, given the nature of the logit link function: although random terms have mean zero on the logit scale, they may translate to probabilities asymmetrically distributed around $\bar{\theta}_s$ except with β_{0s} close to zero.

The concept of synchrony that we consider is not specifically designed to respond to periodic oscillations, as the use of random effects implies that the model sees the order of the years as arbitrary. Actually, an analysis would give the same synchrony results if years were reordered in any random way, as long as the order is kept the same for all species (Figure 2-1, a & b). Alternative methods based on the concept of 'phase synchrony' are better designed to deal with oscillations. Time-lags in species' responses (e.g. prey-predator coupled systems) will also cause the synchrony framework to fail to identify a strong common signal among species (Figure 2-1c), in the same sense as we would not find high correlation between the time series. Again, other techniques ('phase synchrony' methods or cross-correlograms) may be better suited to deal with such situations.

Another case worth discussing is that created by species that show negative correlation in the values of their parameters (there will be an illustration of such a case in Chapter 4, Figure 4-10). Such a relationship cannot be easily decomposed into common and species-specific terms and therefore the model will estimate a low common variance and low synchrony. We note also that synchrony takes into account actual values, and the model will not simply see a strong synchrony in two species with highly correlated values but very different magnitudes (Figure 2-1d). In that example, the species with low variance may be seen as highly synchronous (its variations can be explained as common with the other species), while the species with high variance will have a low index of synchrony, given that most of their variation is not seen as common with the other species. In these last examples, the synchrony framework we use does not define all the species as 'synchronous' given that, despite being obviously affected by a common effect, strictly speaking they do not react in the same direction or with similar strength (magnitude). If a study is concerned with a concept of synchrony that considers such effects as synchronous, then estimating correlations may provide a better approach. This could be achieved for example by specifying a model with only species-specific random terms distributed as multivariate normal, and estimating the covariances. We note nevertheless that covariances and correlations are defined pairwise, while the method we use quantifies synchrony in the complete set of species, which is a different concept (although sometimes related, as we will see in section 4.1.6). We note finally that pairwise correlations do not allow the quantification of the effect of covariates in generating synchrony and asynchrony.

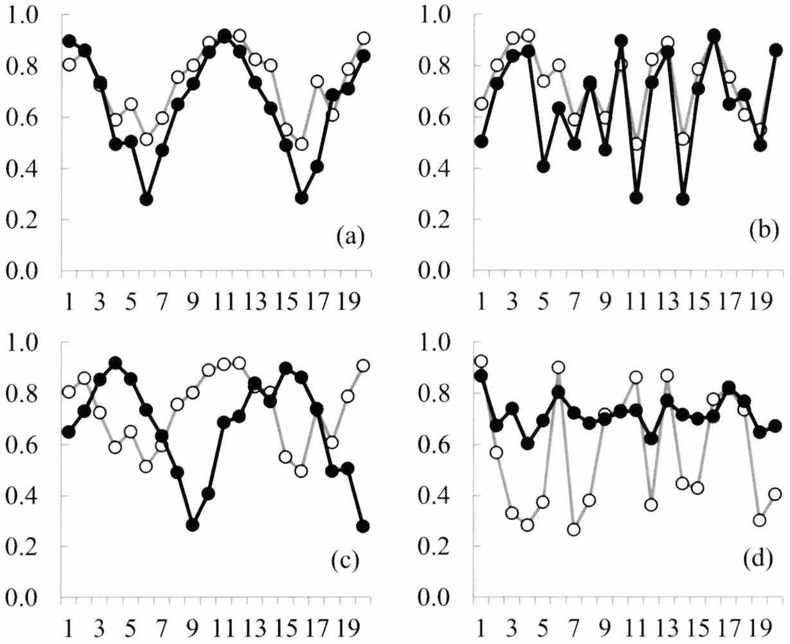


Figure 2-1 Illustrative examples (not based on real data) of variations over time of a demographic parameter for two species: the same amount of synchrony would be estimated in (a), with two in-phase oscillating species, as in (b) where the years have been reordered (equally for both species); (c): same as (a) but with a time-lag of 7 years in one of the species; (d) high correlation but very different variances.

2.3 Multi-species synchrony in adult survival

We demonstrate the framework described above to explore multi-species synchrony with an application to adult survival, using 25 years of mark-resight data for the three auk species at the Isle of May, the Atlantic puffin, the common guillemot and the razorbill. These three auk species have broadly similar life histories and ecology (Gaston & Jones 1998) and birds from breeding populations on the Isle of May show at least partially overlapping winter distributions (Wernham *et al.* 2002): they are thus likely to be exposed to similar environmental stochasticity. Consequently we would expect some degree of synchrony in their response in terms of the temporal variation of demographic parameters. Adult survival probabilities for Isle of May puffins, guillemots and razorbills have previously been analysed separately (Harris *et al.* 1997; Harris, Wanless & Rothery 2000; Crespin *et al.* 2006), but to date no attempt has been made to integrate survival data for these species, and in particular, to look for synchronising and desynchronising agents.

2.3.1 The Cormack-Jolly-Seber model

Our multi-species adult survival synchrony models are based on the standard open-population mark-recapture ('MR') models for estimating apparent survival and recapture probabilities (reviewed in Lebreton *et al.* 1992). In the case of the seabirds at the Isle of May, recaptures are actually resightings so we will refer to 'resight probability'. As the birds are ringed as breeding adults, age is unknown and cannot be modelled. We therefore use the Cormack-Jolly-Seber model (Williams, Nichols & Conroy 2002, p.419), which has year-dependent survival and resight probabilities, defined as

(i) apparent adult survival probability $\phi(t)$: the probability that a bird alive at the resight occasion of year t survives until the resight occasion of year $t+1$;

(ii) resight probability $p(t)$: the probability that a bird that is alive in year t is resighted during resighting occasion t. We note that often $p(t)$ is defined with respect to year $t=2,\dots,T$, instead of resighting occasion $t=1,\dots,T-1$. We prefer the index starting at 1 as it offers a more natural coding for indexing the vector of year-resight probabilities.

We denote this model as $\{\phi(t)p(t)\}$ or 'CJS'. In the case of ringed seabirds at the Isle of May, the 'resight occasions' refer to searches carried out throughout the colony during the breeding season. A number of birds R_i are marked (ringed) and released over a series of years and attempts are made to resight them in successive years. An individual recapture history is constructed with the information collected for all birds, where '0's denote that an animal was not seen and '1's otherwise. Such individual histories can be modelled directly, either by constructing a likelihood for the sequence of 0's and 1's for each bird (King *et al.* 2009, p.25) or alternatively as a state-space model, where a series of latent variables model the state (alive or dead) of each animal at each recapture occasion (King *et al.* 2009, p.339).

When no age-dependence or individual effects are to be modelled, it is common to summarise the detection histories in so-called 'm-arrays' (Figure 2-2). The m-array value m_{ij} represents the number of birds released in year i that were seen alive for the first time at resight occasion j. It is quite possible that some of the R_i birds released in year i are never resighted during the whole period of the study; these can be calculated as $m_{i,T} = R_i - \sum_{k=i}^{T-1} m_{i,k} = R_i - r_i$. Such birds may, or may not, be still alive.

			Resight occasion j					Not resighted
		Released	1	2	3	...	$T-1$	
Release occasion i	1	R_1	$m_{1,1}$	$m_{1,2}$	$m_{1,3}$	...	$m_{1,T-1}$	$m_{1,T}$
	2	R_2	0	$m_{2,2}$	$m_{2,3}$	...	$m_{2,T-1}$	$m_{2,T}$
	3	R_3	0	0	$m_{3,3}$	...	$m_{3,T-1}$	$m_{3,T}$
	...	...	...	...	...	...	...	...
	$T-1$	R_{T-1}	0	0	0	...	$m_{T-1,T-1}$	$m_{T-1,T}$

Figure 2-2 Mark-recapture history summarised as an m-array, with $T-1$ release occasions and $T-1$ resight occasions. The m_{ij} represent the number of birds released in year i that are resighted alive for the first time in resight occasion j.

The cell probability q_{ij}, that is, the probability of a bird released in year i being seen alive for the first time at resight occasion j, is

$$q_{i,j} = \left(\prod_{k=i}^{j-1} [\phi(k)\{1 - p(k)\}] \right) \phi(j)p(j), \qquad j < T$$

$$qi, T = 1 - \sum_{j=1}^{T-1} q_{ij}. \tag{2.6}$$

In practice, to avoid the product of small numbers giving problems in the implementation, equation (2.6) for $j < T$ can be written as

$$q_{i,j} = \exp\left(\sum_{k=i}^{j-1} [\log(\phi(k)\{1 - p(k)\})]\right) \phi(j)p(j), \qquad j < T. \tag{2.7}$$

Each row of the m-array is independently distributed as multinomial, with R_i released birds distributed in T possible outcomes (including r_i birds never resighted), according to cell probabilities $q_{i,j}$

$$\{m_{i,i}, m_{i,i+1}, \dots, m_{i,T-1}, m_{i,T}\} \sim \text{multinomial}\big(R_i, \{q_{i,i}, q_{i,i+1}, \dots, q_{i,T}\}\big), \forall i. \tag{2.8}$$

For $T - 1$ release years and $T - 1$ resighting occasions, and omitting the combinatorial terms that do not include the parameters, the product-multinomial likelihood of the complete data set (m-array $\boldsymbol{m}$) can be written as a function of parameters $\boldsymbol{\phi} = \{\phi(t): t = 1, \dots, T - 1\}$ and $\boldsymbol{p} = \{p(t): t = 1, \dots, T - 1\}$ as

$$L(\boldsymbol{m}|\boldsymbol{\phi}, \boldsymbol{p}) \propto \prod_{i=1}^{T-1} \prod_{j=i}^{T} (m_{i,j})^{q_{i,j}} \tag{2.9}$$

The Cormack-Jolly-Seber model makes a series of assumptions (Williams, Nichols & Conroy 2002):

(i) for a given resight occasion j, all individuals in the population have the same probabilities $\phi(j)$ and $p(j)$;

(ii) The marks (rings in our case) are neither lost nor overlooked, and are recorded correctly;

(iii) The resight occasions are instantaneous (or very short periods). When captures happen, birds are released immediately;

(iv) Emigration from the sampled area is permanent;

(v) The fate of each bird with respect of resighting and survival is independent of that of any other bird.

We assume that (ii) is true for the auks ringed at the Isle of May, and that resightings happen in a relatively short period of time of negligible mortality (iii), although obviously not instantaneously. The data set consists of resightings so that birds are not captured after the first (marking) occasion. Permanent emigration (iv) is confounded with true mortality in the CJS model, as in both cases individuals cease to be available for future resightings. Survival is therefore often termed 'apparent survival'. For the Isle of May auk species, established breeding adults have high colony fidelity so that apparent survival will be close to true survival. Finally, we will test the homogeneity assumed in (i) in section 2.3.4.

2.3.2 Multi-species adult survival synchrony model

Likelihood functions can be constructed individually for each of the species involved in the model according to (2.9). Then common and species-specific year random effects can be added in the logistic regressions of adult survival for all species $s = 1,\dots,S$ in a set and years $t = 1,\dots,T-1$, using a logit link function as described in section 2.2 (where in this case $\boldsymbol{\theta} = \boldsymbol{\phi}$)

$$\text{logit}\big(\phi_s(t)\big) = \beta_{0s} + \delta(t) + \varepsilon_s(t). \tag{2.10}$$

The $\boldsymbol{\delta}$ terms correspond to the amount of between-year variation that is synchronous to all species considered, while the $\boldsymbol{\varepsilon}_s$ terms characterise the asynchronous (species-specific) components. We extend the approach of Grosbois *et al.* (2009) so that the 'year x species' random terms can have different variances for the different species (i.e. σ_s^2 are species-specific) and so the year-to-year variance in adult survival can be partitioned differently for different species.

Once the model parameters have been estimated, species-specific indices of synchrony in adult survival I_s can be calculated based on the variances of the random terms, as described by equation (2.3) in section 2.2.1. These indices represent the proportion of year-to-year variance for each species that is accounted for by the common random effect $\delta(t)$.

2.3.3 *Mark-resight data of adult auks*

Between 1984 and 2007, 543 puffins, 831 guillemots and 153 razorbills were marked using a combination of three colour-rings that unequivocally identifies each marked individual. These were adults breeding in areas located in front of permanent hides. Resightings of these birds took place each year up to 2008. Individuals of all three species rarely breed more than a few metres from where they are marked (M. P. Harris, *personal observation*), so resighting effort was mainly focussed on these areas although regular searches were also made in all nearby areas. We assume that adults remain identifiable through their life.

2.3.4 *Heterogeneity in resight probability*

Before fitting the data in combination, we assess the goodness of fit (GOF) of the general fully time-dependent Cormack-Jolly-Seber (CJS) model $\{\phi(t)p(t)\}$ with program RELEASE (Burnham *et al.* 1987), for each species individually. In this model, both survival and resight probabilities are allowed to vary from year to year. The GOF is very similar for all species studied: the general CJS model fits the data poorly, due mostly to the 2.C component (guillemot: $\chi^2 = 173.49$, $df = 22$; puffin: $\chi^2 = 129.9$, $df = 22$; razorbill: $\chi^2 = 55.35$, $df = 17$; all p-values < 0.001), which indicates heterogeneity in resight probability in the form of 'trap dependence', i.e. birds have different probability of being resighted depending on whether they were seen the previous season. This effect has been previously reported for puffins at the Isle of May (Harris *et al.* 2005). Component 3.SR fits well for all three species (p-values > 0.9), showing no evidence of individual heterogeneity in adult survival, as noted in previous analyses of these species from the Isle of May (Harris, Wanless & Rothery 2000; Harris *et al.* 2005; Grosbois *et al.* 2009).

The trap-dependence in resight probability (Pradel 1993), detected for the three species, is taken into account in the synchrony models by adding a 1-year trap-dependence structure in the following way: for each species s, the resight probability for individual i in year t, $p_s(i,t)$, depends through a logit link on a year-specific resight probability $p_s^*(t)$ and an additive term a_s that is only included if the individual was resighted in the previous occasion

$$\operatorname{logit}(p_s(i,t)) = \log\left(\frac{p_s(i,t)}{1-p_s(i,t)}\right) = p_s^*(t) + a_s T_s(i,t), \qquad (2.11)$$

where the indicator function $T_s(i,t)$ takes value 1 if bird i was resighted in year $t-1$, and 0 otherwise, and can be seen as an individual covariate for each capture occasion. The resight probability in year t would be $p_s(t) = \left(1 + e^{-p_s^*(t)-a_s}\right)^{-1}$ if the individual was resighted in year $t-1$ and $p_s(t) = \left(1 + e^{-p_s^*(t)}\right)^{-1}$ if it was not. The species-specific terms a_s represent the amount of 1-year trap-dependence for each species studied. The multinomial likelihood in (2.9) has to be modified accordingly. Omitting the species subscript for simplicity, and denoting resight probability in i^{th} recapture occasion as $p(i)$ when the bird has not been seen the previous year, and $\bar{p}(i)$ otherwise, the probabilities for the cells in the diagonal of the m-array will be $q_{i,i} = \phi(i)\bar{p}(i)$, $i = 1, \dots, T-1$, as they represent birds known to have been seen the previous year. For cells above the diagonal the multinomial cell probabilities in (2.6) are now calculated as

$$q_{i,j} = \phi(i)\{1-\bar{p}(i)\} \prod_{k=i+1}^{j-1} [\phi(k)\{1-p(k)\}]\, \phi(j)p(j), \quad j < T$$

$$q_{i,T} = 1 - \sum_{j=1}^{T-1} q_{ij}\,. \qquad (2.12)$$

All CJS MR models considered in the following sections have fully time-dependent resight probability with 1-year trap-dependence (heterogeneity) and these are denoted '$p(t+h)$'.

2.3.5 Environmental covariates for survival

We investigate the contribution of two environmental covariates in generating synchrony and asynchrony in adult survival: winter NAO index (wNAO) and a local measure of sea surface temperature (SST). These indices are described in section 1.3. Following Sandvik *et al.* (2005) and Harris *et al.* (2005), we use both wNAO without time lag ('wNAO$_0$'), that reflects the direct effect of weather harshness on survival, and wNAO with a 1-year time lag ('wNAO$_1$'), that reflects the indirect effect of climate, possibly through the food chain. Equally, we include SST with no time lag ('SST$_0$') and with 1-year time lag ('SST$_1$'), that is, the average over January to May of the previous year (Harris *et al.* 2005).

2.3.6 *Bayesian analysis*

All models in this chapter are programmed in WinBUGS (Spiegelhalter *et al.* 2003). We first analyse the multi-species synchrony model without covariates, which we denote $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$ to indicate the dependence of ϕ on species-specific intercepts (β), common ($\boldsymbol{\delta}$) and species-specific ($\boldsymbol{\varepsilon}_s$) year random terms. We calculate indices of synchrony I_s based on the estimated variances of the random effects. Figure 2-3 displays a DAG with the relationship between all variables included in this model.

We then fit a model that includes the covariates described in section 2.3.5, looking at multi-species synchrony on the residual variation in adult survival. For simplicity, we use the same covariates for all three species, but this is in general not a restriction and species-specific covariates could be considered. The vector $cov = \{c_1, c_2, c_3, c_4\} = \{\text{wNAO}_0, \text{wNAO}_1, \text{SST}_0, \text{SST}_1\}$ in the models hereafter refers to the four covariates together, and we denote the resulting synchrony model as $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$. All covariate time series (1984-2008) are standardised prior to inclusion in the models by subtracting the mean of the series and dividing by its standard deviation. We verify first that the covariates do not have high correlation. For adult survival, we consider a logit link function and a linear regression, with the aforementioned set of four standardised covariates c_j and corresponding species-specific regression coefficients β_{js}:

$$\text{logit}\big(\phi_s(t)\big) = \beta_{0s} + \sum_{j=1}^{4}\{\beta_{js}c_j(t)\} + \delta(t) + \varepsilon_s(t). \tag{2.13}$$

Using the estimates of residual and total variances of the random effects (from models with and without the covariates), we calculate the C_δ and C_s coefficients as described in (2.5) which measure the contribution of the environmental covariates to the interspecific synchronous $\boldsymbol{\delta}$ and asynchronous $\boldsymbol{\varepsilon}_s$ components of the between-year variances, respectively.

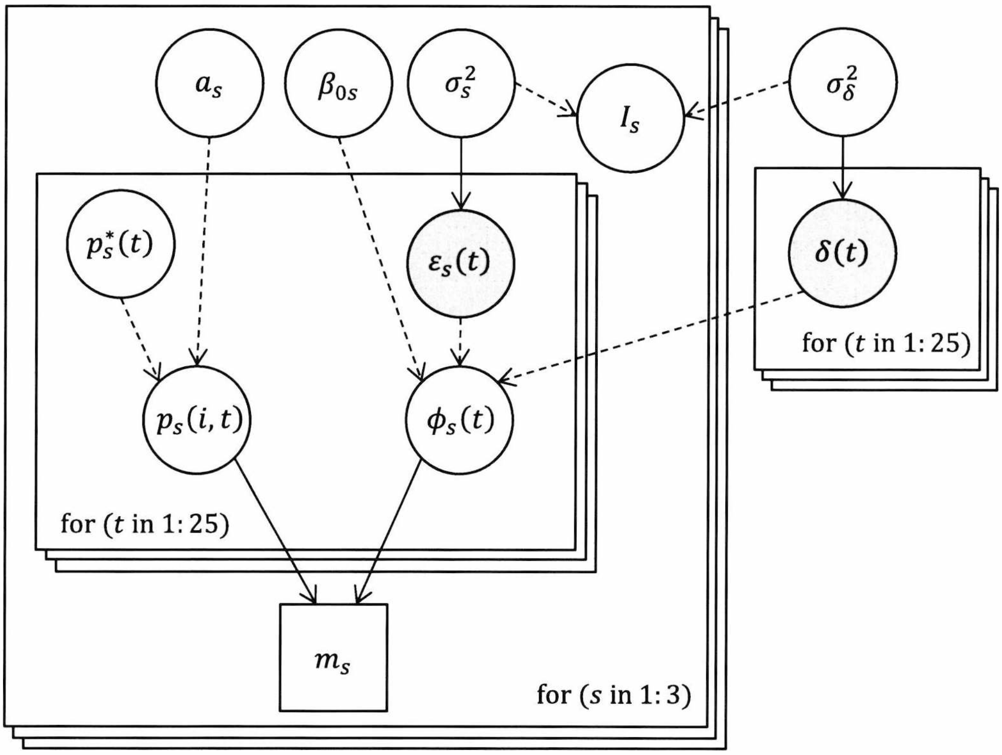


Figure 2-3 Directed Acyclic Graph (DAG) for the Isle of May 3-species adult survival synchrony analysis without covariates, model $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$, where s is species and t is years. Prior parameters have been omitted for clarity. Squares=data; circles=parameters to be estimated, of which grey circles=random effects; solid arrows=stochastic relationships; dotted arrows=deterministic relationships.

We note that, in their single-species multi-population model, Grosbois *et al.* (2009) use a single common covariate that takes different values for each colony, while in this study each common covariate has the same value for all the species considered (as the geographical location is the same), but each species might have a different combination of covariates.

For both analyses, the MCMC chains are run for 150000 iterations after a burn-in of 100000 samples, storing the samples of one iteration out of three to avoid memory problems. Convergence is assessed with the Brooks-Gelman-Rubin statistic (Brooks & Gelman 1998), after starting three chains with dispersed initial values for all variables. The statistic suggests that convergence had been achieved after the 100000 samples of the burn-in. We use low information priors for all variables, to reflect the lack of prior knowledge

(i) flat uniform priors for the regression coefficients $\beta_{is} \sim \mathrm{U}(-5,5)$ and trap-dependence coefficients $a_s \sim \mathrm{U}(-5,5)$;

(ii) vague normal priors for the year-specific component of resight probabilities $p_s^*(t) \sim \mathrm{N}(0,10^4)$;

(iii) flat uniform priors for the standard deviations of the $\boldsymbol{\delta}$ and $\boldsymbol{\varepsilon}_s$ random terms: $\sigma \sim \mathrm{U}(0,3)$.

We conduct a prior sensitivity study for the random-effect variances by specifying conventionally-used vague inverse-gamma priors as an alternative to uniform priors, for the model without covariates. We also check marginal posterior distributions for the parameters with uniform priors to verify that the interval is not too restrictive.

2.3.7 Results

For the model that includes all the covariates, $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$, estimated survival probabilities (Figure 2-4) differ substantially for the three species, although most values remain relatively high, as is typical for long-lived seabirds. Note that the size of the 95% credible intervals reflects the amount of data available for each species, being widest for razorbill (153 birds) and very narrow for guillemots (831 birds). Survival is relatively stable over the years for guillemots, shows wider variation for razorbills, with pronounced peaks in a few particular years, while estimates for puffins are intermediate. The estimated trap-dependence coefficients a_S are all positive for the three species (Table 2-1) and therefore the probability of seeing a bird is higher if it is seen the previous year; this is usually termed 'trap-happiness'. Using the estimates of a_S and p_S^* we derive the resight probabilities for the three species (Figure 2-5), for the case when a bird was seen the year before ($\bar{p}$), and for when it was not (p). The 'trap-happiness' is evident in these estimates. Note that resight probability is one for the three species in the last year. When the study is repeated excluding 2008, this effect appears again associated with the last year, in this case 2007. This suggests that the survival estimates for the last year should be discarded, as they are biased low due to the boundary estimate in recapture probability. We note that the Cormack-Jolly-Seber model is parameter-redundant, even when trap-dependence in resight probability is included (Choquet & Cole 2012); the addition of random effects might make the model weakly identifiable.

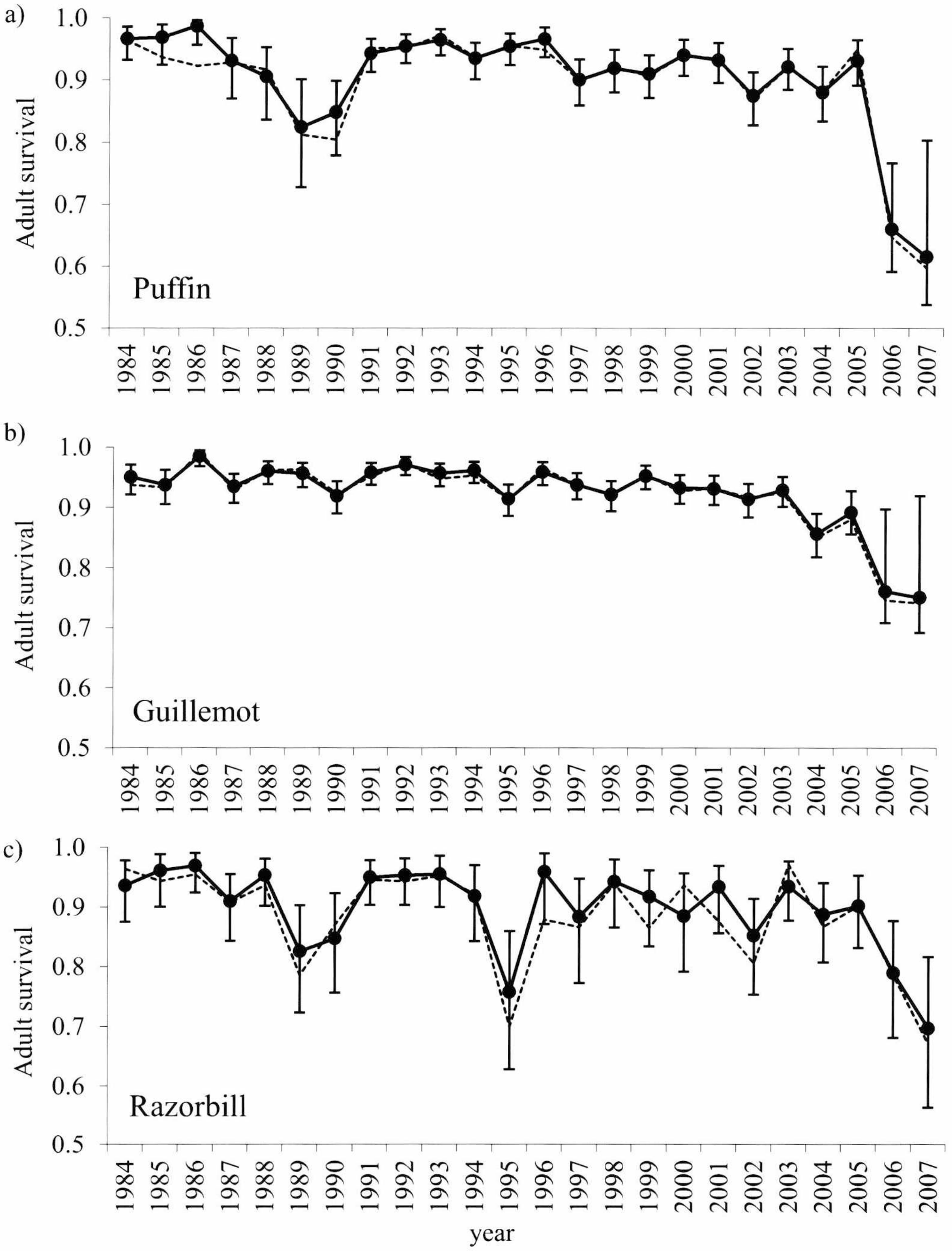


Figure 2-4 Estimated apparent adult survival (medians and 95% CIs) from model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$ for a) puffin, b) guillemot and c) razorbill. The dotted lines represent survival estimates from the fully time-dependent model $\{\phi(t)p(t + h)\}$ obtained with WinBUGS for each species separately, indicating a slight effect of shrinkage due to the random effects (more discussion in section 5.5.6).

In the case of razorbill, four other years have resight probabilities estimated to be one. The number of marked razorbills is substantially lower than for the two other species, and these estimates reflect years for which all birds known to be alive the previous year were either seen or never seen again.

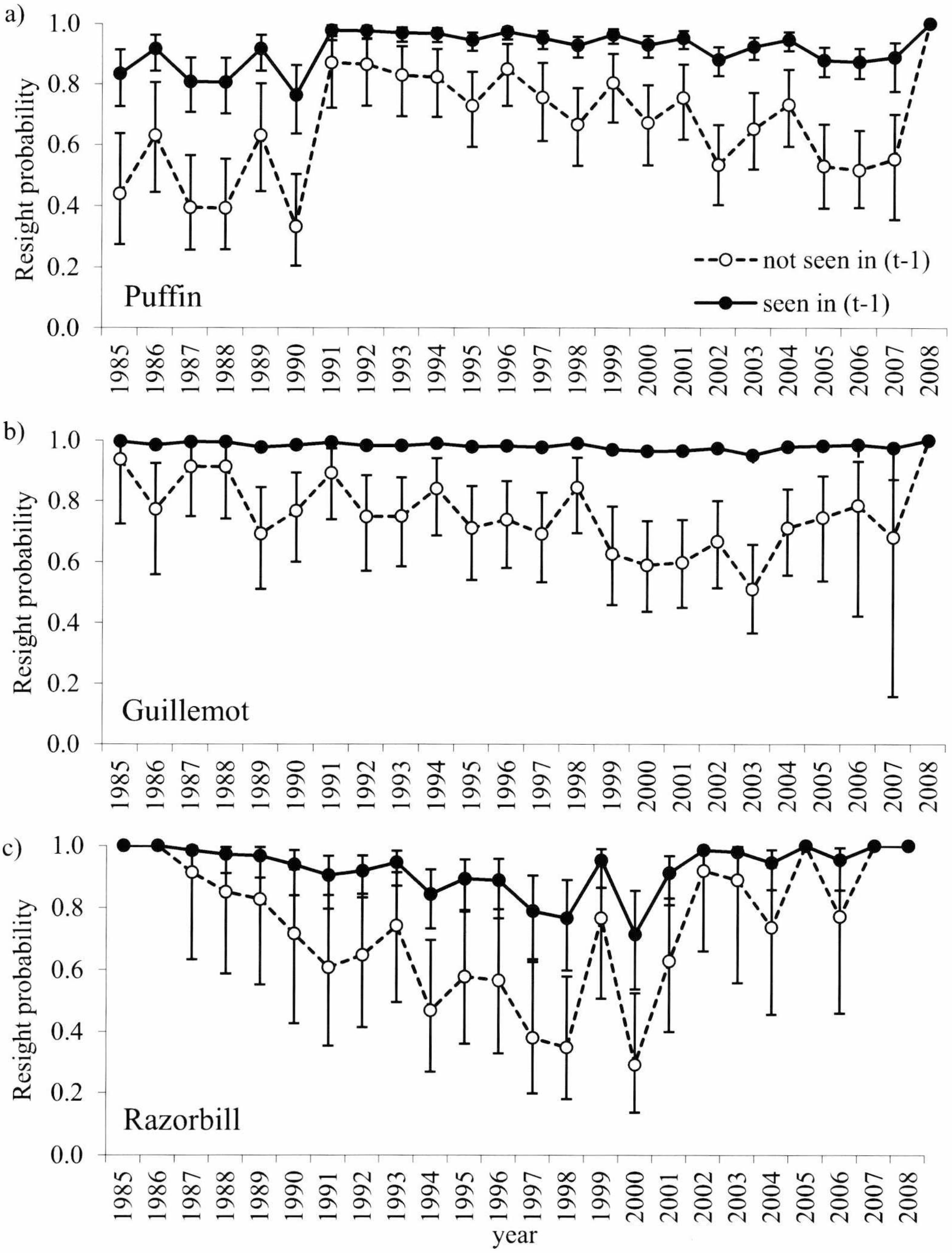


Figure 2-5 Estimated resight probabilities (median and 95% CI) for a) puffin, b) guillemot and c) razorbill at the Isle of May, according to model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$. Solid lines represent the values when the animal has been seen (captured or resighted) the year before; the opposite case is shown with dashed lines.

Most of the point estimates for the regression coefficients are below zero (Table 2-1), denoting a negative relationship between adult survival and the corresponding covariate. Note that most of the 95% credible intervals span both sides of zero. In the particular case of 1-year time-lagged SST for razorbill, the regression coefficient (β_4) is very close to zero, indicating a lack of strong influence of that covariate on razorbill survival. The fact that some of the regression coefficients corresponding to the time-lagged versions of wNAO and SST are far from zero suggests that they also have an indirect effect on adult survival, acting possibly through the food chain (Harris *et al.* 2005; Sandvik *et al.* 2005).

Table 2-1 Median (and 95% CIs) of the marginal posterior distribution of the regression and 1-year trap-dependence coefficients of model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$. For the covariates, regression coefficients whose 95% CI excludes zero (or includes it very close to the interval limit) are marked in bold.

	puffin	guillemot	razorbill
β_0 (intercept)	2.51 (2.22, 2.81)	2.68 (2.39, 2.97)	2.36 (2.02, 2.76)
$\beta_1(\text{wNAO}_0)$	-0.14 (-0.47, 0.18)	0.15 (-0.16, 0.45)	0.27 (-0.13, 0.67)
$\beta_2(\text{wNAO}_1)$	-0.19 (-0.56, 0.18)	0.08 (-0.27, 0.43)	**-0.43 (-0.91, 0.03)**
$\beta_3(\text{SST}_0)$	**-0.47 (-0.93, 0.02)**	-0.11 (-0.55, 0.31)	-0.46 (-1.06, 0.11)
$\beta_4(\text{SST}_1)$	-0.31 (-0.75, 0.11)	**-0.40 (-0.81, -0.01)**	-0.04 (-0.58, 0.48)
a	1.86 (1.54, 2.18)	2.94 (2.54, 3.35)	1.81 (1.22, 2.41)

The inter-specific synchrony indices I_s, calculated from the estimates of the full model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$ and the model without covariates $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$ are shown in Tables 2-2 and 2-3. For the full model the residual variances of the species-specific random terms $\hat{\sigma}_\varepsilon^2(res)$ are all substantially lower than that of the common random term $\hat{\sigma}_\delta^2(res)$ which is also noticeable when looking at the estimates of the random terms for each year of the study (Figure 2-6). I_s values are consequently high, which suggests that most of the variation unexplained by the environmental covariates is synchronous to the three species.

Table 2-2 Estimates (median and 95% CI) of the random effects synchronous and asynchronous total variances and derived synchrony indices I_S for each species, for model $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$. Subscript 'P' refers to puffins, 'G' to guillemots and 'R' to razorbills. 95% Credible Intervals are shown in brackets. Based on the MCMC samples, the probabilities of $\hat{\sigma}_S^2 < \hat{\sigma}_\delta^2$ are 0.78, 0.86 and 0.74 respectively.

	Total variances	Indices of synchrony
Species-specific asynchronous variance component	$\hat{\sigma}_P^2(tot) = 0.191\ (0.017, 0.628)$	$I_P = 0.667\ (0.173, 0.965)$
	$\hat{\sigma}_G^2(tot) = 0.137\ (0.008, 0.487)$	$I_G = 0.735\ (0.245, 0.982)$
	$\hat{\sigma}_R^2(tot) = 0.202\ (0.005, 0.849)$	$I_R = 0.665\ (0.117, 0.987)$
Inter-specific synchronous variance component	$\hat{\sigma}_\delta^2(tot) = 0.386\ (0.066, 0.885)$	

Table 2-3 Estimates (median and 95% CI) of the random effects synchronous and asynchronous residual variances and derived synchrony indices I_S for each species, for model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$. Subscript 'P' refers to puffins, 'G' to guillemots and 'R' to razorbills. 95% Credible Intervals are shown in brackets. Based on the MCMC samples, the probabilities of $\hat{\sigma}_S^2 < \hat{\sigma}_\delta^2$ are 0.95, 0.90 and 0.82 respectively.

	Residual variances	Indices of synchrony
Species-specific asynchronous variance component	$\hat{\sigma}_P^2(\text{res}) = 0.036\ (0.000, 0.346)$	$I_P = 0.894\ (0.304, 0.999)$
	$\hat{\sigma}_G^2(\text{res}) = 0.079\ (0.001, 0.377)$	$I_G = 0.787\ (0.350, 0.996)$
	$\hat{\sigma}_R^2(\text{res}) = 0.082\ (0.001, 0.660)$	$I_R = 0.785\ (0.205, 0.998)$
Inter-specific synchronous variance component	$\hat{\sigma}_\delta^2(\text{res}) = 0.288\ (0.091, 0.711)$	

In model $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$, all $\hat{\sigma}_S^2(\text{tot})$ and $\hat{\sigma}_\delta^2(\text{tot})$ total variances increase compared to the model with covariates, to accommodate the extra variation created by the lack of covariates. The species-specific variances increase more, in proportion, and therefore the indices of synchrony decrease to below 80%. The fraction of the synchronous variance accounted for by the set of covariates is $C_\delta = 0.256$, that is, about a quarter of the variation that is synchronous to the three auk species is explained by components of the climate related to wNAO and SST. Climate is acting to some extent as a synchronising agent in the survival of puffins, guillemots and razorbills but there is still about 75% of synchronous variation that is not explained by these covariates. The environmental covariates are also responsible for a large part of the asynchronous variation, as shown by the values of the C_s coefficients. For puffins and razorbills, the values are very high ($C_P = 0.810$ and $C_R = 0.595$ respectively), implying that most of the between-year variation asynchronous to the other auk species is related to these climatic covariates. For guillemots on the other hand, less than half of the asynchronous variation in adult survival is explained by these covariates ($C_G = 0.425$). Thus it appears that the same climatic factors can act simultaneously as synchronising and desynchronising agents for adult survival of these species at the Isle of May. There is some indication that both wNAO and SST can act indirectly on survival (Harris *et al.* 2005). It is therefore possible that the oceanographic effects reflected in wNAO and SST can act through different indirect causation paths, some of them affecting the three species in synchrony, some others affecting them differently or only affecting some of the species.

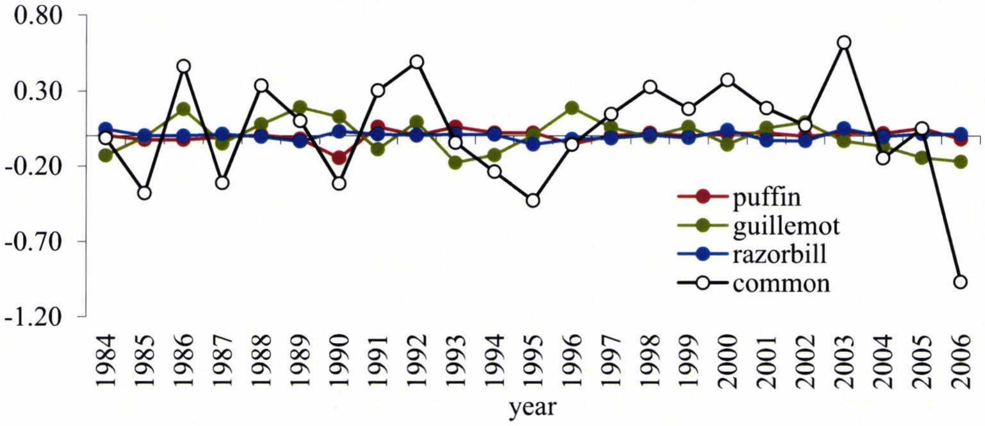


Figure 2-6 Value of the random effect terms (on the logistic scale) estimated for each year by the model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$, showing the common year random terms $\delta(t)$ and the species-specific random terms $\varepsilon_s(t)$ for each species.

Regarding prior sensitivity in the model without covariates $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$, the use of inverse-gamma priors for the random- effect variances appears to be slightly more informative than specifying uniforms U(0,3) for their standard deviation, and the posterior distributions are sensitive to the choice of the gamma distribution parameters, as has been noted in previous studies (Gelman 2006; Royle 2008) including for guillemot MR data from the Isle of May (Reynolds *et al.* 2009). The effect is particularly noticeable for razorbills, the species with least data. These results support the selection of uniform priors for these parameters. The Appendix shows a number of comparisons of priors and marginal posteriors. We also test low-information normal priors for the regression intercepts β_s and the trap-dependence parameters a_s instead of the uniform priors used in the analyses, but these parameters appear robust to such changes.

2.3.8 Goodness-of-fit

To check the goodness-of-fit for the model $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$, we conduct posterior predictive checks, calculating Bayesian p-values (Gelman *et al.* 2004, p.162; King *et al.* 2009, p.138). These are based on the comparison of a statistic calculated for both the observed m-array $\boldsymbol{O}$ (the data) and a simulated m-array $\boldsymbol{S}$, generated using the parameter values obtained at each iteration of the MCMC chains. For an observed m-array $\boldsymbol{O}$ (with cell values $O_{ij} = m_{ij}$) and a set of estimated parameters $\boldsymbol{\theta}$, the basic algorithm is as follows

(i) Calculate the expected number of birds E_{ij}^n in each cell $\{i, j\}$ of the m-array, according to the parameter values $\boldsymbol{\theta}_n$ from the n^{th} MCMC iteration;

(ii) Simulate an m-array S^n according to parameter values $\boldsymbol{\theta}_n$, with the simulated number of birds in each cell $\{i, j\}$ denoted S_{ij}^n;

(iii) Calculate the 'observed discrepancy' between observed data and expected values $D_O^n(O_{ij}, E_{ij}^n)$, for each iteration n of the MCMC chain;

(iv) Calculate the 'simulated discrepancy' between simulated data and expected values $D_S^n(S_{ij}^n, E_{ij}^n)$;

(v) Repeat for all MCMC iterations n;

(vi) Compute the Bayesian p-value as the proportion of MCMC iterations where $D_O^n(O_{ij}, E_{ij}^n) < D_S^n(S_{ij}^n, E_{ij}^n)$. Extreme values (close to 0 or 1) are indicative of lack of fit.

We use the Freeman-Tukey test statistic as a measure of discrepancy (see an example in the mark-recapture context in Brooks, Catchpole & Morgan 2000)

$$F_X^n = \sum_i \sum_j \left(\sqrt{X_{ij}^n} - \sqrt{E_{ij}^n}\right)^2,$$

where X_{ij}^n represents either the observed (O_{ij}) or the simulated (S_{ij}^n) data. Note that the Freeman-Tukey statistics F_O^n and F_S^n can be conveniently calculated within WinBUGS for each iteration of the MCMC. The Bayesian p-values obtained for the fit to each species' MR data set (Figure 2-7) do not show strong evidence of lack of fit for any of the three auk species: 0.851, 0.855 and 0.767 for puffin, guillemot and razorbill respectively.

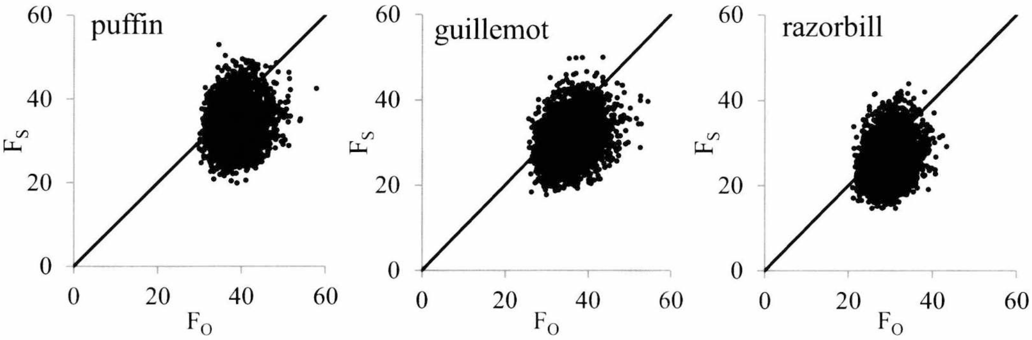


Figure 2-7 Scatterplot for the Freeman-Tukey statistic of the observed data versus that of the simulated data, for the 3-auk adult survival synchrony model without covariates $\{\phi(\beta + \delta + \varepsilon)p(t + h)\}$. For clarity, only the 5000 first samples are shown of an analysis with 150000 MCMC iterations (with burn-in of 100000). The corresponding Bayesian p-values for each data set are 0.851, 0.855 and 0.767 for puffin, guillemot and razorbill respectively.

2.3.9 *Simulation study*

We use simulations to study the performance of the proposed method in fitting a set of data derived from known parameters, as a way of checking parameter identifiability (Gimenez *et al.* 2004). We select the full model structure $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$ from the previous section and choose parameter values based on the best model obtained in the Isle of May auk study as well as the same number of animals as in the real data set, in order to stay within ecological realism. Mark-resight data are generated 20 times, given that the processing time required for the MCMC sampling is prohibitive for a much larger simulation study. The random effects terms are generated independently in each data set, but using the same variances; intercepts and resight probabilities are kept constant. The model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$ is fitted to the 20 data sets using WinBUGS (50000 MCMC iterations after a burn-in of 100000).

Table 2-4 Results of the simulation study with model $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$ for the following variables: trap-dependence coefficient a_s; logistic regression coefficients β_{is}; variances of the random effects σ^2. Obtained from 20 simulations. Subscripts P, G and R denote puffin, guillemot and razorbill respectively. Bias is computed as the average of the absolute value of the difference between the point estimate (median) and the true value.

	True value	Mean of medians	SE of medians	Bias	Bias (%)
a_P	1.9	1.95	0.23	0.051	2.7%
a_G	2.9	2.99	0.23	0.094	3.3%
a_R	1.8	1.72	0.26	-0.077	-4.3%
β_{0P}	2.50	2.60	0.14	0.098	3.9%
β_{0G}	2.70	2.74	0.15	0.043	1.6%
β_{0R}	2.40	2.52	0.14	0.123	5.1%
$\beta_{1P} - \text{wNAO}_0$	-0.10	-0.09	0.16	0.006	-5.7%
$\beta_{1G} - \text{wNAO}_0$	0.10	0.12	0.15	0.017	16.7%
$\beta_{1R} - \text{wNAO}_0$	0.30	0.32	0.21	0.025	8.2%
$\beta_{2P} - \text{wNAO}_1$	-0.20	-0.19	0.23	0.007	-3.6%
$\beta_{2G} - \text{wNAO}_1$	0.10	0.10	0.22	0.001	1.2%
$\beta_{2R} - \text{wNAO}_1$	-0.40	-0.36	0.26	0.036	-9.1%
$\beta_{3P} - \text{SST}_0$	-0.50	-0.55	0.28	-0.049	9.8%
$\beta_{3G} - \text{SST}_0$	-0.10	-0.08	0.21	0.022	-21.8%
$\beta_{3R} - \text{SST}_0$	-0.40	-0.36	0.29	0.036	-8.9%
$\beta_{4P} - \text{SST}_1$	-0.30	-0.30	0.20	0.000	0.1%
$\beta_{4G} - \text{SST}_1$	-0.40	-0.43	0.19	-0.031	7.8%
$\beta_{4R} - \text{SST}_1$	0.04	-0.03	0.27	-0.067	-167.8%
σ_δ^2	0.300	0.338	0.13	0.038	12.8%
σ_P^2	0.040	0.070	0.07	0.030	76.0%
σ_G^2	0.080	0.094	0.06	0.014	17.6%
σ_R^2	0.080	0.149	0.12	0.069	86.0%

The simulation results (Table 2-4) indicate that bias is generally small for the regression and trap-dependence coefficients. Three parameters have larger bias (β_{1G}, β_{3G} and particularly β_{4R}) but note these are associated with parameters that are close to zero. Bias in survival estimates is in almost all cases below 3% and is again in general largest for razorbills (smallest data set) and smallest for guillemots (largest data set). Apart from these, the largest bias values appear with the estimation of the random effects variances. In relation to the species-specific random terms, it is worth noting that as expected the largest bias is associated with the species with least data (razorbill, 153 marked individuals) while the smallest corresponds to guillemots (with 831 birds). These differences disappear when the simulations are repeated with 831 individuals for each of the species.

2.4 Discussion

Although recent decades have seen much development of statistical methods to estimate demographic parameters such as reproduction, and survival and migration probabilities, the focus is usually on the estimation of these parameters for individual species. This is despite the fact that several species may live in close proximity, sometimes competing for the same resources. There is therefore a great need for new methods that enable a better integration of demographic data, e.g. the study of synchrony between sympatric species, which are subject to common environmental stochasticity and potentially similar biotic interactions. The growing interest in multi-species aspects is visible both in ecological theory (McCarthy 2011; Mutshinda, O'Hara & Woiwod 2011) and application (Frederiksen, Mavor & Wanless 2007).

In this chapter, we present a framework for quantifying the degree of multi-species synchrony in a demographic parameter, adapting the model used for a multi-population study by Grosbois *et al.* (2009) to the multi-species situation. We demonstrate it with a study of synchrony in adult survival between three auk species that breed at the Isle of May but, as we will see in the next chapter, the framework is readily adapted to other parameters such as productivity. We also calculate the contribution of environmental covariates as synchronising and desynchronising agents. Although this method does not directly shed light into the typically complex mechanisms that underlie the observed synchronisation or desynchronisation between different species, it can be used to provide insight into community dynamics and to point out further avenues of investigation in terms of environmental covariates.

The survival estimates obtained in our study with the model with environmental covariates $\{\phi(cov + \delta + \varepsilon)p(t + h)\}$ are consistent with previous analyses of the three species individually (Harris, Wanless & Rothery 2000; Harris *et al.* 2005). However estimates of a species' survival from a more integrated study have the potential for borrowing strength from the rest of the ensemble, with the consequent gain in precision. Some of the estimated regression coefficients are consistent with the existence of indirect environmental effects, possibly through the food web, as noted in Sandvik *et al.* (2005): regression coefficients are negative for SST with no delay and others with 1-year lag are away from zero. Some of the estimated regression coefficients are low and have 95% CIs that included zero, possibly pointing to the lack of a strong influence of the corresponding environmental covariates on that particular species' survival. We do not attempt a systematic covariate selection process prior to the modelling as the primary aim at this stage is to develop the statistical model for studying multi-species synchrony and demonstrate the potential of this framework. There is a significant proportion of variance not explained by our set of covariates, which indicates that there is scope for further investigation. This may include the existing environmental covariates with longer time lags (Harris *et al.* 2005) or averaged over different periods of the year or broader areas in which auks overwinter (Sandvik *et al.* 2005). Biotic covariates, like prey stock estimates (Harris *et al.* 1997), could also be considered, as well as non-linear or non-parametric relationships with the covariates (Gimenez *et al.* 2006). Our study lays the methodological groundwork for this.

Improved understanding of how the environment synchronises and desynchronises demographic parameters can be of great value in generating ecological hypotheses, especially when coupled with biological knowledge of these species. Links between demography and environmental conditions are complex, with variables acting simultaneously as synchronising and desynchronising agents. In the case of the auks considered here, it is likely that to understand the processes involved, more information will have to be incorporated. The results of synchrony could for example be related to similarities in wintering grounds, as new research clarifies the picture of where these birds spend the winter months (Harris *et al.* 2009; Fauchald *et al.* 2011). Models like the one presented by Grosbois *et al.* (2009) for multi-populations and its adaptation for multi-species introduced in this chapter represent new steps towards more integrative approaches to study demographic parameters. Methods to study multi-species relations are urgently needed given the changing environmental conditions and may play an important role in increasing our understanding of how climate change may affect communities' composition, as sympatric species react in similar or different ways to changes in their environment.

3 MULTI-SPECIES SYNCHRONY IN PRODUCTIVITY

In this chapter we adapt the multi-species synchrony framework to another important demographic parameter: productivity. Productivity (or breeding success), commonly defined as the average number of offspring produced per breeding attempt, is an integrated measure made up of sequential events, ranging from an individual's decision to breed through to the offspring becoming independent of parental care. For birds, these components may include clutch size, hatchability and chick survival (Rockwell *et al.* 1993).

We start by looking at multi-species synchrony in overall productivity, using long-term breeding success data for five seabird species at the Isle of May. We also explore the contribution of large-scale and local environmental covariates to synchronising and desynchronising productivity in this community. We discuss how the common terms obtained from the multi-species synchrony productivity analysis can potentially be used as a community-based integrative indicator of the local environmental conditions. We then demonstrate how synchrony can be studied in different components of productivity, using more detailed data collected for two of the species as well as simulations. The last section looks at a different type of data, still related to breeding success: the distribution of clutch sizes. Given that this distribution is typically underdispersed compared to a Poisson or binomial distribution, we model underdispersion in clutch sizes and explore synchrony in both the mean clutch size and the amount of underdispersion between kittiwakes and shags, for which clutch sizes in a subset of the monitored nests have been recorded for a number of years.

3.1 Multi-species synchrony in overall productivity

In this section we look at overall productivity, which encompasses the complete breeding process, from laying eggs to fledging of chicks. In the following sections, s denotes the species and t the year.

3.1.1 Overall productivity as a probability: binomial model

Given that clutch sizes are bound by a species-specific maximum value, we propose modelling the number of chicks fledged from $K_s(t)$ monitored pairs of species s that attempt breeding in year t, as a binomial variable:

$$F_s(t) \sim \text{Bin}\big(K_s(t)c_s, \rho_s(t)\big). \tag{3.1}$$

Here c_s is the species-specific maximum clutch size. According to this formulation, 'overall productivity' ρ is a measure of breeding success that represents the probability of each potential egg in a clutch (out of the maximum possible c_s) becoming a fledged chick. This model is suitable when only the number of fledglings is recorded, a situation that frequently occurs in seabird monitoring programs where determining clutch size is often difficult and time consuming (later we address the case where the number of eggs is also recorded). The model assumes that the fate of each potential egg is an independent Bernoulli trial and as a consequence is equally applicable to obligate single-egg breeders as well as to species with variable clutch size ($c_s = 1$ and $c_s > 1$ respectively). We also assume that clutch fate is monitored from laying until fledging, avoiding potential biases that require special care (Mayfield 1961; Heisey & Nordheim 1995).

3.1.2 Overall productivity synchrony model

In order to study synchrony in productivity in a set of species for which the total number of fledglings from a number of monitored pairs has been recorded, we adapt the structure of common and species-specific year random terms described in section 2.2.1 for multi-species synchrony in survival. Applying the binomial model in (3.1) to each species, year random terms can be incorporated into productivity on the logit scale (as in this model ρ is defined as a probability)

$$\text{logit}\big(\rho_s(t)\big) = \beta_{0s} + \delta(t) + \varepsilon_s(t), \tag{3.2}$$

where β_{0s} are species-specific intercepts, $\delta(t)$ are random year terms common to all species and $\varepsilon_s(t)$ species-specific random year terms. All random terms are assumed to be independent and normally distributed, with no correlation between terms

$$\delta(t) \sim N\left(0, \sigma_\delta^2(\text{tot})\right), \ \varepsilon_s(t) \sim N\big(0, \sigma_s^2(\text{tot})\big).$$

Both σ_δ^2 and the σ_s^2 are 'total variances' ('tot'), that is, together they have to explain all the year-to-year variation as the model does not have covariates. σ_δ^2 represents the synchronous variation, while the species-specific σ_s^2 represent the asynchronous variations. Thanks to this structure of random year effects, the year-to-year variation in productivity is effectively partitioned for each species into common (synchronous) and species-specific (asynchronous) terms. Synchrony indices I_s, representing the amount of synchrony in the year-to-year variations in productivity on the logit scale, can be defined following (2.3)

$$I_s = \frac{\hat{\sigma}_\delta^2(\text{tot})}{\hat{\sigma}_\delta^2(\text{tot}) + \hat{\sigma}_s^2(\text{tot})}.$$

This quantity effectively represents the proportion of the year-to-year variation in productivity that is common to the other species in the set under consideration.

Now, we can introduce J covariates $c_j(t)$ in the logistic regression in (3.2) to estimate the contribution of the environment

$$\text{logit}\big(\rho_s(t)\big) = \beta_{0s} + \sum_{j=1}^{J} \{\beta_{js} c_j(t)\} + \delta(t) + \varepsilon_s(t), \tag{3.3}$$

where the β_{js} are the corresponding regression coefficients. The estimated variances of the new δ and ε_s terms, the residual variances $\hat{\sigma}_\delta^2(\text{res})$ and $\hat{\sigma}_s^2(\text{res})$, will be smaller than the total variances estimated previously from the model without covariates, $\hat{\sigma}_\delta^2(\text{tot})$ and $\hat{\sigma}_s^2(\text{tot})$. By comparing these, a set of common (C_δ) and species-specific (C_s) coefficients can be calculated, as done in (2.5) for adult survival

$$C_\delta = 1 - \frac{\hat{\sigma}_\delta^2(\text{res})}{\hat{\sigma}_\delta^2(\text{tot})} \quad \text{and} \quad C_s = 1 - \frac{\hat{\sigma}_s^2(\text{res})}{\hat{\sigma}_s^2(\text{tot})},$$

which measure respectively the contribution of the set of covariates to synchronising and desynchronising the year-to-year variations in productivity.

A commonly used alternative definition of overall productivity is the mean number of fledglings per pair, particularly for species that can lay more than one egg. Such a variable $\lambda_s(t)$ can be derived from the binomial model as $\lambda_s(t) = c_s \rho_s(t)$. For species that lay only one egg, $\lambda = \rho$: the mean number of fledglings per pair is equal to the probability of fledging one chick. Note that λ can take values greater than 1 but is of course bounded by c_s. If the interest lies in studying synchrony directly in λ, an appropriate link-function would be a type of generalised logistic function, which maps the regression with values $(-\infty, \infty)$ to $\lambda_s \in [0, c_s]$

$$\log\left(\frac{\lambda_s(t)}{c_s - \lambda_s(t)}\right) = \beta_{0s} + \delta(t) + \varepsilon_s(t). \tag{3.4}$$

By substituting $\lambda = c_s \rho_s$ we obtain

$$\log\left(\frac{\lambda_s(t)}{c_s - \lambda_s(t)}\right) = \log\left(\frac{\rho_s(t)}{1 - \rho_s(t)}\right) = \text{logit}\big(\rho_s(t)\big). \tag{3.5}$$

Since (3.5) is the same as (3.3), we conclude that synchrony in the probability of 'each potential egg being laid and surviving until fledging', is mathematically equivalent to that of the 'mean number of fledglings', and thus no specific modelling is required to estimate the latter.

Productivity defined as the mean number of fledglings per breeding pair is sometimes modelled with a Poisson distribution. We will look at this option in section 3.1.8.

3.1.3 The Isle of May productivity data set

We fit the models of overall productivity synchrony described above to data for five of the commonest members of the seabird community on the Isle of May: the three auks (puffin, guillemot and razorbill), the kittiwake and the shag. During the breeding season these species share a common prey base which around the Isle of May consists mainly of lesser sandeels *Ammodytes marinus* and sprat *Sprattus sprattus* (Frederiksen *et al.* 2006). We note that similarities in productivity have been reported for these species at broader geographical scales: all five species considered in this study appear in the same cluster (together with Northern fulmar *Fulmarus glacialis*) after principal component analysis of the productivity time-series of 15 seabird species from several colonies around Scotland (Parsons *et al.* 2008).

Data on breeding success were collected for these species at the Isle of May between 1986 and 2009. $K_s(t)$ pairs that attempted breeding were monitored during the season to ensure that the fate of offspring was known until fledging, enabling the total number of fledglings $F_s(t)$ to be recorded. Details of standardized methods can be found in Walsh *et al.* (1995). The number of breeding pairs monitored varied from year to year, with the following minima/mean/maxima: puffins 35/122/147; guillemots 731/842/1014; razorbills 84/140/194; kittiwakes 423/775/1327; shags 42/131/288. Clutch sizes tend to be small in seabirds. The three auks are obligate single-egg breeders. For these species, only pairs that laid were monitored and thus K equals the number of eggs E. Clutch sizes for kittiwakes and shags are variable, but on the Isle of May typical maxima are $c_K = 3$ and $c_S = 4$ eggs respectively. However, as in many monitoring programs, it is not possible to record the actual numbers of eggs laid by these two species at all the monitored sites and only the total number of fledglings was recorded.

3.1.4 Bayesian analysis

We first analyse the 24 years of data for the five species using the binomial model with synchrony defined for productivity ρ and no covariates. Analyses are conducted within the Bayesian framework in program JAGS v2.2.0 (Plummer 2003). We assess convergence of the MCMC chains with the Gelman–Rubin diagnostic $\hat{R}$ (Gelman & Rubin 1992) calculated in the R package CODA (Plummer *et al.* 2006) with three chains for all variables started at different values, which suggests that a burn-in period of 100000 samples ensures convergence ($\hat{R} < 1.02$ for all parameters). In this (and subsequent analyses in this chapter) 500000 MCMC samples are drawn from the posterior distribution of all parameters after a conservative burn-in of 500000. As in

Chapter 2, we define uninformative priors in the form of uniform distributions for all parameters and hyperparameters (standard deviations) to reflect our lack of strong prior beliefs about the demographic parameters to be estimated (logistic regression intercepts: $\beta_{0S} \sim \mathrm{U}(-5,5)$; $\mathrm{U}(0,3)$ for SDs of all random terms). The limits of these uniform distributions are selected after a shorter trial analysis to ensure they are wide enough to include all probable values of the corresponding MCMC chains. Figure 3-1 shows a generic Directed Acyclic Graph that represents the relationship of the parameters and hyperparameters in a productivity synchrony analysis for S species and T years. For our analysis of the Isle of May, $S = 5$ and $T = 24$.

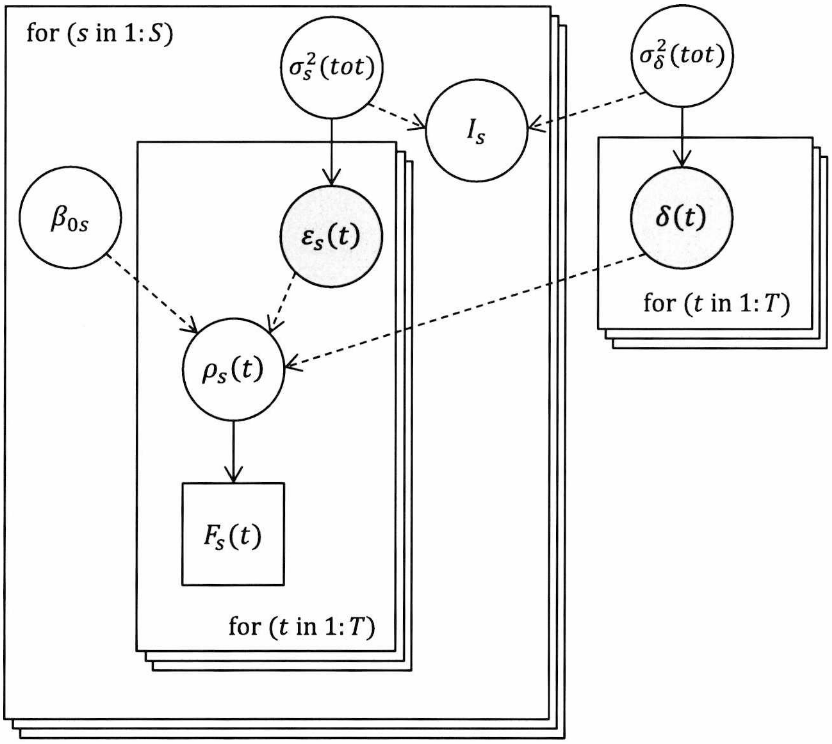


Figure 3-1 Directed Acyclic Graph (DAG) for a productivity synchrony analysis with S species and T years. Priors have been omitted for clarity. Squares=data; circles=parameters to be estimated, of which grey circles=random terms; solid arrows=stochastic relationships; dotted arrows=deterministic relationships.

3.1.5 Estimates of overall productivity

Figure 3-2 shows productivity estimates (median of the marginal posterior distributions with 95% CI) for each year for the five species. The baseline productivities $\bar{\rho}_s = \text{ilogit}(\hat{\beta}_s)$ on the linear scale (with 95% CI) are: 0.706 (0.648, 0.760) for puffins; 0.728 (0.673, 0.777) for guillemots; 0.661 (0.622, 0.700) for razorbills; 0.139 (0.090, 0.202) for kittiwakes; and 0.220 (0.157, 0.297) for shags.

Thus, in terms of productivity quantified as a probability (ρ_s), kittiwakes and shags do poorly compared to the auks (Figure 3-3). However, this reflects also the fact that species that lay multi-egg clutches typically produce fewer eggs than what they are physiologically capable of (maximum clutch size c_s) and thus productivity may appear low even if all eggs laid survived until fledging.

The more commonly reported measure of productivity, the number of fledglings per breeding attempt $\lambda_s(t)$, can be easily derived as $c_s \rho_s(t)$ (Figure 3-4). The mean number of fledglings per pair fluctuates around similar values for all five species (< 1) but with both kittiwakes and shags displaying a much wider variation than the auks.

The estimated random effects variances and synchrony indices (Table 3-1) indicate that productivity is appreciably synchronised for razorbills (87% of the year-to-year variation is synchronous with the other four species) but less so for puffins (30%) and guillemots (29%); kittiwakes and shags show even lower values (9% and 12%). Note that synchrony for each species is related to the year-to-year variations over the mean value and therefore the lower synchrony values for kittiwakes and shags are not mathematically related to their lower average productivity (the intercept in the logistic regression).

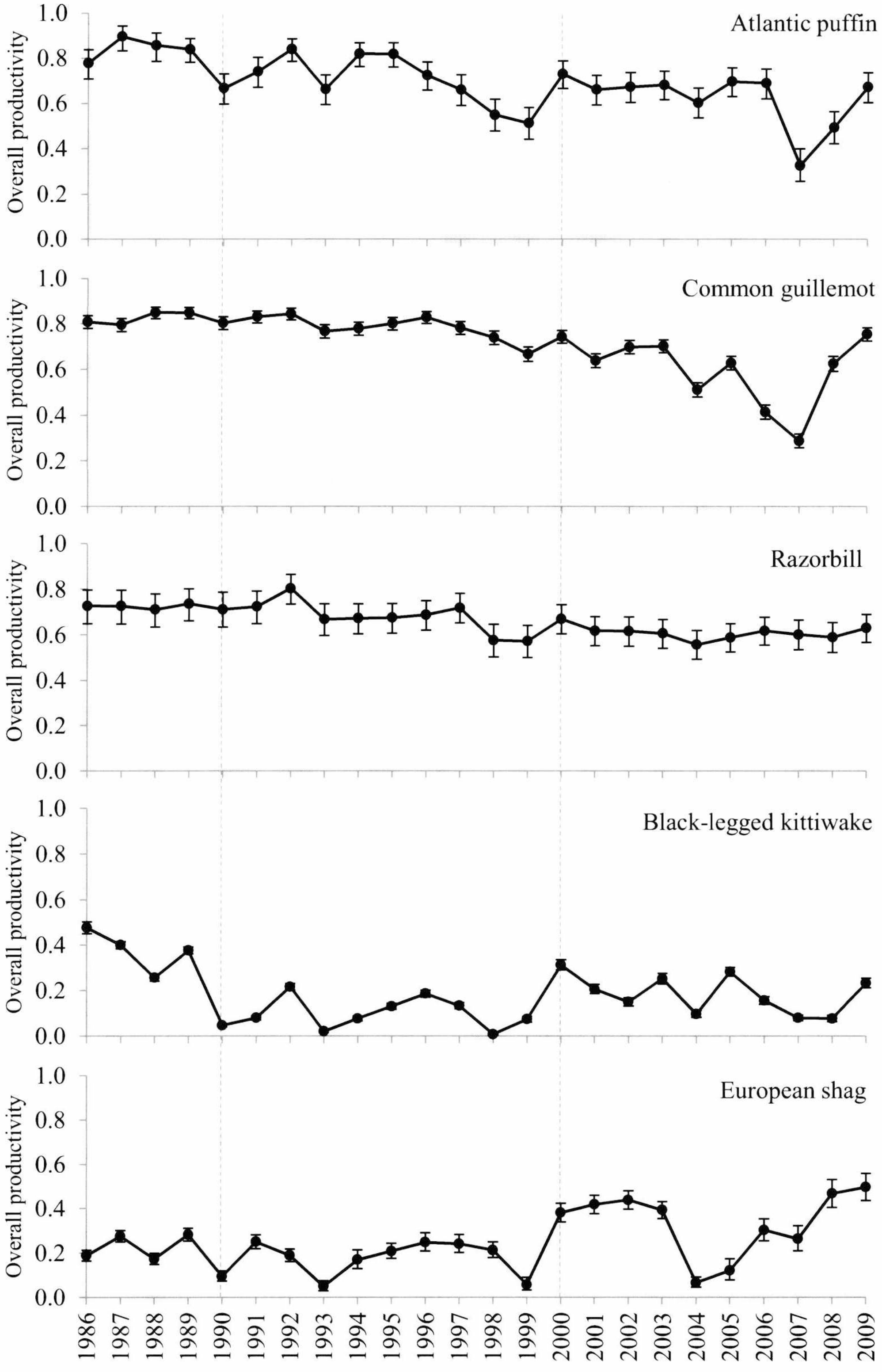


Figure 3-2 Estimates of yearly productivity ρ (defined as the probability of each potential egg in a clutch ending up as a fledged chick) with 95% CI for puffin, guillemot, razorbill, kittiwake and shag. Note the smaller CIs for species with most monitored nests: kittiwake, guillemot and shag.

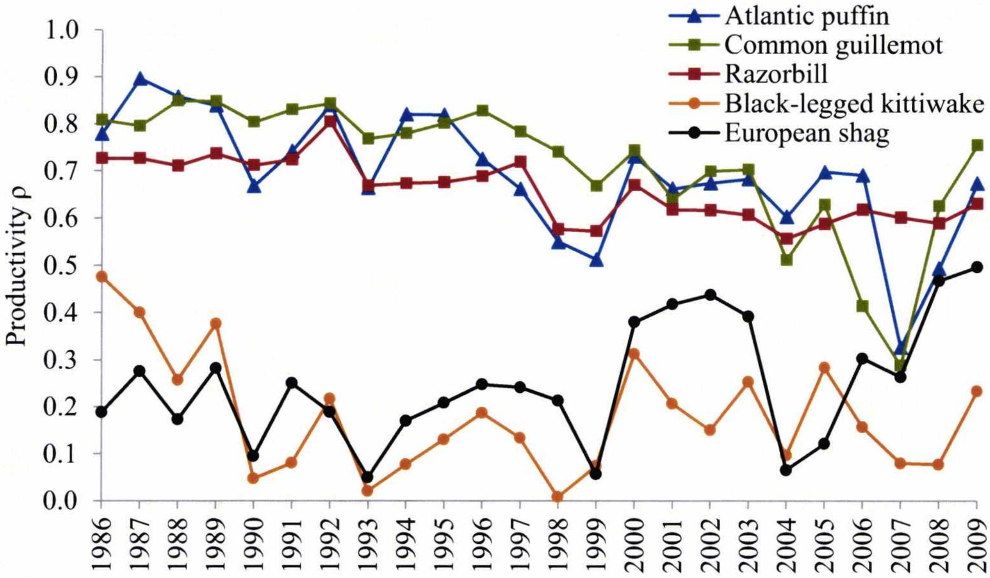


Figure 3-3 Point estimates (medians of marginal posterior distributions) of yearly productivity for puffins, guillemots, razorbills, kittiwakes and shags, with productivity defined as the probability of each potential egg in a clutch ending up as a fledged chick, $\rho_s(t)$. CIs have been omitted for clarity.

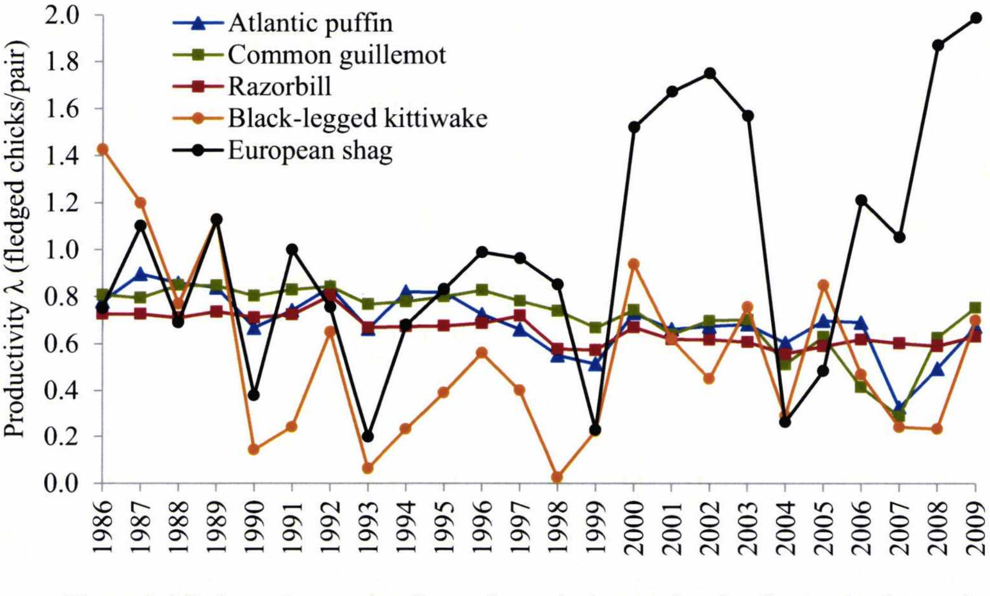


Figure 3-4 Point estimates (medians of marginal posterior distributions) of annual productivity for puffins, guillemots, razorbills, kittiwakes and shags, with productivity defined as the mean number of fledglings per breeding pair, $\lambda_s(t)$. CIs have been omitted for clarity.

Razorbill productivity shows relatively less year-to-year variation, which is mostly explained as common variance and leads to its high synchrony index, as discussed in section 2.2.2. The opposite occurs for kittiwakes and shags where most year-to-year variation is species-specific. Puffins and guillemots show intermediate results.

It is important to realize that synchrony is inherently related to the set of species used. For example, if analysis is conducted for a subset of puffins, kittiwakes and shags, estimated synchrony differs ($I_{PUF} = 41\%, I_{KIT} = 21\%, I_{SHA} = 25\%$).

Table 3-1 Estimates (median and 95% CI) of the random effects synchronous and asynchronous total variances and derived synchrony indices I_s for each species (based on the MCMC samples). Species numbers refer to Atlantic puffin (1), common guillemot (2), razorbill (3), black-legged kittiwake (4) and European shag (5).

	Variances	Index of synchrony
Asynchronous	$\hat{\sigma}_1^2(tot) = 0.272\ (0.114, 0.623)$	$I_1 = 0.295\ (0.097, 0.636)$
	$\hat{\sigma}_2^2(tot) = 0.277\ (0.139, 0.581)$	$I_2 = 0.292\ (0.102, 0.594)$
	$\hat{\sigma}_3^2(tot) = 0.018\ (0.000, 0.125)$	$I_3 = 0.870\ (0.448, 1.000)$
	$\hat{\sigma}_4^2(tot) = 1.127\ (0.627, 2.240)$	$I_4 = 0.092\ (0.030, 0.234)$
	$\hat{\sigma}_5^2(tot) = 0.833\ (0.456, 1.686)$	$I_5 = 0.120\ (0.044, 0.276)$
Synchronous	$\hat{\sigma}_\delta^2(tot) = 0.115\ (0.046, 0.278)$	

3.1.6 *The common trend*

Figure 3-5 displays the estimated synchronous and asynchronous random terms. The common terms $\delta(t)$ show a decline over the study period. The behaviour of the species-specific terms depends on the species. These have small values for razorbills (giving a small asynchronous variance, as discussed above) and have the most variation in shags and kittiwakes (largest asynchronous variances).

To support our theoretical results in section 3.1.2 that synchrony estimated directly in the derived parameter λ (3.4) is equivalent to that estimated in ρ, we repeat the analysis of the five species with synchrony defined directly in λ (fledglings per pair). As expected, the estimates of synchrony obtained are identical (to the second decimal place) to the ones for synchrony defined in ρ.

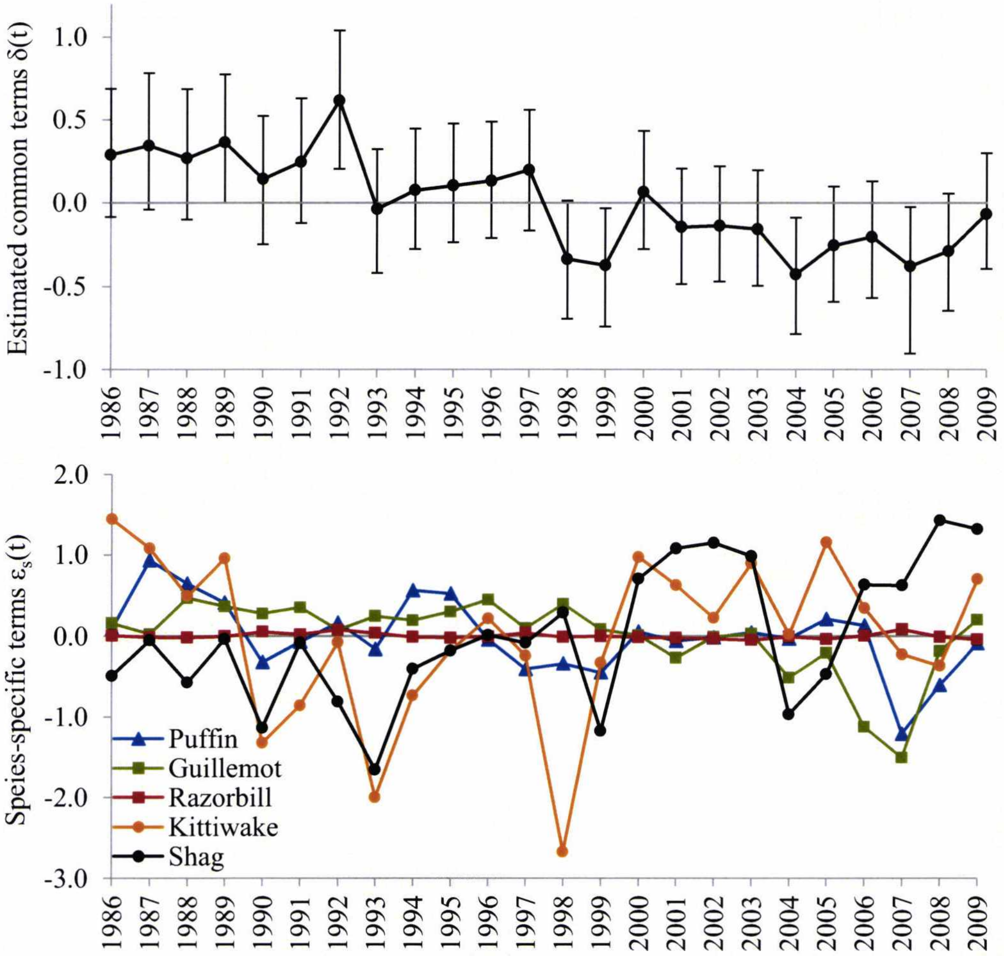


Figure 3-5 Common (synchronous) random terms $\delta(t)$ (top panel, with 95% CI) and species-specific (asynchronous) random terms $\varepsilon_s(t)$ (bottom panel) estimated in the analysis of the model of productivity ρ without covariates. Random terms are shown and estimated on the logistic scale.

The common terms represent the part of the yearly variation that is synchronous to all the species in the set, that is, the common signal in the overall productivities of the community. This can be viewed as an integrative summary that could potentially be used as a multi-species indicator. We compare these terms with another 'seabird index' proposed by Frederiksen, Mavor & Wanless (2007) based on Principal Component Analysis (Jolliffe 1986). While the latter includes productivity estimates from the same five species at the Isle of May, two additional variables (mass of nearfledged puffin and guillemot chicks) are also incorporated and their analysis covers a shorter time period compared to our study. We therefore apply the Frederiksen, Mavor & Wanless (2007) approach to our data, using only the productivity estimates for the 5 species, and look at the first principal component (PC1). We fit a linear trend to both indices:

(i) 'Synchrony index': $\hat{\delta}(t) = 0.388 - 0.031t$

(ii) Frederiksen, Mavor & Wanless (2007) 'seabird index': $\widehat{PC1} = 2.299 - 0.184t$

Note that the scale of $\hat{\delta}(t)$ and $\widehat{PC1}$ (and therefore the slopes reported above) are not necessarily comparable, but in any case the coefficient of determination is $R^2 = 0.619$ and 0.622 respectively ($p < 0.001$), that is, both indices show a statistically significant decline over the study period. Figure 3-6 compares the estimated terms.

Alternatively to fitting a linear trend to the point estimates of the common terms $\delta(t)$, the common trend can be estimated explicitly, and synchrony can be defined based on the 'residual common terms' $\delta'(t)$

$$\text{logit}\big(\rho_s(t)\big) = (\beta'_{0s} + \alpha\bar{t}\,) + \delta'(t) + \varepsilon_s(t),$$

where the random terms are $\delta'(t) \sim N\big(0, \sigma^2_{\delta'}\big)$, $\varepsilon_s(t) \sim N(0, \sigma^2_s)$, $\forall t, \forall s$. Here $\bar{t}$ is the standardised year (z-score), α is the common slope, and β'_s are the new intercepts (which have the intercept of the common decline confounded with the species-specific intercepts β'_{0s} from the original binomial model). New synchrony indices can be defined taking into account the 'residual variance' $\sigma^2_{\delta'}$ after the slope has been estimated. When we fit this model to the 5-species productivity data, we obtain an estimated slope $\hat{\alpha} = -0.303\ [-0.425, -0.197]$ and smaller indices of synchrony from the residual common terms ($I'_1 = 0.077$, $I'_2 = 0.084$, $I'_3 = 0.618$, $I'_4 = 0.017$, $I'_5 = 0.022$), indicating that this trend accounts for an important part of the common variation.

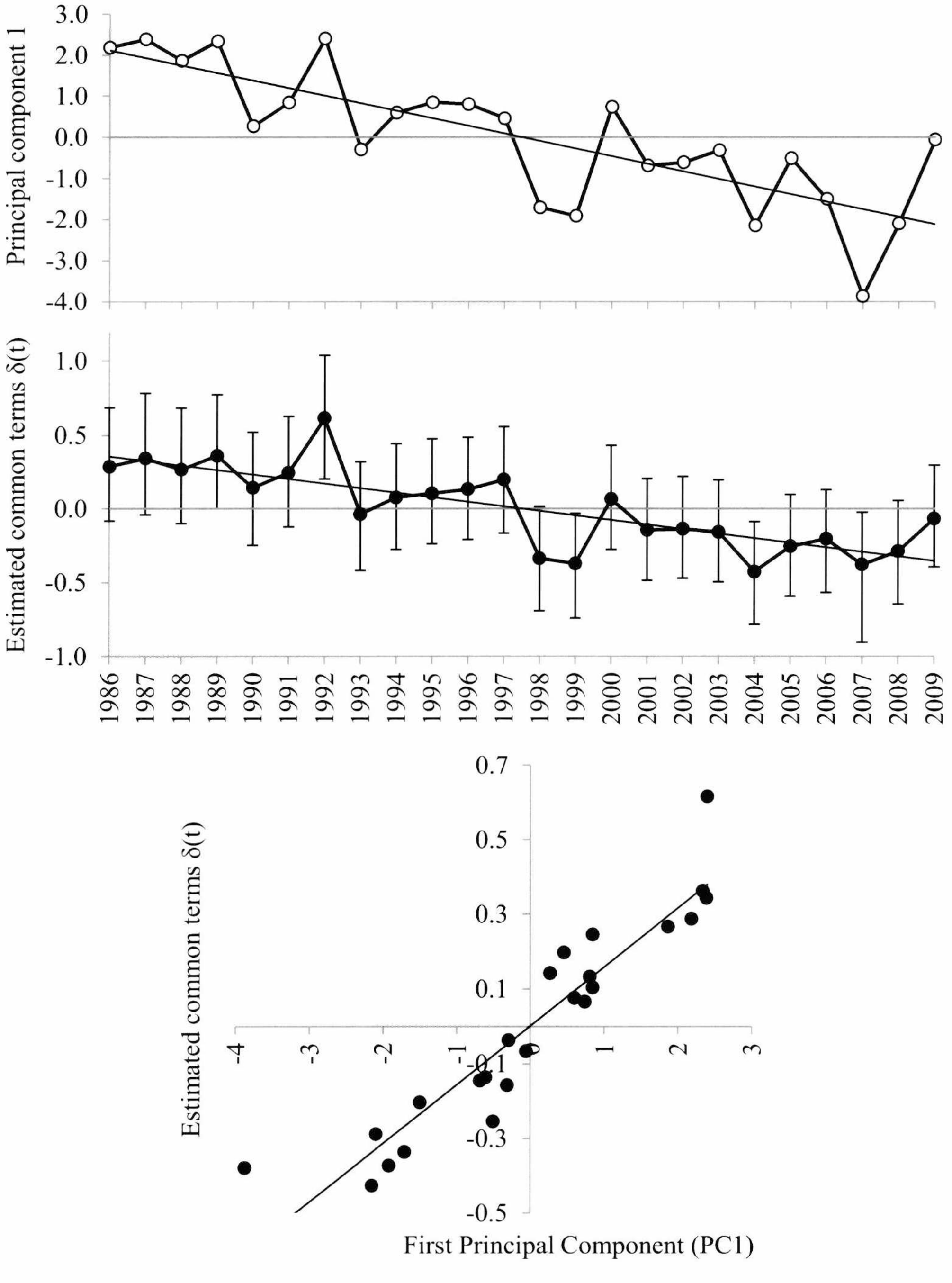


Figure 3-6 Comparison of the first principal component from PCA of the 5-species productivity estimates time series (top panel; obtained applying the methods in Frederiksen, Mavor & Wanless 2007) and the common random terms $\delta(t)$ estimated in the analysis of the model without covariates (with 95% CI; central panel). The linear regressions with time fitted to both indices are also shown. The bottom panel shows a scatterplot of both variables. Note that the random terms are shown and estimated on the logistic scale. The common terms of the synchrony model has the advantage of providing a measure of uncertainty around the estimates, while the PCA is based on point estimates.

3.1.7 *Environmental contributions to synchrony*

In order to study the contribution of environmental factors to synchronising and desynchronising the year-to-year variations in overall productivity ρ of our set of species, we fit the binomial model including covariates in the logistic regression. We investigate the effect of winter NAO index (wNAO) and the sea surface temperature (SST) around the Isle of May; these data sets are described in section 1.3.1. As in Chapter 2, we include time-lagged versions (1 and 2 years, denoted by subscripts in our covariates) to allow for potential indirect effects acting through the food chain (Frederiksen *et al.* 2006; Sandvik & Erikstad 2008). We also consider the presence of a commercial sandeel fishery that operated close to the Isle of May between 1990 and 1998 since it has been shown to influence breeding success of kittiwakes in this region (Frederiksen *et al.* 2004).

To avoid spurious effects by introducing covariates with little predictive power, a preliminary analysis is conducted with all covariates included for the five species and the covariates that have little support are subsequently removed from the analysis. As an ad hoc rule, we considered a covariate to have 'little support' if the probability in the part of the marginal posterior distribution of the regression coefficient that crosses over zero is greater than 1/3 (i.e. $\Pr(\beta_{js} < 0) > 1/3$ if median $\hat{\beta}_{js} > 0$, or $\Pr(\beta_{js} > 0) > 1/3$ if $\hat{\beta}_{js} < 0$). In the final analysis with covariates, the estimated regression coefficients whose 95% CIs do not include 0 (or is close to the limit) are

(i) for puffins: NAO_1: 0.180 (-0.057, 0.420); SST_1: -0.566 (-0.849, -0.290);

(ii) for guillemots: SST_2: -0.297 (-0.583, -0.019);

(iii) for razorbills: NAO_0: 0.129 (0.004, 0.256); NAO_2: 0.173 (0.025, 0.325);

(iv) for kittiwakes: NAO_2: 0.372 (-0.012, 0.764); SST_1: -0.464 (-0.826, -0.069); 'fishery': -1.880 (-2.654, -1.101);

(v) for shags: no significant covariates.

Figures 3-7 and 3-8 plot the estimated effect of these covariates.

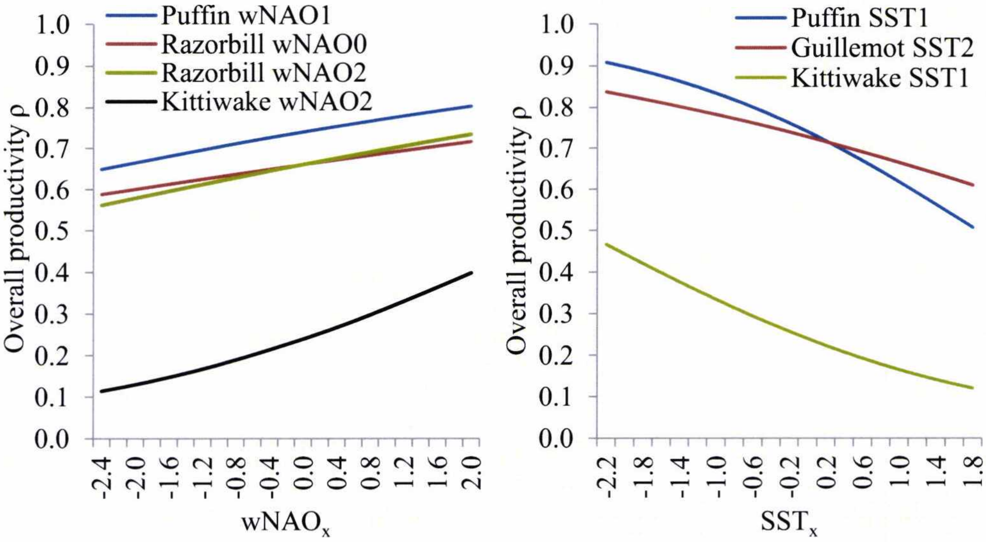


Figure 3-7 Effect of winter NAO and February-March SST on productivity of the different species, with covariates considered in isolation (all other covariates being zero, which represents an average value given that covariates have been standardised). The number after NAO and SST refers to the time-lag in years.

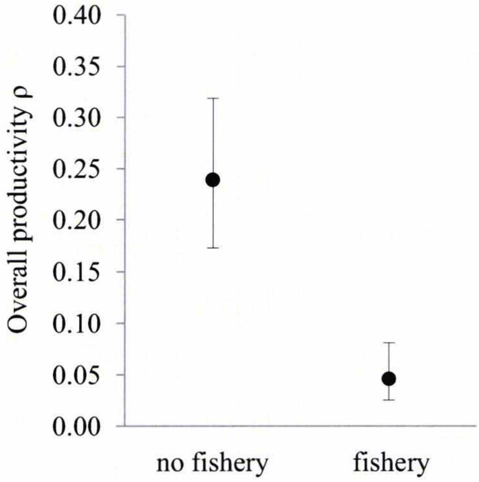


Figure 3-8 Effect of the presence (covariate = 1) of a local sandeel fishery on kittiwake productivity (all other covariates being zero), with 95% CI.

Although different species appear affected by different aspects of the climatic variables, the direction of the responses is consistent, with the contribution of NAO always positive and SST always negative. The presence of the local sandeel fishery is only significant for kittiwake productivity, as previously noted by Frederiksen, Mavor & Wanless (2007) for a shorter time series.

In terms of their contribution to synchrony (Table 3-2), the analysis shows evidence of climatic covariates explaining a large part (64%) of the common signal (although this variance was originally small). The contribution to desynchronising productivity varies from species to species, from 18% for razorbills to 55% for kittiwakes (the only species clearly affected by the sandeel fishery), and is very small for shags, consistent with the lack of significant covariates (C_5 is not exactly 0 as, although non-significant, covariates are still included for shag productivity so that the model can estimate some spurious degree of contribution of these covariates).

Table 3-2 Estimates (median and 95% CI) of the random effects synchronous and asynchronous residual variances and the derived contribution of covariates to synchronising (C_δ) and desynchronising (C_s) productivity (calculated using the point estimates of the residual variances in this table and total variances from Table 3-1). Species numbers refer to Atlantic puffin (1), common guillemot (2), razorbill (3), black-legged kittiwake (4) and European shag (5).

	Variances	Contribution of covariates
Asynchronous	$\hat{\sigma}_1^2(\text{res}) = 0.159\ (0.057, 0.401)$	$C_1 = 0.413$
	$\hat{\sigma}_2^2(\text{res}) = 0.213\ (0.096, 0.509)$	$C_2 = 0.232$
	$\hat{\sigma}_3^2(\text{res}) = 0.014\ (0.000, 0.104)$	$C_3 = 0.183$
	$\hat{\sigma}_4^2(\text{res}) = 0.506\ (0.261, 1.105)$	$C_4 = 0.551$
	$\hat{\sigma}_5^2(\text{res}) = 0.762\ (0.379, 1.730)$	$C_5 = 0.085$
Synchronous	$\hat{\sigma}_\delta^2(\text{res}) = 0.041\ (0.005, 0.125)$	$C_\delta = 0.643$

3.1.8 Poisson distribution as an alternative to the proposed binomial

A commonly used distribution for modelling breeding success when clutch sizes are larger than one is the Poisson distribution. If the number of fledglings from pair i is $F_s^i(t) \sim \text{Pois}\big(\lambda'_s(t)\big)$, with λ' the mean number of chicks of species s fledging per breeding pair in year t, the total number of fledglings from $K_s(t)$ monitored pairs is also Poisson

$$F_s(t) \sim \text{Pois}\big(K_s(t)\lambda'_s(t)\big). \tag{4.6}$$

Importantly, this approach makes an implicit approximation: if maximum clutch size c_s is modelled explicitly, the number of fledglings per pair is actually a truncated Poisson

$$F_s^i(t) \sim \text{TPois}(\lambda_s'(t)),$$

with maximum value c_s. When we sum over all $K_s(t)$ monitored pairs to obtain the total number of fledglings of species s in year t, we have

$$F_s(t) \sim \sum_{i=1}^{K_s(t)} \text{TPois}(\lambda_s'(t)). \tag{4.7}$$

This distribution is not the same as that in (4.6), even for large values of $K_s(t)$, although it will be similar when the amount of truncation is small. Using (4.6) instead of (4.7) is a very convenient approximation as it simplifies model fitting in general, and specifically in programs like WinBUGS or JAGS where a sum of truncated Poisson distributions would be more complicated to code and time-consuming to analyse compared to the standard Poisson distribution.

Multispecies synchrony in λ' can be studied in the approximated Poisson model (4.6) using random terms in a similar way to λ in the binomial model, except that here the link function would be a generalised logistic function, to take into account the maximum value c_s

$$\log\left(\frac{\lambda_s'(t)}{c_s - \lambda_s'(t)}\right) = \beta_s + \delta(t) + \varepsilon_s(t),$$

defining the synchronous and asynchronous random terms and deriving indices of synchrony as in section 3.1.2. For demonstration purposes, we analyse productivity for kittiwakes and shags using this approximated Poisson model. The point estimates (Figure 3-9) are practically identical to those obtained from the binomial model (Figure 3-4), as are the indices of synchrony ($I_{KIT} = 27.0\%$ vs. 28.7%, $I_{SHA} = 50.7\%$ vs. 51.4%, for Poisson and binomial respectively).

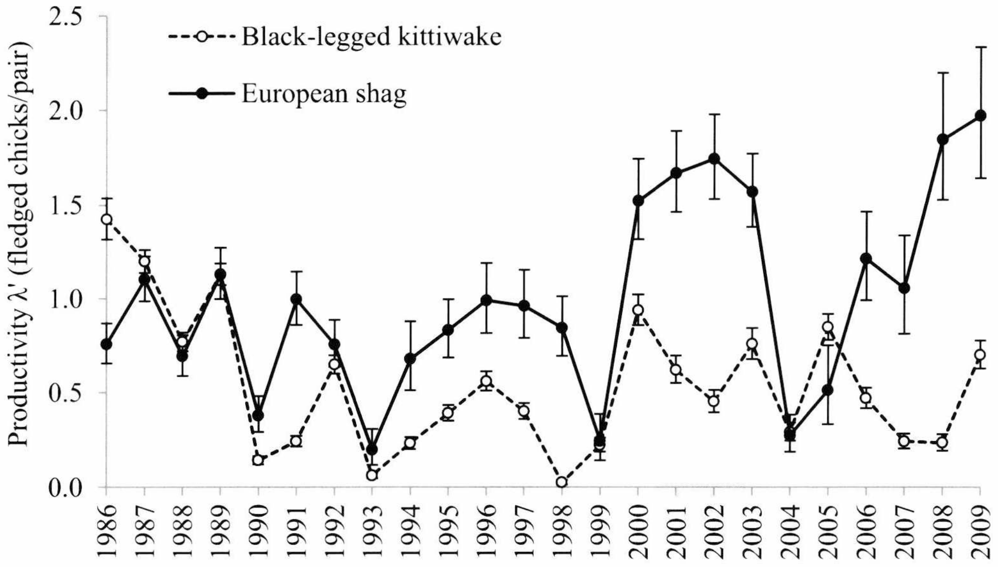


Figure 3-9 Kittiwake (white dots) and shag (black dots) productivity estimates and 95% credible intervals, with productivity λ_s' defined as average number of fledglings per breeding pair in the Poisson model. Note how λ_s' are far from their upper limit (maximum clutch sizes c_4=3 and c_5=4). Compare to Figure 3-4, where λ_s are derived from the binomial model.

3.2 Multi-species synchrony in components of productivity

3.2.1 Compartmental model

The models and results presented in section 3.1 are based on data restricted to the number of chicks fledging from the monitored breeding sites. However, in some cases information about intermediate stages of breeding may be available and thus multi-species synchrony can be estimated for components of productivity. There is a tradition of modelling "nest survival" based on the successive stages, including when not all nests are observed from nest construction through to fledging (Mayfield 1961; Heisey & Nordheim 1995).

The compartment model in Rockwell *et al.* (1993) can be adapted for our case study of the seabirds at the Isle of May. If we define fledglings as chicks that survive to leave the breeding site, synchrony can be estimated for any *transition probability* in the model, including egg survival, hatchability and chick survival (or compounds of these) depending on data availability on the different *state variables* (number of eggs laid, eggs at hatching, chicks hatched and fledglings, respectively).

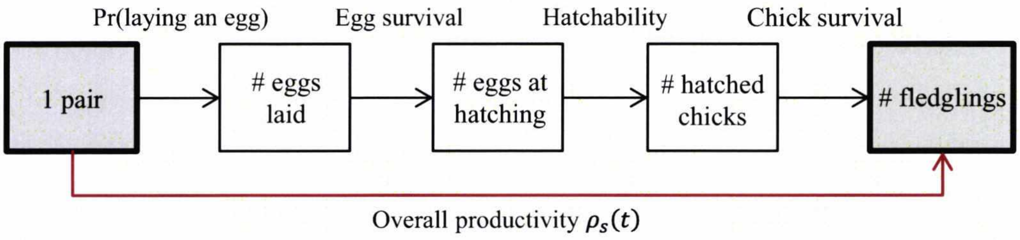


Figure 3-10 Block diagram of the different stages in the reproductive process, from the breeding pair to the number of fledglings, adapted from Rockwell *et al.*(1993) for the Isle of May seabird community. Overall productivity ρ encompasses all these stages. The greyed blocks represent the data in the overall productivity analysis (number of breeding pairs and number of fledglings).

3.2.2 *Components of productivity for guillemots and razorbills*

We illustrate the study of synchrony in components of productivity using a model to quantify synchrony for two particular components, defined for each species s and year t (Figure 3-11):

(i) hatchability $h_s(t)$, the probability of a chick hatching from a laid egg (note that this definition is different from that in Figure 3-10);

(ii) chick survival $f_s(t)$, the probability of a hatched chick surviving until fledging.

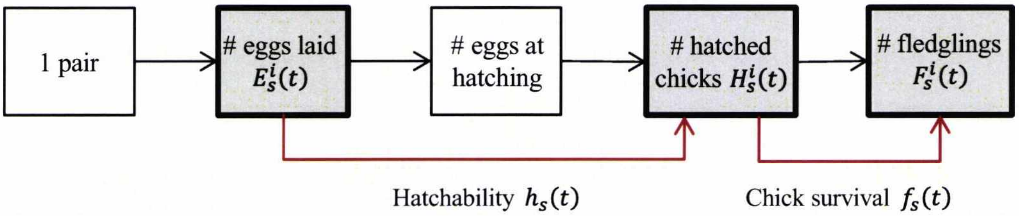


Figure 3-11 Block diagram of the different data sets (greyed blocks) and probabilities estimated (red arrows) in the study of synchrony in components of productivity for guillemots and razorbills at the Isle of May.

This partition of productivity is used for example in Tavecchia *et al.* (2008). The model can be modified easily for other stages of productivity. We apply the model to guillemots and razorbills at the Isle of May (1986-2009), for which we have appropriate data: eggs laid $E_s(t)$, hatched chicks $H_s(t)$ and fledglings $F_s(t)$. The number of laid eggs monitored varied from year to year, with minima/mean/maxima of 731/842/1014 for guillemots and 81/140/194 for razorbills. The total number of hatched and fledged chicks can be modelled as binomial variables

$$H_s(t) \sim \text{Bin}\big(E_s(t), h_s(t)\big),$$

$$F_s(t) \sim \text{Bin}\big(H_s(t), f_s(t)\big).$$

To estimate synchrony for both h and f, we again use logistic regressions with common (δ_h and δ_f) and species-specific (ε_{hs} and ε_{fs}) year random terms

$$\text{logit}\big(h_s(t)\big) = \beta_{hs} + \delta_h(t) + \varepsilon_{hs}(t),$$

$$\text{logit}\big(f_s(t)\big) = \beta_{fs} + \delta_f(t) + \varepsilon_{fs}(t),$$

where β_{hs} and β_{fs} are species-specific intercepts for h and f, and the year random terms are assumed independent and identically distributed as: $\delta_h(t) \sim \text{N}\big(0, \sigma_{\delta h}^2\big)$, $\delta_f(t) \sim \text{N}\big(0, \sigma_{\delta f}^2\big)$, $\varepsilon_{hs}(t) \sim \text{N}(0, \sigma_{hs}^2)$ and $\varepsilon_{fs}(t) \sim \text{N}\big(0, \sigma_{fs}^2\big)$. We define synchrony indices for h and f based on the estimated variances of the random terms

$$I_{hs} = \frac{\hat{\sigma}_{\delta h}^2}{\hat{\sigma}_{\delta h}^2 + \hat{\sigma}_{hs}^2} \quad \text{and} \quad I_{fs} = \frac{\hat{\sigma}_{\delta f}^2}{\hat{\sigma}_{\delta f}^2 + \hat{\sigma}_{fs}^2}.$$

The contribution of environmental covariates can be quantified by comparing these variances to the residual variances obtained from a model that includes covariates, as explained for overall productivity in section 3.1.2.

In the analysis we use uninformative uniform priors $\text{U}(-5,5)$ for the regression intercepts β_{hs} and β_{fs}, and $\text{U}(0,3)$ for SD of the random terms ($\sigma_{\delta h}, \sigma_{\delta f}, \sigma_{hs}$ and σ_{fs}). The Gelman–Rubin diagnostic suggests that a burn-in period of 250000 samples is sufficient to ensure convergence ($\hat{R} < 1.01$ for all parameters).

The results show that the variations in h are much more similar in the two species than those in f (Figure 3-12). Particularly notable is 2006-2007, when guillemot chick survival declines dramatically, while for razorbill it is only slightly lower than average. A comparison of this figure to Figure 3-2 indicates that the differences in overall productivity ρ are driven by chick survival, with hatchability playing a minor role.

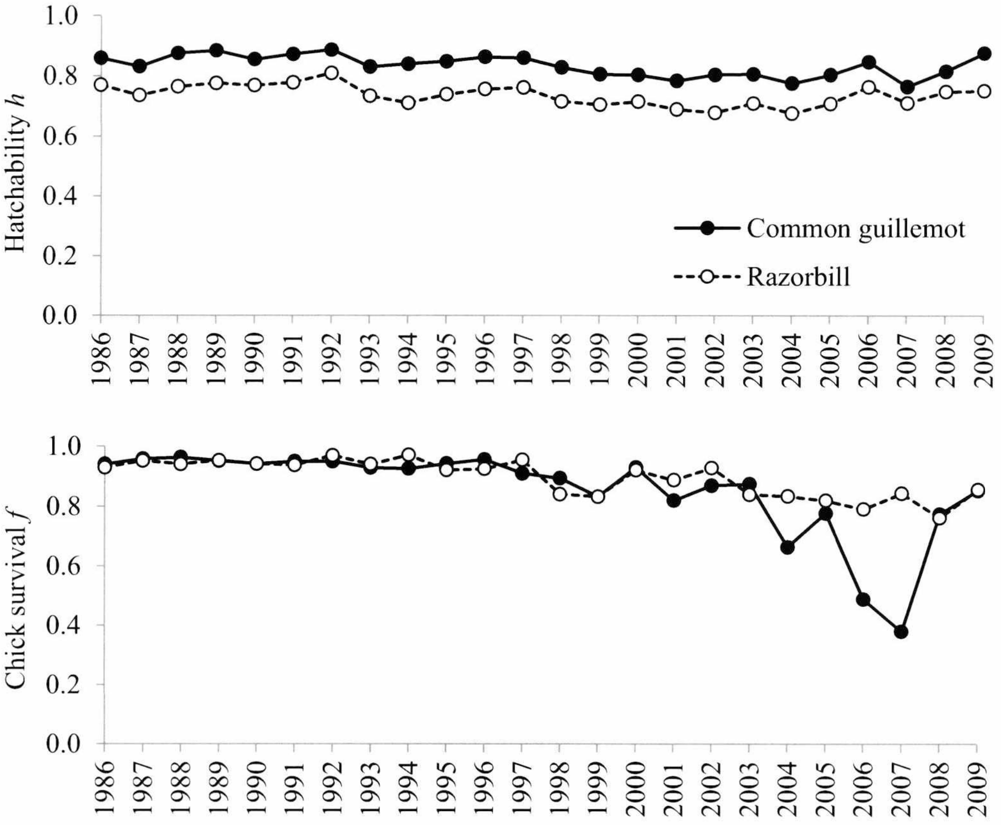


Figure 3-12 Estimates of the components of productivity (hatchability h and chick survival f) for common guillemots (black dots) and razorbills (white dots).

The estimated synchrony indices (median and limits of the 95% CI)

(i) $I_h = 0.612$ (0.132, 0.984) and $I_f = 0.509$ (0.213, 0.817) for guillemots,

(ii) $I_h = 0.874$ (0.280, 1.000) and $I_f = 0.888$ (0.410, 1.000) for razorbills, indicate that a large part of the razorbill year-to-year variation in both hatchability and chick survival is shared with guillemots, while for guillemots a larger part of the variation is species-specific; note nevertheless the large CIs. These results suggest that under the conditions that have operated over the last 24 years, the chick stage has been more sensitive than the egg stage to environmental variations (probably some aspect of food availability), with guillemots less well buffered than razorbills, resulting in the latter displaying larger variation, particularly at the chick stage.

Interestingly, we find statistically significant declines over time in the common terms of both hatchability and chick survival, stronger in f than in h (Figure 3-13).

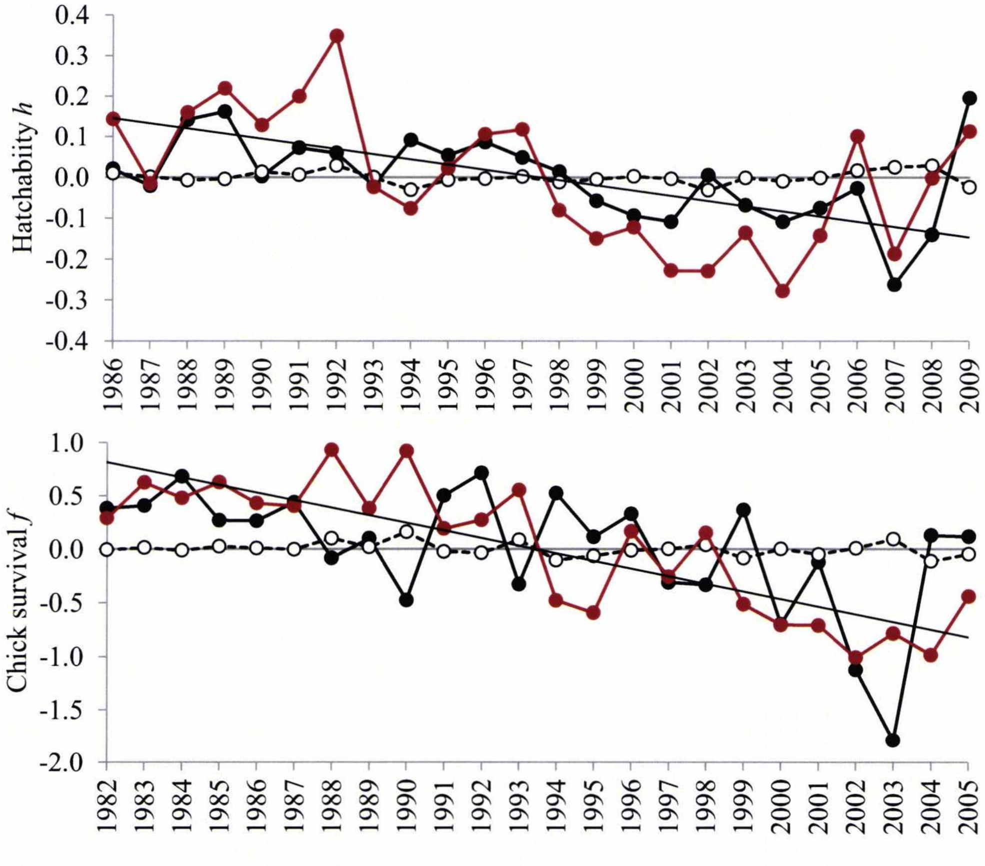


Figure 3-13 Common (δ, red line) and species-specific (ε_s, black solid line for guillemot and dashed line for razorbill) random terms estimated for hatchability h (top panel) and chick survival f (bottom panel). A linear temporal trend is fitted to the common terms ($R^2 = 0.296$ and 0.688 for h and f respectively, with p-values 0.006 and <0.001).

An interesting effect can be noticed when comparing the estimates of h and f obtained from independent species-specific and multi-species synchrony models (Figure 3-14). Despite the overall similarity, there is a slight smoothing of the series in the synchrony models, particularly for razorbills. This results from the property of shrinkage due to the random effects used in the synchrony model (Gelman *et al.* 2004) which pulls the species that contributes the least data (razorbills here, with almost a factor of 10 smaller data set than guillemots) towards the species 'mean'. Note that in our model this does not mean they tend towards each other (as species-specific intercepts may be different), but rather that the year-to-year variations tend to become similar. As in general razorbills show more variability (except for the 2004-2007 dip in guillemot f) and contribute less data, in practice this translates into razorbill variations being smoothed slightly, as observed in the figure.

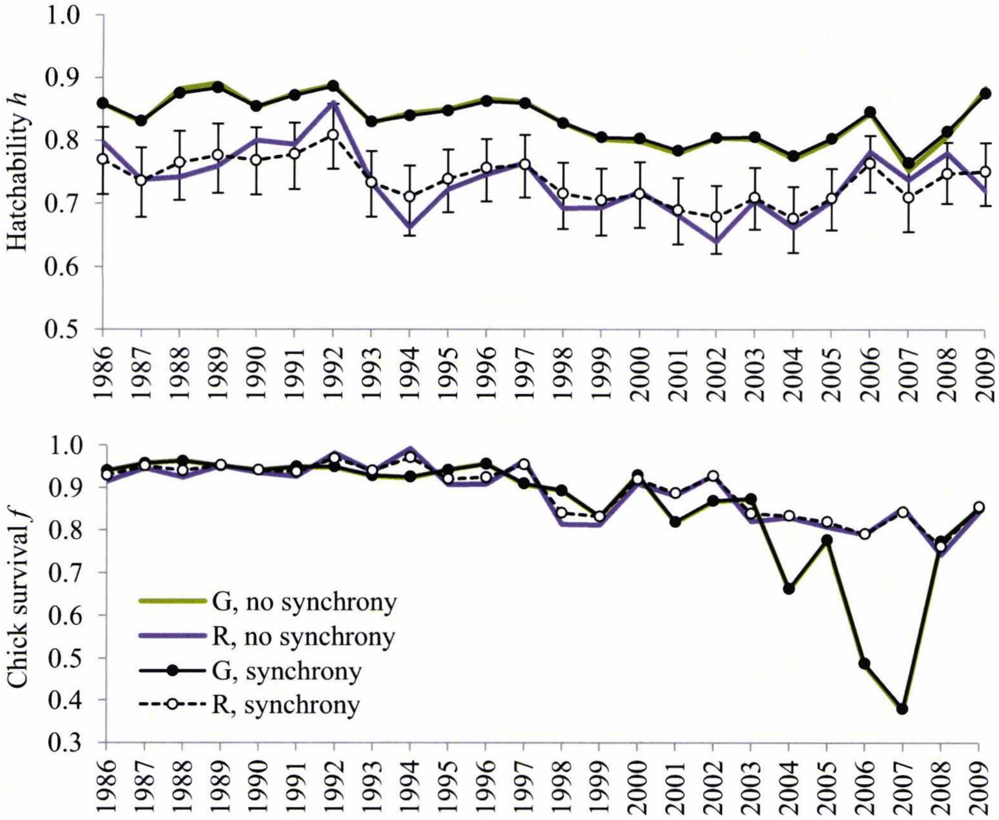


Figure 3-14 Comparison of the point estimates (median of marginal posterior distributions) of hatchability h and chick survival f from a model with random effects to estimate synchrony (black solid and dashed lines for guillemots 'G' and razorbills 'R' respectively), and model without random effects (green and purple lines for guillemots 'G' and razorbills 'R' respectively).

To study the contribution of environmental covariates to synchrony and asynchrony in h and f, we repeat the analysis, now incorporating the same environmental covariates used for the 5-species overall productivity analysis: wNAO and SST (including 1 and 2 year time-lags), and the presence of the sandeel fishery. We find no significant covariates for hatchability h (i.e. zero not included in their 95% CI). For chick survival f, wNAO_0 is significant for razorbill ($\beta_{f(wNAO)} = 0.302\ (0.062, 0.577)$) and SST_2 for guillemot ($\beta_{f(SST2)} = -0.413\ (-0.824, -0.011)$). These covariates coincide with the ones found significant for these species for overall productivity ρ, including their sign.

The comparison of the total variances of the random terms obtained from the model without covariates to the residual variances from the model with environmental covariates, indicates that these make a large contribution to synchrony in chick survival f ($C_{f\delta} = 0.855$), a medium contribution to asynchrony in razorbills ($C_{fR} = 0.435$) and a low contribution to asynchrony in guillemots ($C_{fM} = 0.095$; possibly because none of the covariates properly explains the drop in 2006-07). We do not assess the contribution to synchronising hatchability, given the lack of significant covariates. Overall, the relationship of overall productivity with these covariates appears to be driven primarily by chick survival.

3.2.3 *Simulation study*

We use simulations to verify that the framework proposed for studying synchrony in components of productivity is able to recover the parameters of interest (Gimenez *et al.* 2004). We simulate and analyse data for two different components of productivity (Figure 3-15):

(i) probability of laying an egg γ (out of the maximum clutch size possible),

(ii) combined hatching-fledging success ϕ (probability of an egg surviving until fledging, a combination of hatchability h and chick survival f).

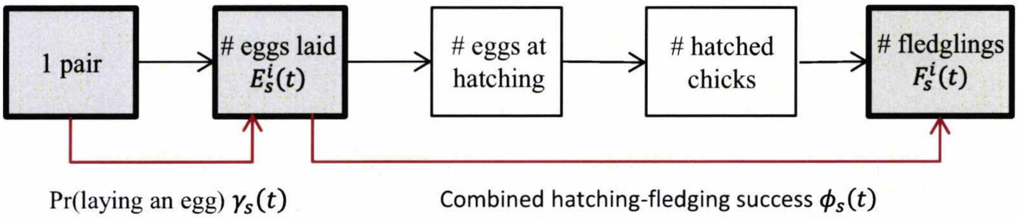


Figure 3-15 Block diagram of the different data sets (greyed blocks) and probabilities estimated (red arrows) in the study of synchrony in components of productivity for simulated data.

These productivity components are a partition of the overall productivity ρ defined in section 3.1, i.e. $\rho_s(t) = \gamma_s(t)\phi_s(t)$. Apart from knowing the number of monitored breeding pairs $K_s(t)$ and the total number of fledglings $F_s(t)$, the extra information required for this model is the total number of eggs $E_s(t)$ laid at the monitored nests.

Using the probabilities defined above and given species-specific maximum clutch sizes c_s, we model both the number of eggs and fledglings as binomial variables:

$$E_s(t) \sim \mathrm{Bin}\big(c_s K_s(t), \gamma_s(t)\big),$$

$$F_s(t) \sim \mathrm{Bin}\big(E_s(t), \phi_s(t)\big).$$

To estimate synchronies, we express the probabilities as logistic regressions with common and species-specific year random terms

$$\mathrm{logit}\big(\gamma_S(t)\big) = \beta_{\gamma S} + \delta_\gamma(t) + \varepsilon_{\gamma S}(t),$$

$$\mathrm{logit}\big(\phi_S(t)\big) = \beta_{\phi S} + \delta_\phi(t) + \varepsilon_{\phi S}(t),$$

and define species-specific synchrony indices for γ and ϕ as a function of the estimated random effects variances

$$I_{\gamma s} = \frac{\hat{\sigma}_{\delta\gamma}^2}{\hat{\sigma}_{\delta\gamma}^2 + \hat{\sigma}_{\gamma s}^2} \quad \text{and} \quad I_{\phi s} = \frac{\hat{\sigma}_{\delta\phi}^2}{\hat{\sigma}_{\delta\phi}^2 + \hat{\sigma}_{\phi s}^2}.$$

We simulate a data set consisting of 25 years monitoring of three sympatric species in a hypothetical breeding community, with maximum clutch sizes of 3, 4 and 5 eggs respectively. Data consist of the numbers of eggs $E_s(t)$ and numbers of chicks fledged $F_s(t)$ from $K_s(t) = 1000$ nests monitored per year. We choose synchronous and asynchronous variances to create low synchrony in γ but high synchrony in ϕ (Table 3-3), representing an ecologically realistic scenario where species adjust clutch size according to overwintering conditions that differ between species, but have a synchronised success in fledging chicks given a dependency on common resources.

Table 3-3 Values of the parameters (intercepts and variances of the random terms for both γ and ϕ) used to simulate a data set of numbers of eggs and fledged chicks, and resulting indices of synchrony.

	Species 1	Species 2	Species 3	common
Intercept $\beta_{\gamma s}$	0.1	0.2	0.12	NA
Variance $\sigma^2_{\gamma s}$	0.4	0.3	0.5	0.05
Index $I_{\gamma s}$	0.111	0.143	0.091	NA
Intercept $\beta_{\phi s}$	1.6	1.1	1.2	NA
Variance $\sigma^2_{\phi s}$	0.2	0.25	0.1	0.8
Index $I_{\phi s}$	0.800	0.762	0.888	NA

The simulated data set can be seen in Table 3-4. For the analysis in JAGS, a convergence assessment using the Gelman-Rubin statistic suggests that the burn-in period of 500000 samples is sufficient to ensure convergence ($\hat{R} \leq 1.03$ for all parameters). We obtain very precise estimates of the components of productivity $\gamma_s(t)$ and $\phi_s(t)$, with the absolute value of the error below 0.04, which is expected given the large amount of data. The model is also able to separate the random terms of these two components: 95% CI of all intercepts, random effects variances and synchrony indices include the true value (Figure 3-16).

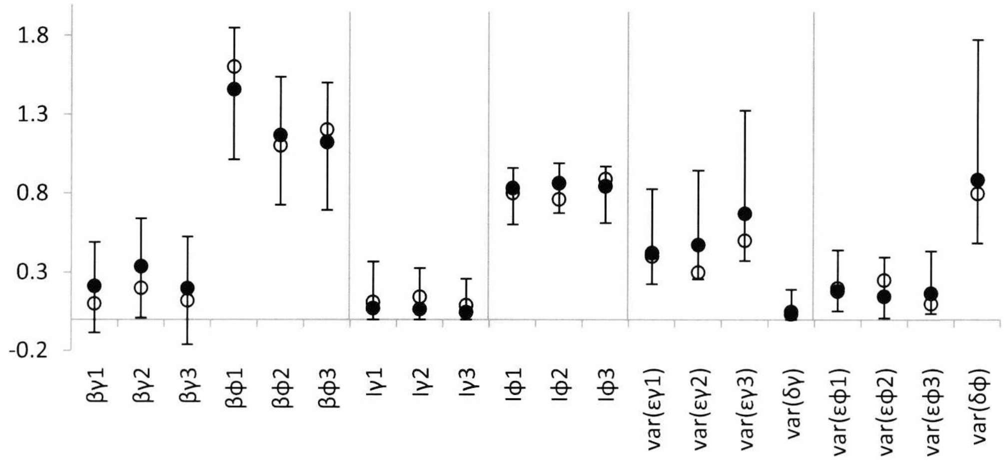


Figure 3-16 True (solid circles) and estimated (open circles) values and 95% CI for: regression intercepts (β), synchrony indices (I_S) and random effect variances for the three species and parameters: probability of laying an egg (γ) and hatching-fledging success (ϕ).

We conclude the simulation study with a test regarding the identifiability of the parameters of interest when the total number of eggs is not recorded (akin to our Isle of May 5-species breeding success data set). As expected, the model is not able to estimate the missing data (a hidden parameter in this model) or the components of productivity, obviously rendering the study of synchrony impossible. The parameters γ and ϕ are confounded: the model cannot distinguish whether an increase in fledglings is due to a larger clutch, a better fledging success or a combination of both. For each year and each species, only the product $\gamma_s(t)\phi_s(t)$ is estimable.

3.3 Multi-species synchrony in clutch size underdispersion

We have so far considered breeding success data consisting of total counts of different (at least two) stages of productivity. In some cases of intensive monitoring, more detailed data may be collected on breeding success of particular species. In this section we deal with the particular case where the number of eggs laid by each monitored pair is recorded, which contributes information about the distribution of clutch sizes for each year. The study of clutch size in birds has a long history in ecological and evolutionary biology (Moreau 1944). The relationship of clutch size to a species' traits, environment and ecology is still a source of investigations (Jetz, Sekercioglu & Boehning-Gaese 2008). Less attention has been paid to intraspecific variation in clutch size. In general, there is little variability in the size of clutches for a given species, so that it appears underdispersed compared to e.g. a Poisson distribution (Ridout & Besbeas 2004). In more extreme cases, some bird species lay a fixed number of eggs (for instance obligate single-egg breeders, like the auks in our study), or may lay k or $k+1$ eggs for some appropriate integer k (Heyde & Schuh 1978). We consider here an underdispersed distribution to model clutch size, and explain how to quantify multi-species synchrony in both the mean clutch size and the amount of underdispersion, when clutch size data are collected for several sympatric species.

Table 3-4 Simulated data set of eggs laid (E) and fledglings (F), for species 1, 2 and 3 species and 25 years, with $K = 1000$ monitored nests per species per year.

	Eggs			Fledglings		
year	E1	E2	E3	F1	F2	F3
1	2129	1812	1632	1556	1089	1009
2	2181	2642	1906	1438	1129	965
3	1115	1087	2387	754	645	1521
4	1855	1780	2707	1114	894	2008
5	1268	2305	2599	848	1615	1557
6	1737	2683	3465	1557	2096	2764
7	1003	1690	2822	526	893	1345
8	1128	2411	2939	1013	2000	2274
9	1785	2797	4414	1587	2135	2996
10	737	3212	2654	622	2701	2266
11	1962	1323	2856	1834	1113	2594
12	2184	2817	3968	1855	2386	3299
13	1315	2659	2672	993	1724	1712
14	2199	2730	2772	2022	2493	2563
15	913	3097	1829	234	1632	573
16	1499	2196	1598	621	1037	588
17	1446	1366	2725	1292	1237	1859
18	1950	2121	3601	1918	1999	3473
19	1935	1943	4520	1272	1358	3475
20	1461	3420	2525	1180	2729	2038
21	1680	2010	3016	1597	1802	2812
22	1298	2300	2236	925	1828	1279
23	1993	2287	1262	1724	1984	989
24	2256	2973	2733	1944	2261	2336
25	2135	1859	1354	1953	1575	1207

3.3.1 *Exponentially weighted Poisson model (EWP)*

Ridout & Besbeas (2004) propose a 3-parameter exponentially weighted Poisson distribution (EWP3) which they fit to clutch-size data. According to this model, letting λ be the average clutch size, the probability of clutch size k in a nest taking value x is

$$\Pr(k = x) = \frac{e^{-\lambda}\lambda^{x}}{x!} \cdot \frac{w_x}{W}, \qquad x \geq 0, \lambda > 0$$

where w_x is an exponential weight function of two underdispersion parameters β_1 and β_2

$$w_x = \begin{cases} e^{-\beta_1(\lambda - x)} & if\ x \leq \lambda \\ e^{-\beta_2(x-\lambda)} & if\ x > \lambda \end{cases} \tag{3.8}$$

and the normalizing factor is

$$W = \sum_{x=0}^{\infty} \frac{e^{-\lambda}\lambda^{x} w_x}{x!}. \tag{3.9}$$

The resulting distribution is underdispersed compared to the Poisson if $\beta_1, \beta_2 > 0$. The model can be simplified by setting $\beta_1 = \beta_2$, which gives a 2-parameter exponentially weighted Poisson distribution (EWP2). In that case, the exponential weight function can be written using the absolute value of $(\lambda - x)$,

$$w_x = e^{-\beta|\lambda - x|} \tag{3.10}$$

This expression does not incorporate a condition and is therefore easier to implement in programs like WinBUGS/JAGS than (3.8).

Clutch sizes in a data set may have minimum value different from zero (e.g. when only pairs that laid at least one egg are monitored), and they will typically have a maximum value (maximum clutch size), characteristic of the species. In such cases, the normalizing factor W can be modified to take this into account, giving a truncated EWP (TEWP) distribution, although the truncation may have a relatively small effect under strong underdispersion. Given minimum and maximum clutch sizes *a* and *b*, the normalizing factor (3.9) becomes

$$W_T = \sum_{x=a}^{b} \frac{e^{-\lambda}\lambda^x w_x}{x!}.$$

3.3.2 *Synchrony in mean clutch size and underdispersion*

The distribution of clutch sizes may vary from year to year according to intrinsic or extrinsic conditions. When clutch size data are available for a series of years and for a set of species (as we will see in the next section, this is the case at the Isle of May for kittiwakes and shags) synchrony in the year-to-year variations can be studied for both mean clutch size λ and amount of underdispersion β. Assuming for simplicity that $\beta_1 = \beta_2$, for each species *s* and year *t*, clutch size of nest *i* will be distributed

$$k_s^i(t) \sim \mathrm{TEWP2}\big(\lambda_s(t), \beta_s(t)\big).$$

Mean and underdispersion can then be modelled with common and species-specific random effects terms, in the same way as for other demographic parameters, using appropriate link functions $f_{\lambda s}(x)$ and $f_{\beta s}(x)$

$$f_{\lambda s}\big(\lambda_s(t)\big) = \alpha_{\lambda s} + \delta_\lambda(t) + \varepsilon_{\lambda s}(t),$$

$$f_{\beta s}\big(\beta_s(t)\big) = \alpha_{\beta s} + \delta_\beta(t) + \varepsilon_{\beta s}(t),$$

where all random terms $\delta_\lambda(t)$, $\delta_\beta(t)$, $\varepsilon_{\lambda s}(t)$ and $\varepsilon_{\beta s}(t)$ are assumed independent and identically distributed for all s and t with normal distributions. Multi-species synchrony coefficients can be defined for each species, separately for each parameter (here λ and β), using the estimated variances of the corresponding random terms

$$I_{\lambda s} = \frac{\hat{\sigma}^2_{\delta\lambda}}{\hat{\sigma}^2_{\delta\lambda} + \hat{\sigma}^2_{\lambda s}} \quad \text{and} \quad I_{\beta s} = \frac{\hat{\sigma}^2_{\delta\beta}}{\hat{\sigma}^2_{\delta\beta} + \hat{\sigma}^2_{\beta s}}.$$

3.3.3 *Data set*

For the Isle of May seabird community, detailed clutch size data (counts of monitored nests with different clutch sizes) have been collected for shags (years 1997-2011, except 2000, 2003 and 2004) and kittiwakes (years 1992-2011) in a subset of the monitored nests. In order to study synchrony between the two species, only the years in common between both data sets (12 in total) are retained for this analysis: 1997-1999, 2001-2002, 2005-2011 (Table 3-5). As mentioned in section 2.2.2, the fact that these years are not consecutive is not an issue because we define synchrony on the variation over the species' baseline, not with respect to the previous year's value.

Table 3-5 Data of kittiwake and shag clutch sizes for the different years at the Isle of May, including the total number of nests monitored.

	Kittiwakes						Shags					
Year	0	1	2	3	4	#nests	1	2	3	4	5	#nests
1997	2	16	91	25	0	134	2	11	110	12	1	136
1998	51	55	169	5	0	280	0	33	151	13	0	197
1999	2	0	23	0	0	25	0	11	38	2	0	51
2001	0	11	57	6	0	74	0	21	159	8	0	188
2002	15	27	167	27	0	236	0	17	164	10	0	191
2005	21	59	287	1	0	368	8	31	68	0	0	107
2006	39	86	227	1	0	353	5	40	164	6	1	216
2007	23	40	236	21	0	320	10	49	170	10	0	239
2008	27	50	302	5	0	384	4	17	107	1	0	129
2009	21	81	198	3	0	303	1	10	137	3	0	151
2010	28	35	288	157	1	509	0	31	195	38	2	266
2011	16	37	203	84	0	340	6	28	219	26	1	280

There is only one kittiwake nest (out of 3326, 0.03%) with four eggs, and five shag nests (out of 2151, 0.23%) with five eggs, so we did not model these uncommon categories. Note also that we do not have data for shag nests with no eggs. This is due to historical reasons of how the monitoring of that species is conducted, but in any case clutch sizes of zero eggs are rare in shags (F. Daunt, *personal communication*). Therefore, kittiwake clutch sizes are modelled from zero to three eggs, and shag clutch sizes from one to four eggs. The distribution of clutch sizes shows evidence of underdispersion compared to a Poisson or binomial distributions for both species (Figure 3-17).

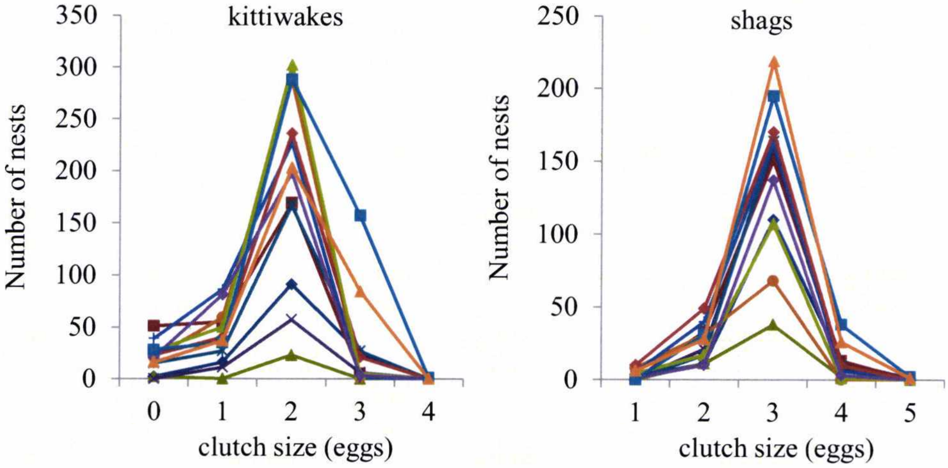


Figure 3-17 Clutch size distribution for different years, for kittiwakes and shags at the Isle of May. Colours denote different years.

As a quantitative example, we fit the kittiwake clutch size data of year 2011 to a binomial, truncated Poisson, truncated Poisson and TEWP2 distributions (Figure 3-18).

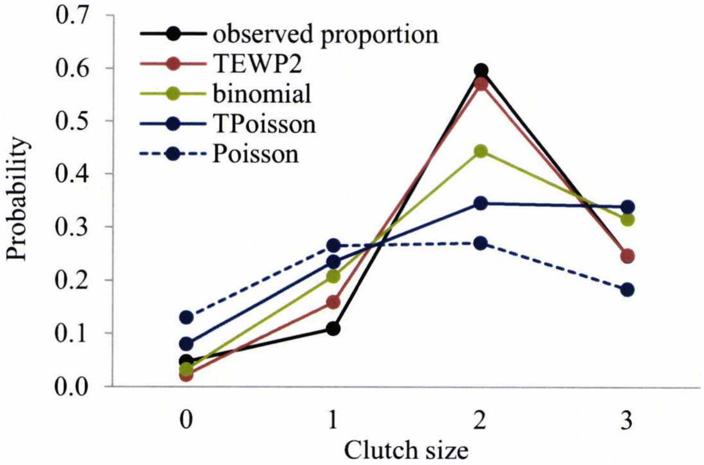


Figure 3-18 Probabilities of each clutch size for kittiwakes in year 2011, based on the estimates obtained from analysing the number of nests of each clutch size with a) TEWP2 distribution (red), b) a binomial distribution with n=3 trials (green), c) a truncated Poisson distribution (solid blue) and d) a Poisson distribution (dotted blue). The observed proportions (number of nests of each clutch size divided by the total number of nests) are shown in black. Note that the Poisson distribution has mass outside the range of clutch sizes considered, so that the sum of the probabilities in the 0-3 range is only 0.85. Estimates under the different models obtained in JAGS using 20000 MCMC iterations after a burn-in of 10000.

We choose to model $\beta_1 = \beta_2$, and consequently use (3.10), for implementation simplicity. The underdispersion and the better fit of the TEWP2 distribution can be clearly observed when the probabilities of the different clutch sizes under the different models are compared to the observed frequencies.

3.3.4 Implementation issues

The TEWP2 distribution is not one of the standard distributions found in software programs WinBUGS or JAGS, so it has to be coded manually. This is done using the so-called 'zeros' trick (Spiegelhalter *et al.* 2003) to specify the contribution of each sample in the data to the likelihood. Let L_i be the term that each observation x_i contributes to the likelihood. We use a new variable y with all observations $y_i = 0$. We declare $y_i \sim \text{Pois}(\phi_i)$, where $\phi_i = -\log(L_i) + C$, and C is a constant defined to ensure that all ϕ_i terms are positive. As the value of y is always zero, the contribution of each 'Poisson-distributed' observation y_i to the likelihood in the WinBUGS program will be: $e^{-\phi_i} = e^{\log(L_i)-C} = k \cdot L_i$, that is, proportional to the likelihood of the original data x_i. This is a 'trick' in the sense that it uses a distribution that exists in WinBUGS/JAGS to create a tailored likelihood expression, instead of for creating a real Poisson model. The method can be applied to each sample in the data set (one by one iteratively), or lumped series of data samples, if their combined contribution to the likelihood is more convenient to write. As an example, we show here the WinBUGS/JAGS code for the 'zeros trick' for a data set consisting of `N` samples, each contributing a factor `LX[i]` to the log likelihood:

```
C <- 1000  # constant for the zeros trick
for (i in 1:N){
    # log-likelihood contribution of data sample i
    LL[i] <- LX[i]
    # 'zeros trick'
    zeros[i]<-0
    phi[i] <- -LL[i]+C
    zeros[i] ~ dpois(phi[i])
}
```

The contribution to the likelihood of each observation x_i from a TEWP2 distribution, truncated between values *a* and *b* ($a \leq x_i \leq b$), is

$$L(x_i|\lambda,\beta) = \frac{e^{-\lambda}\lambda^{x_i}}{x_i!} \cdot \frac{w_{x_i}}{W} = \frac{e^{-\lambda}\lambda^{x_i}}{x_i!} \cdot \frac{e^{-\beta|\lambda-x_i|}}{\sum_{j=a}^{b} \frac{e^{-\lambda}\lambda^j e^{-\beta|\lambda-j|}}{j!}} = \frac{\lambda^{x_i}}{x_i!} \cdot \frac{e^{-\beta|\lambda-x_i|}}{\sum_{j=a}^{b} \frac{\lambda^j e^{-\beta|\lambda-j|}}{j!}}.$$

In terms of log-likelihood

$$\mathcal{L}(x_i|\lambda,\beta) = x_i \log(\lambda) - \log(x_i!) - \beta|\lambda - x_i| - \log\left(\sum_{j=a}^{b} \frac{\lambda^j e^{-\beta|\lambda-j|}}{j!}\right).$$

The WinBUGS/JAGS function *logfact(x)* can be used to implement $\log(x_i!)$ efficiently. For our data sets, the previous expression becomes

(i) for shags ($1 \leq x_i \leq 4$):

$$\mathcal{L}_S(x_i|\lambda,\beta) = x_i \log(\lambda) - \log(x_i!) - \beta|\lambda - x_i| \\ - \log\left(\lambda e^{-\beta|\lambda-1|} + \frac{\lambda^2}{2} e^{-\beta|\lambda-2|} + \frac{\lambda^3}{6} e^{-\beta|\lambda-3|} + \frac{\lambda^4}{24} e^{-\beta|\lambda-4|}\right),$$

(ii) for kittiwakes ($0 \leq x_i \leq 3$):

$$\mathcal{L}_K(x_i|\lambda,\beta) = x_i \log(\lambda) - \log(x_i!) - \beta|\lambda - x_i| \\ - \log\left(e^{-\beta\lambda} + \lambda e^{-\beta|\lambda-1|} + \frac{\lambda^2}{2} e^{-\beta|\lambda-2|} + \frac{\lambda^3}{6} e^{-\beta|\lambda-3|}\right),$$

where we drop species and year subscripts for simplicity, i.e. $\lambda \equiv \lambda_s(t), \beta \equiv \beta_s(t)$.

These expressions could be used for the 'zeros' trick if using each nest count one by one. For improved efficiency, we model the summaries (counts of number of nests of each clutch size) so that if $n_s^c(t)$ is the number of nests of species *s* with clutch size *c* in year *t*, the full log-likelihood of the complete data set $H_s(t)$ for each species s and year *t* can be written as

(i) for shags ($1 \leq x_i \leq 4$):

$$\begin{aligned}
&\mathcal{L}_S\big(H_S(t)\big|\lambda_S(t),\beta_S(t)\big) \\
&\qquad = n_S^1(t)\big\{\log\big(\lambda_S(t)\big) - \beta_S(t)|\lambda_S(t)-1| - Z_S(t)\big\} \\
&\qquad + n_S^2(t)\big\{2\log\big(\lambda_S(t)\big) - \log(2) - \beta_S(t)|\lambda_S(t)-2| - Z_S(t)\big\} \\
&\qquad + n_S^3(t)\big\{3\log\big(\lambda_S(t)\big) - \log(6) - \beta_S(t)|\lambda_S(t)-3| - Z_S(t)\big\} \\
&\qquad + n_S^4(t)\big\{4\log\big(\lambda_S(t)\big) - \log(24) - \beta_S(t)|\lambda_S(t)-4| - Z_S(t)\big\},
\end{aligned}$$

where

$$\begin{aligned}
Z_S(t) = \log\Bigg\{&\lambda_S(t)e^{-\beta_S(t)|\lambda_S(t)-1|} + \frac{\lambda_S(t)^2}{2}e^{-\beta_S(t)|\lambda_S(t)-2|} \\
&+ \frac{\lambda_S(t)^3}{6}e^{-\beta_S(t)|\lambda_S(t)-3|} + \frac{\lambda_S(t)^4}{24}e^{-\beta_S(t)|\lambda_S(t)-4|}\Bigg\};
\end{aligned}$$

(ii) for kittiwakes ($0 \leq x_i \leq 3$):

$$\begin{aligned}
&\mathcal{L}_K\big(H_K(t)\big|\lambda_K(t),\beta_K(t)\big) \\
&\qquad = n_K^0(t)\{-\beta_K(t)\lambda_K(t) - Z_K(t)\} \\
&\qquad + n_K^1(t)\big\{\log\big(\lambda_K(t)\big) - \beta_K(t)|\lambda_K(t)-1| - Z_K(t)\big\} \\
&\qquad + n_K^2(t)\big\{2\log\big(\lambda_K(t)\big) - \log(2) - \beta_K(t)|\lambda_K(t)-2| - Z_K(t)\big\} \\
&\qquad + n_K^3(t)\big\{3\log\big(\lambda_K(t)\big) - \log(6) - \beta_K(t)|\lambda_K(t)-3| - Z_K(t)\big\},
\end{aligned}$$

where

$$\begin{aligned}
Z_K(t) = \log\Bigg\{&e^{-\beta_K(t)\lambda_K(t)} + \lambda_K(t)e^{-\beta_K(t)|\lambda_K(t)-1|} \\
&+ \frac{\lambda_K(t)^2}{2}e^{-\beta_K(t)|\lambda_K(t)-2|} + \frac{\lambda_K(t)^3}{6}e^{-\beta_K(t)|\lambda_K(t)-3|}\Bigg\}.
\end{aligned}$$

The choice of link functions for the regression of λ and β with the random terms depends on the range of values we expect possible for these parameters. The mean clutch size λ lies within the range of possible clutch sizes, and we expect $\beta > 0$ (which represents underdispersion; negative values would mean overdispersion). We do not expect values of $\beta > 6$, which represents extreme underdispersion (almost all nests having the same number of eggs). Accordingly, we select link functions so that

$\lambda_s(t)\epsilon[0,4]$ and $\beta_s(t)\epsilon[0,6]$. We use the 'generalised logit', so that if a variable θ can take values between *a* and *b*

$$\log\left(\frac{\theta - a}{b - \theta}\right) = X \quad \to \theta = \frac{a + be^X}{1 + e^X}.$$

When applied to the case of kittiwakes and shags, the regressions with common and species-specific random terms are, for species *s* and year *t*

$$\log\left(\frac{\beta_s(t)}{6 - \beta_s(t)}\right) = a_{\beta s} + \delta_\beta(t) + \varepsilon_{\beta s}(t),$$

$$\log\left(\frac{\lambda_s(t)}{4 - \lambda_s(t)}\right) = a_{\lambda s} + \delta_\lambda(t) + \varepsilon_{\lambda s}(t),$$

where $a_{\beta s}$ and $a_{\lambda s}$ are species-specific intercepts and

$$\delta_\beta(t) \sim N(0, \sigma_{\delta\beta}^2), \quad \delta_\lambda(t) \sim N(0, \sigma_{\delta\lambda}^2),$$

$$\varepsilon_{\beta s}(t) \sim N(0, \sigma_{\beta s}^2), \quad \varepsilon_{\lambda s}(t) \sim N(0, \sigma_{\lambda s}^2).$$

3.3.5 Results

The analysis of the shag and kittiwake clutch size data is carried out in JAGS v2.2.0 (Plummer 2003) using the model described above, setting uninformative uniform priors to the random-effect standard deviations and intercepts. We run the MCMC chains for 1 million iterations (keeping 1 out of 10 samples to reduce memory requirements) after a discarded burn-in of 1 million iterations. The JAGS analysis takes about 1.5 hours on a 3.4 GHz desktop. Convergence is assessed using the Gelman-Rubin statistic (Gelman & Rubin 1992) using the R package CODA (Plummer *et al.* 2006) based on 2 overdispersed chains for all variables. No evidence of lack of convergence is observed after 1 million iterations (all $\hat{R} \leq 1.01$ for all estimated parameters).

Figure 3-19 shows the estimates (with 95% CI) of mean clutch size λ and underdispersion parameter β for shags and kittiwakes for the different years. The estimates of λ are much more precise than those of β.

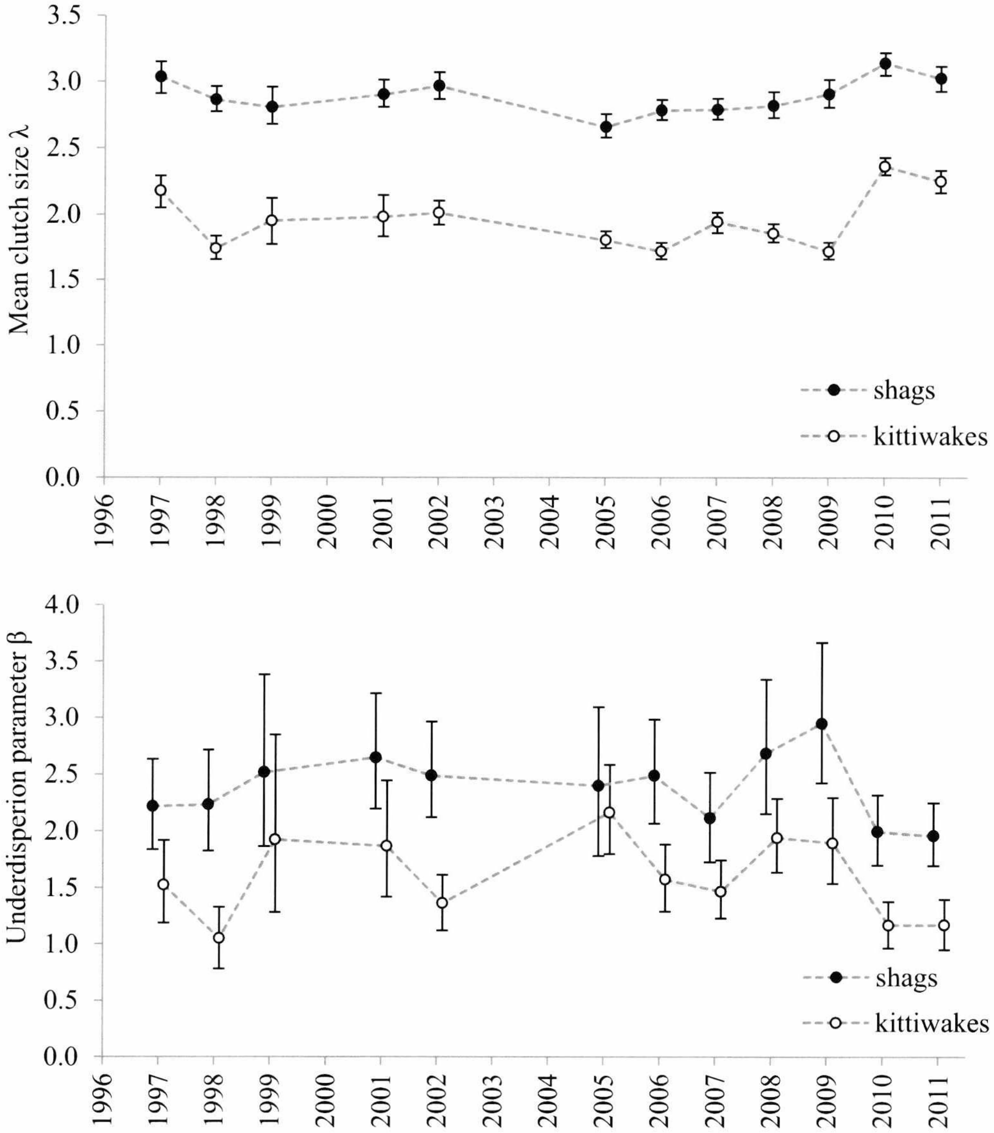


Figure 3-19 Estimates (with 95% CI) of mean clutch size λ (top panel) and underdispersion parameter β (bottom panel) for shags (black dots) and kittiwakes (white dots) for the different years. Note the different scales and that not all estimated years are consecutive.

The estimated variances are shown in Table 3-6, together with the corresponding multi-species indices of synchrony in both λ and β. The year-to-year variation in shag mean clutch size is mostly common ($I_{\lambda S} = 0.860$) with that of kittiwakes, while kittiwakes have slightly higher species-specific variation ($I_{\lambda K} = 0.642$). The values are slightly lower for underdispersion, which is mostly synchronous for shags ($I_{\beta S} = 0.728$), but less so for kittiwakes ($I_{\beta K} = 0.418$). Note nevertheless that the estimates are very imprecise, which could be related to the fact that we only model 12 years, compared for instance to the 24 years in the studies of synchrony in productivity (section 3.1) and the 25 years in the case of adult survival (Chapter 2). With fewer years to estimate the variance of the random terms, the estimation of synchrony indices becomes less precise.

Table 3-6 Estimated variances and indices of synchrony for mean clutch size λ and underdispersion parameter β (with 95% CI) for shags ('S') and kittiwakes ('K').

Parameter	Variance of random terms	Species-specific index of synchrony
λ	$\hat{\sigma}^2_{\lambda S} = 0.006\ (0.000, 0.048)$	$I_{\lambda S} = 0.860\ (0.219, 1.000)$
	$\hat{\sigma}^2_{\lambda K} = 0.019\ (0.001, 0.079)$	$I_{\lambda K} = 0.642\ (0.130, 0.989)$
	$\hat{\sigma}^2_{\delta\lambda} = 0.034\ (0.007, 0.112)$	
β	$\hat{\sigma}^2_{\beta S} = 0.023\ (0.000, 0.205)$	$I_{\beta S} = 0.728\ (0.011, 0.999)$
	$\hat{\sigma}^2_{\beta K} = 0.080\ (0.001, 0.370)$	$I_{\beta K} = 0.418\ (0.005, 0.992)$
	$\hat{\sigma}^2_{\delta\beta} = 0.057\ (0.001, 0.266)$	

We conduct an exploratory investigation of the relationship of each estimated variable with environmental covariates, using correlation of the point estimates (medians) obtained in the previous analysis. Note that the uncertainty of the estimates is not taken into account in this simple exploration and that some of the estimates have relatively wide credible intervals, particularly those of the underdispersion parameters.

In accordance with the substantial amount of common variance, there is a significant amount of interspecies correlation in both β and λ, which is positive for both variables (Figure 3-20, top panels). By contrast, there is no clear statistical evidence of intraspecific correlation between β and λ in either species, although higher values of λ are in general related to low values of β, that is, more spread in clutch sizes.

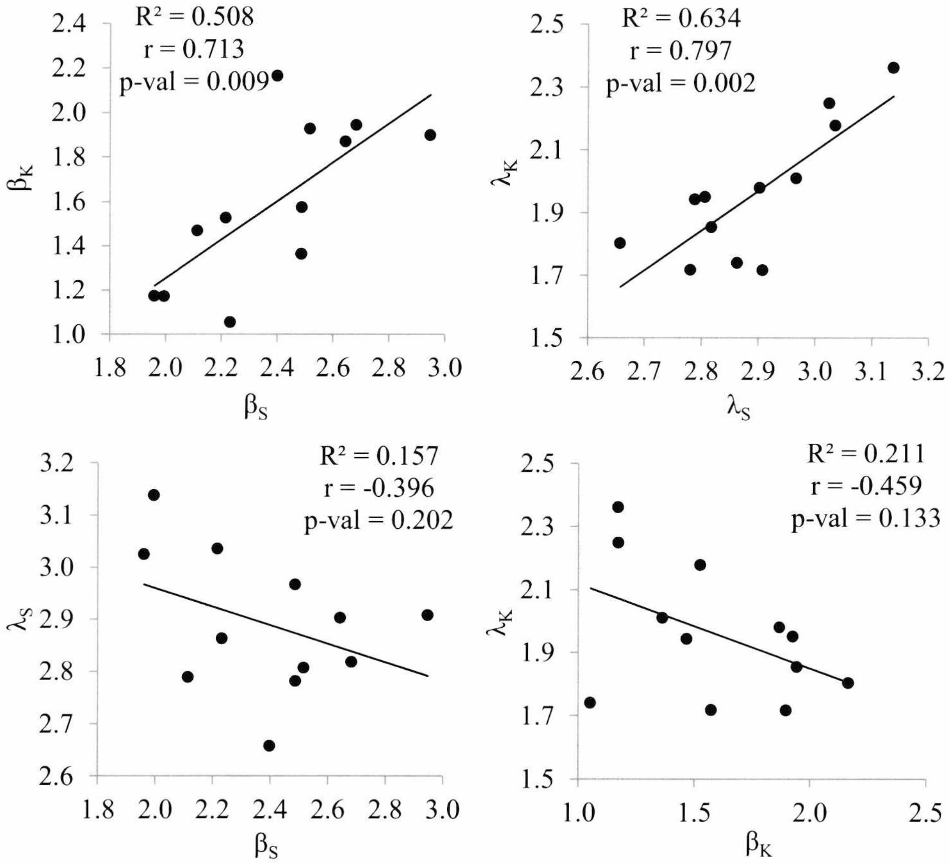


Figure 3-20 Scatterplots of different combinations of mean clutch size λ and underdispersion parameter β for shags (left panel) and kittiwakes (right panel). Pearson's correlation coefficient r and associated p-value (2-tailed), as well as the linear regression line and regression coefficient R^2 are also shown for each panel.

Interestingly, no statistical evidence of correlation is apparent between the estimates of mean clutch size and overall productivity (Figure 3-21) for either species; some statistical evidence indicates nevertheless some degree of correlation with the underdispersion parameter β.

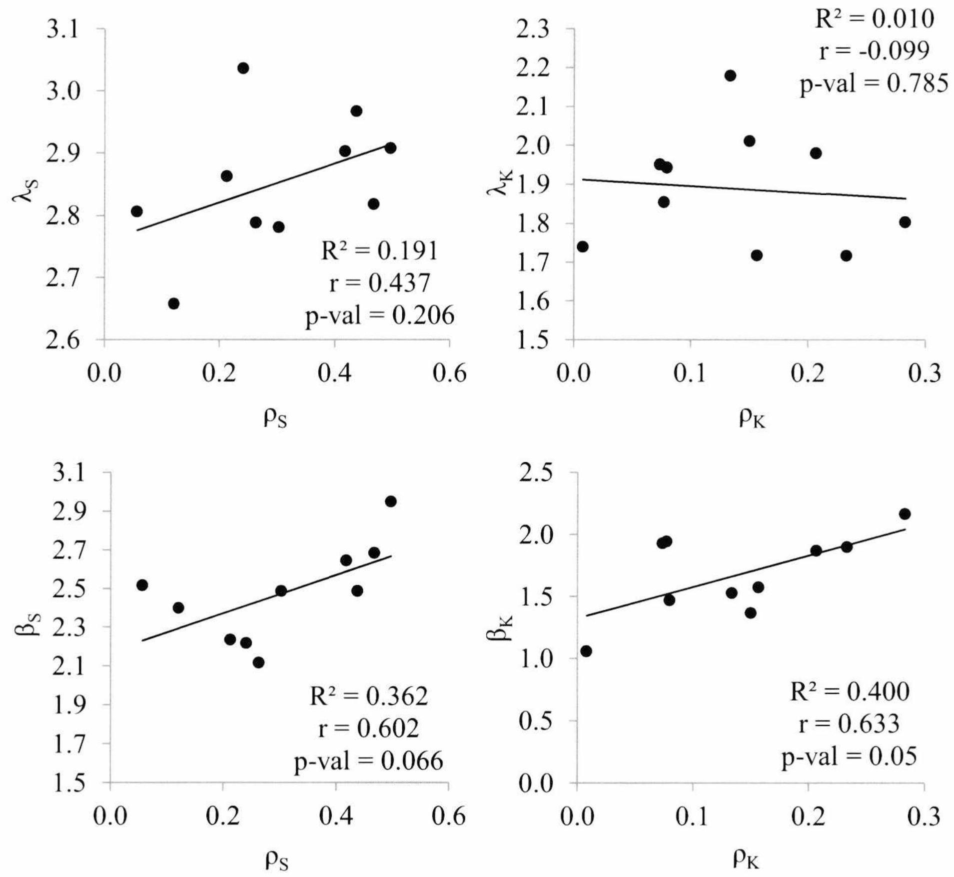


Figure 3-21 Scatterplots of overall productivity ρ (estimated in section 3.1.5) with respect to either mean clutch size λ (top panels) or underdispersion parameter β (bottom panels), for shags (left panels) and kittiwakes (right panels). Pearson's correlation coefficient r and associated p-value (2-tailed), as well as the linear regression line and regression coefficient R^2 are also shown for each panel.

We also calculate the correlation between mean clutch size and underdispersion with the environmental variables used in the study of overall productivity synchrony: winter NAO (wNAO) and February to March Sea Surface Temperature (SST), including 1 and 2 year time lags (see section 3.1.7 for details about these covariates). Correlation is only significant ($\alpha = 0.05$) for four combinations, with $|r| > 0.65$ (Figure 3-22).

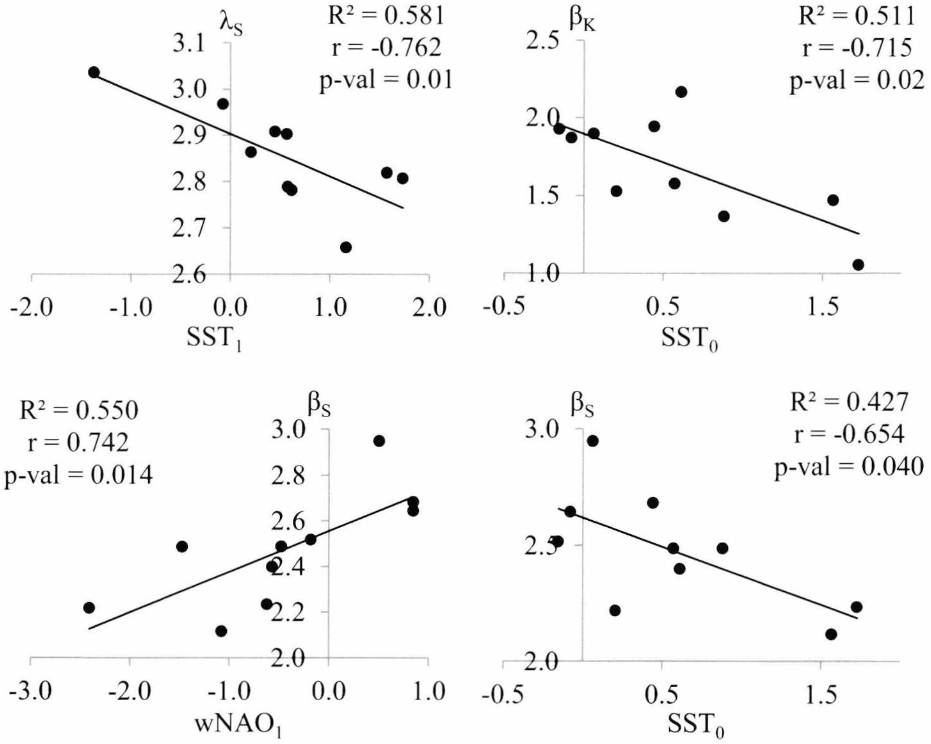


Figure 3-22 Scatterplots of either mean clutch size λ or underdispersion parameter β with the environmental covariates for which the regression is significant at the $\alpha = 0.05$ level. Pearson's correlation coefficient r and associated p-value (2-tailed), the linear regression line and coefficient R^2 are also shown for each panel. Years 2010 and 2011 are not included in this plot as we did not have the corresponding values of wNAO and SST.

These correlations indicate that:

(i) Colder sea surface temperatures around the Isle of May in the winter of the year before breeding (SST_1) are associated with a larger mean clutch size in shags.

(ii) Higher winter NAO values (representing mild and wet winters) one year before breeding, appear to increase underdispersion in shag clutch sizes (i.e. the number of eggs in most nests is close to the mean).

(iii) Colder sea surface temperatures around the Isle of May in the winter previous to breeding (SST_0) appear to increase underdispersion in both shag and kittiwake clutch sizes.

We note that none of these covariates appears significant in explaining overall productivity in the respective species.

3.4 Discussion

In this chapter we adapt the synchrony framework presented in Chapter 2 to the study of multi-species synchrony in different aspects of breeding success, including overall productivity, its components and clutch size underdispersion. Unlike survival which, being a probability, is naturally bounded between zero and one, productivity is commonly defined as the average number of offspring produced by a breeding female and thus can exceed one. A novel feature of the approach proposed is that, using a binomial distribution and the maximum clutch size, it can accommodate inter-specific clutch size variation so that the models are valid even if the community under study is a mix of species that lay both single- and multiple-egg clutches. The models proposed for overall productivity and its components do not require nest-by-nest counts but only total counts of fledglings (and potentially other intermediate state variables like eggs) produced by a number of monitored breeding pairs of several species for a series of common years. The method is widely applicable, and we demonstrate it in a case study typical of many seabird monitoring programs (Walsh *et al.* 1995; Dragoo, Byrd & Ironsa 2006). Other long-term detailed data sets like the British Trust for Ornithology's Nest Record Scheme (Crick, Baillie & Leech 2003) would allow estimation of synchrony at different stages of the breeding process.

3.4.1 Productivity and its components

In our case study the five species that comprise the seabird community share a common long-term productivity decline. Superimposed on this trend is year-to-year variation that tends to be only weakly synchronised among the species, although some good (e.g. 1992 &2000) and poor (e.g. 1993 &2004) breeding seasons are shared by all five species. Extreme non-linear cases of only exceptionally bad or good seasons inducing synchrony may require different model structures (Cattadori, Haydon & Hudson 2005). Food supply is an important extrinsic factor affecting seabird breeding success (Frederiksen, Mavor & Wanless 2007), often acting via thresholds in prey availability (Cury *et al.* 2011). Given that productivity of our species is thought to differ in sensitivity to variation in prey abundance, in particular sandeels (with kittiwakes considered the most sensitive and shags the least; Furness & Tasker 2000), varying responses with different thresholds are plausible. In addition, the species with multiple egg clutches show greater capacity for year-to-year variation, with recurrent seasons of low productivity. There are also marked differences in breeding strategies (e.g. guillemot and razorbill chicks only spend three weeks at the colony and leave when unable to fly, completing their development at sea, while in the other three species chicks fledge when only slightly below adult size). In terms of climatic influences, despite consistency among the species in the sign of the responses to winter NAO and local SST, these do not have great explanatory power for overall productivity. These covariates are likely to reflect climatically induced changes in food availability. Ideally abundances of key forage fish in the North Sea food web, e.g. sandeels or sprats, would be incorporated to the study. However, the fact that different time-lags appear important for different species highlights the need for empirical studies to identify the mechanisms involved, including differences in species and/or age classes of prey taken (Frederiksen *et al.* 2006) or differences in feeding area or foraging depth. Moreover, some potentially extreme short-lived climatic effects such as storms, not reflected in these covariates, may affect the species in contrasting ways (e.g. heavy rain will flood puffin burrows while gales are more likely to impact on cliff-nesting species), which will further contribute to asynchrony. The marked differences existing in wintering areas (with kittiwakes showing the greatest dispersal range and shags the least, Wernham *et al.* 2002) could also desynchronise productivity, with the species potentially starting the breeding season in different body condition due to carry-over effects (Harrison *et al.* 2011). In addition to environmental and trophic covariates, intrinsic covariates such as density may also affect productivity via competition for high quality breeding sites and/or food.

The study and modelling of productivity components is an area of interest in ecology (Martin, Hannon & Rockwell 1989; Tavecchia *et al.* 2008) and conservation (Rockwell & Barrowclough 1995), and asynchronous allocations of reproductive effort in response to environmental change have been recorded even in closely related sympatric species (Sandercock, Lank & Cooke 1999; Wilson & Martin 2010). Our study of productivity components highlights that observed changes in overall productivity can be driven by particular stages of breeding. This approach can help identify which stage is the main driver and focus on key environmental or intrinsic mechanisms.

3.4.2 The common terms as indicator

The interest in indicators for monitoring and assessment of marine ecosystem health is widespread. Given their position as top predators in the marine food web, seabirds have been used as indicators to assess fish stocks, study climatic fluctuations and detect ecosystem change (Piatt, Sydeman & Wiese 2007; Parsons *et al.* 2008; Einoder 2009). Breeding success is a widely used metric since it is likely to be linked to prey availability and thus reflect changes at lower trophic levels and in abiotic conditions (Frederiksen, Mavor & Wanless 2007; Cook *et al.* 2011).

The common terms of overall productivity may convey information about variations in the marine environment around the Isle of May that affect the breeding success of the five species synchronously. The long-term decline found probably reflects a general deterioration in conditions in the North Sea with consequent effects for successful breeding. The validity of this result is reinforced by the fact that, despite important methodological differences, it coincides broadly with the decline seen in the 'seabird index' proposed by Frederiksen, Mavor & Wanless (2007) based on Principal Component Analysis (PCA) of the productivities of the same five species (Figure 3-6). Being model-based (versus the a posteriori approach of PCA on the estimates), our method has the advantage of obtaining measures of uncertainty and permits the explicit estimation of the species-specific asynchronous components, that is, the differing response of each species with respect to the set. It also provides a way of generating potential multi-species based indices, although more careful examination of their properties would be required on a case by case basis before their application in management (Einoder 2009).

Parsons *et al.* (2008) divide seabird-based indicators into three types according to the target aspect to be monitored: species status, local marine ecosystem health, or food availability as a proxy for the impact of ecosystem pressures. Abundance is recommended as an indicator of seabird species status, but does not necessarily reflect immediately marked changes in the availability of food. Therefore productivity will generally be a better variable as indicator of both food availability and local marine ecosystem health, while still being relatively easy to monitor. All the species we considered feed exclusively at sea and, on the Isle of May, are not subject to predation by terrestrial mammals. They are thus suitable as indicators of marine health since the influence of confounding factors is unlikely to be large. The common signal in overall productivity synchrony is therefore a strong candidate for an integrated response indicative of this avian predator community. For indicators of food availability as proxy for the impact of ecosystem pressures, Parsons *et al.* (2008) recommend targeted single-species indicators (e.g. kittiwake breeding success as indicator of the impact of an industrial fishery in the North Sea; Frederiksen *et al.* 2004), arguing that their response may be more specific, unless the species in a set respond similarly to the same pressures. In this context, it may be worth investigating the use of the common signal, although we note again the different sensitivity of the species to prey availability (Furness & Tasker 2000).

3.4.3 Clutch size underdispersion

In this chapter we have also considered synchrony in clutch size underdispersion for shags and kittiwakes at the Isle of May. Data on individual clutch size are recorded less commonly and to our knowledge, underdispersion in this state variable has rarely been investigated. Our analyses indicated that overall most of the year-to-year variation in both mean clutch size and underdispersion is largely synchronous between shags and kittiwakes (synchrony indices ranging from 42% to 86%), although the time-series available was shorter than for other productivity analyses and thus did not allow the estimation of precise indices.

Some interesting relationships also emerge from exploratory comparisons of each species' mean clutch size λ, underdispersion β, overall productivity (ρ, related to the average number of chicks fledged per breeding pair) and the environmental covariates considered. First of all, there was no clear relationship between mean clutch size and underdispersion (Figure 3-20, lower panels). The analysis suggests that good years in terms of average number of eggs per nest would be associated with greater spread (lower β). Note also the lack of significant correlation between mean clutch size λ and overall productivity ρ (Figure 3-21, top panels), which indicates that, for these species, years of higher average number of eggs are not necessarily associated with years with higher average number of fledglings per nest. Given data on all stages of the breeding process, further analyses could explore at which stage the relationship between greater investment in egg production and higher overall breeding success breaks down. Surprisingly, there is some evidence of correlation between overall productivity and the underdispersion parameter (Figure 3-21, bottom panels), although note that the estimates of β have relatively wide credible intervals. For instance, kittiwake productivity was practically zero in 1998, which is the year with the lowest recorded β corresponding to a wide spread of clutch sizes (and in this case mean clutch size was low). Also, their relatively high productivity in 2005 corresponded to the highest β recorded, i.e. clutch sizes closer to the mean. Years 2010 and 2011 are somehow unusual in that they combine the highest values recorded for λ with the lowest values for β. The lack of clear patterns suggests that in this system environmental conditions may change through the season in complex ways that vary between years.

A negative correlation between mean clutch size λ and sea surface temperature in winter of the previous year (SST_1) is consistent with an indirect relationship operating via prey that are one year old, most likely sandeels of that age group, which are important prey for shags throughout the year, as well as for kittiwakes in the early part of the season (Lewis *et al.* 2001; Frederiksen *et al.* 2006). It is more difficult to find intuitive ecological explanations for the relationship found between the environmental covariates and underdispersion (β). The analysis suggests that, for both species, a larger spread in the distribution of clutch sizes (lower β) is related both to poorer overall productivity (higher ρ) as well as higher SST_0; at least for the kittiwake, this is consistent with previous studies (Frederiksen *et al.* 2004 found a negative relationship between breeding success and SST_0 in that species). On the other hand, we do not have a clear explanation for the correlation between high underdispersion and high $wNAO_1$. It appears that certain conditions have an equalizing effect on clutch size distribution while others increase the variation. A fuller understanding of these issues may require incorporating appropriate trophic covariates e.g. measures of sandeel abundance and/or the proportion of sandeels in the diet, in order to look for stronger more direct relationships.

Of course one should be aware of the danger of over-interpreting the patterns found, given the relatively small number of years in the study. Also, parameter uncertainty is not accounted for in this simple exploration. As an example, we calculate posterior correlation for the pairs $(\beta_K - \beta_S)$ and $(\lambda_K - \lambda_S)$, by obtaining a correlation coefficient for each MCMC iteration. The resulting distributions have the following medians (and 25th and 75th percentiles): $\hat{r}_{\beta K-\beta S} = 0.58\ (0.03, 0.95)$ and $\hat{r}_{\lambda K-\lambda S} = 0.75\ (0.54, 0.89)$. Although these values are in line with the correlation coefficients found from the point estimates (see top panels in Figure 3-20) it is clear that, when uncertainty is taken into account (using the full posterior distributions of the parameters), there is much less evidence for correlation between β_K and β_S. A strong positive correlation between λ_K and λ_S still appears supported by these results.

3.4.4 Conclusions

The framework presented here to quantify multi-species synchrony in productivity is extremely flexible and, as we have demonstrated, can readily be adapted for different components of productivity and for clutch size underdispersion, as long as suitable data are available. Furthermore, the framework can also be adapted to single-species multi-population cases, i.e. synchrony in productivity of geographically separated populations (as Grosbois *et al.* 2009 do for adult survival) and also to different age classes, based on age-specific data (Rockwell *et al.* 1993). The binomial form also makes it possible to consider multi-parameter synchrony for a single species, e.g. between productivity and other demographic parameters like survival (as we discuss in section 4.2.6), or between different components of productivity (e.g. between hatchability and chick survival). Although the terminology in this chapter refers to avian breeding (e.g. 'clutch', 'fledgling'), the methods are equally valid for non-avian communities. The study of productivity synchrony may help elucidate ecological hypotheses and such models can be important tools in understanding the response of species communities in the face of environmental change. Finally, the study of synchrony and its potential role in the development of multi-species environmental indicators highlights the relevance of long-term monitoring programs from which long time series of demographic parameters such as productivity can be estimated.

The logical extension to this approach is to consider synchrony in several demographic parameters by analysing them simultaneously and incorporating time-series of abundance, in an integrated population modelling framework (Besbeas, Freeman & Morgan 2005). The joint likelihood of such analysis would extend over demographic parameters and different species, an analysis that to our knowledge has so far not been attempted. This will be the subject of the Chapter 5.

4 SYNCHRONY: PROPERTIES, PERFORMANCE AND EXTENSIONS

This chapter focuses on the concept of multi-species synchrony as defined in this thesis, with the aim of clarifying its meaning and offering guidance on when and how to use it. We investigate the properties and performance of multi-species synchrony under different scenarios that may typically be encountered in ecological studies (e.g. how many years or how many species). Several extensions are also discussed. The various simulation studies in this chapter use productivity as the demographic parameter of interest for illustration purposes, but we note that results are general and equally applicable when using the framework for other demographic parameters.

4.1 Model performance and properties

We have already shown using simulations that the modelling framework of this thesis is able to recover the parameters used to simulate synchronous data (section 2.3.9 for survival and 3.2.3 for productivity). In this section, we investigate further the performance and properties of the synchrony framework with respect to several practical aspects that may occur in ecological studies. We do this by performing a series of simulation studies, based on the following general setup:

(i) A set of S species that have a single-egg clutch (like the auks in the Isle of May study).

(ii) Estimation of 'overall productivity' ρ for a series of T years, based on the number of monitored eggs E and the number of fledglings F produced, using a binomial model as explained in section 3.1.1 so that, for species s and year t,

$$F_s(t) \sim \mathrm{Bin}\big(E_s(t), \rho_s(t)\big).$$

(iii) Estimation of multi-species indices of synchrony (I_s) in overall productivity ρ, based on the estimated variances of synchronous ($\delta(t)$) and asynchronous ($\varepsilon_s(t)$) year random terms, as explained in section 3.1.2

$$\mathrm{logit}\big(\rho_s(t)\big) = \beta_s + \delta(t) + \varepsilon_s(t)$$

$$I_s = \frac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2}$$

This setup is chosen because the binomial model for estimating productivity is simple and, given enough monitored eggs (which is not a problem in simulations), the estimates of productivity are very precise, allowing us to concentrate on the study of the properties of synchrony itself.

Data are simulated with $E = 2000$ eggs per year for all species, from which the number of fledglings F is obtained following (ii), using values of productivity that have been calculated based on values of synchrony, variances and intercepts that depend on the particular simulation study to be carried out. This procedure of data simulation and analysis is repeated a number of times, and bias and root mean square error (RMSE) calculated using the known true values of the species-specific intercepts β_s, synchronous (σ_δ^2) and asynchronous (σ_s^2) variances and derived indices of synchrony I_s, and the median of the marginal posterior distributions as point estimates. All data analyses in this section are performed in WinBUGS, run from MATLAB (with 50000 MCMC iterations after 50000 burn-in, unless otherwise specified).

4.1.1 Number of years

Since the quantification of synchrony is based on the estimation of the variances of random effects, we can expect that short time series will produce rather imprecise estimates of synchrony indices. We test this by simulating and analysing productivity data sets for $S = 3$ species and an increasing number of study years $T \in \{5, 10, 25, 50,100\}$. Bias and RMSE are calculated over 100 simulations per value of T, with the following parameters: intercepts $\beta_s = [1, 1.5, 2.5]$, $\sigma_\delta^2 = 1$, $\sigma_s^2 = [0.5, 0.4, 0.4]$ (consequently, $I_s = [0.67, 0.71, 0.71]$). Figure 4-1 shows a typical set of values for ρ produced with these parameter values and $T = 40$.

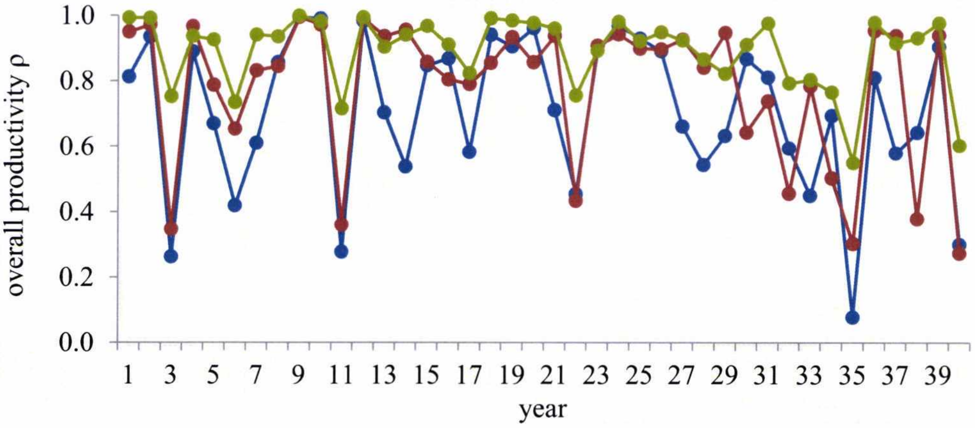


Figure 4-1 Example of overall productivity ρ values produced for 3 species (1: blue; 2: red; 3: green) and T=40 years with the following parameter values: intercepts $\beta_s = [1, 1.5, 2.5]$, $\sigma_\delta^2 = 1$, $\sigma_s^2 = [0.5, 0.4, 0.4]$ (and consequently, $I_s = [0.67, 0.71, 0.71]$).

The simulation results (Figure 4-2) show how all estimates become more precise as the number of years increases, with a steeper reduction of RMSE for up to approximately $T = 25$ years. At least for three species and this combination of intercepts and variances, estimates of synchrony with $T < 10$ years appear positively biased and rather imprecise.

We would expect variance to decrease with a factor $1/T$ as the number of years in the study T increases. We verify that this is the case in our simulation study: we calculate the variance we would expect for $T = [10, 25, 50, 100]$ by scaling the variance obtained for $T = 5$. The resulting values are similar to the variance of the point estimates over the 100 simulations (Figure 4-3).

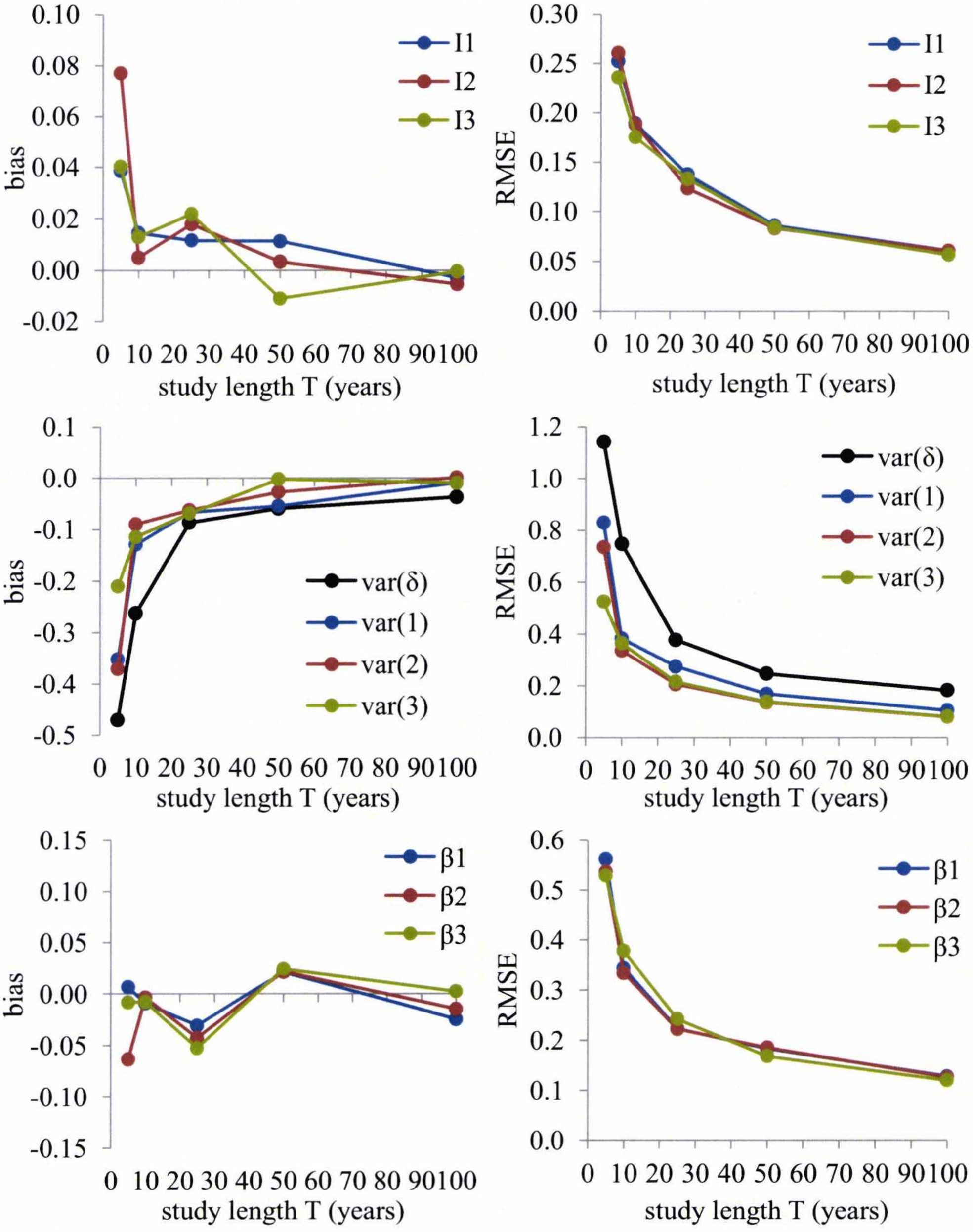


Figure 4-2 Bias (left panels) and RMSE (right panels) of the indices of synchrony (I_S), common (σ_δ^2; denoted 'var(δ)') and species-specific (σ_S^2; denoted 'var(s)') variances, and regression intercepts (β_S), calculated for 100 simulations and study length values T ranging from 5 to 100 years.

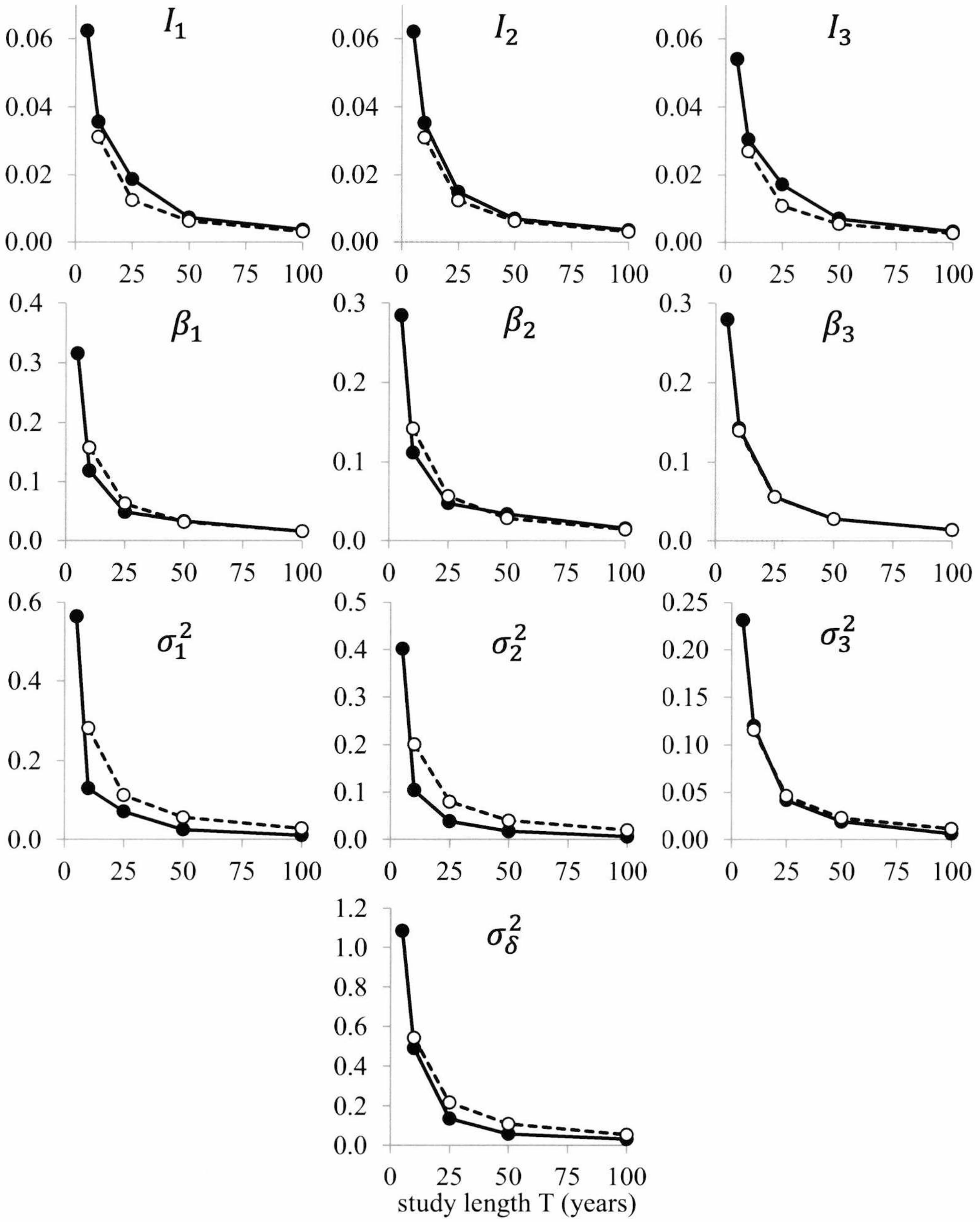


Figure 4-3 Estimated variances over 100 simulations of the median of marginal posterior distributions (solid lines), compared to the expected variance according to a scaling by 1/T of the value estimated for T=5 (dashed lines). Parameters: indices of synchrony (I_s), regression intercepts (β_s), species-specific (σ_s^2) and common (σ_δ^2) variances.

4.1.2 Number of species

In order to explore whether there is an effect of having more or fewer species in the set, we simulate productivity data sets with an increasing number of species (from 2 to 9), for $T = 5$ and $T = 20$ years (50 simulations for each combination). All species shared the same variances and intercepts: $\beta_s = 1.5, \sigma_\delta^2 = 1,\ \sigma_s^2 = 0.4$ (so that synchrony is $I_s = 0.71$ for all species).

Figure 4-4 shows that bias and RMSE (averaged over all species in each set) do not change significantly when more species are added to the set, for either 5 or 20 years. The expected effect of having a longer time series is also visible.

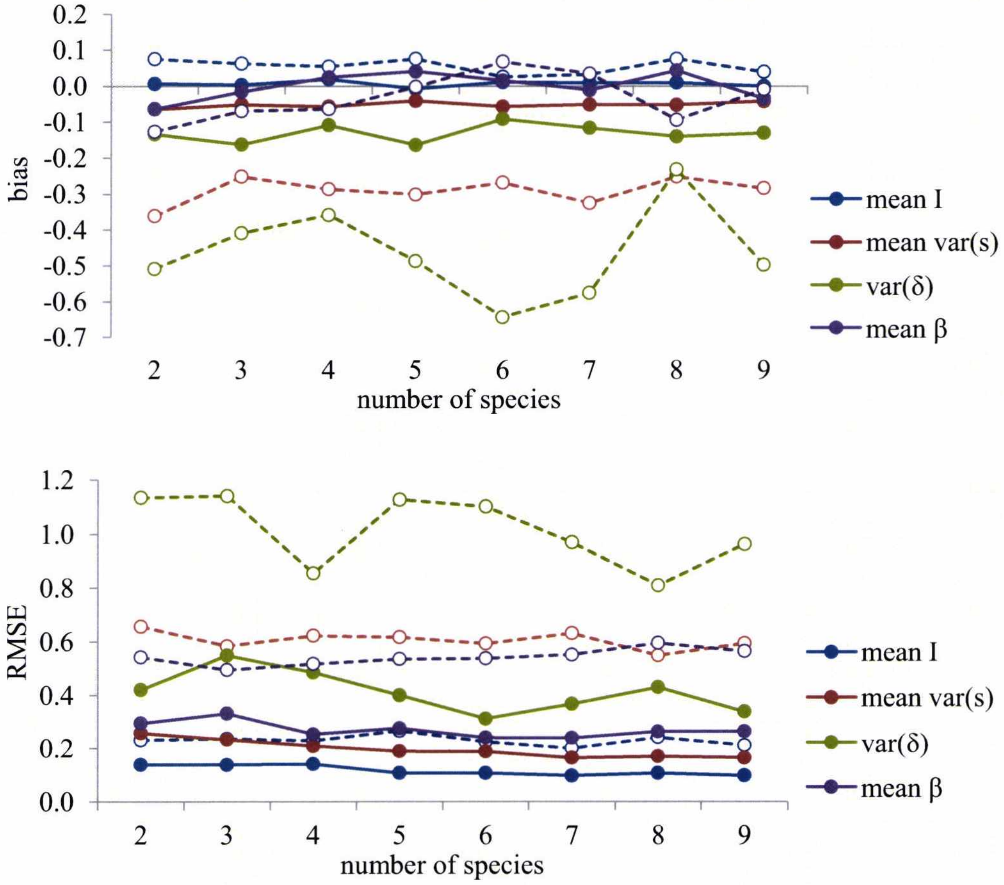


Figure 4-4 Bias (top panel) and RMSE (bottom panel) of indices of synchrony (I), regression intercepts (β), species-specific (σ_s^2) and common (σ_δ^2) variances, for $T = 5$ (dashed lines) and $T = 20$ (solid lines). Except for σ_δ^2, the values represent averages over the S species.

These species are synchronous by design (as these are simulated data sets), so adding more species, if anything, could help improve the estimation of the common terms, but should in any case not harm the estimation of synchrony. This is different from analysing synchrony for a larger set of real species, which in general will not be synchronous by design. In such a situation, the more species that are added, the larger the chances of including a species that is less synchronous with the rest. If such a species is added, the amount of common variation in the set would decrease, resulting in smaller indices of synchrony for the species already present in the set (but not necessarily for the new species added, as discussed in section 2.2.2).

4.1.3 Robustness to different intercepts

When the baseline value of the parameter under study (here productivity) is very different for different species, the same magnitude of variation on the logistic scale will translate into different magnitudes on the probability scale (see an example in Figure 4-5). As synchrony is calculated on the logistic scale but the data relate more directly to overall productivity ρ, which is defined on the probability scale, we test here whether the estimation of synchrony becomes more difficult when the species in a set have very different intercepts.

We simulate data for $S = 5$ species and $T = 20$ years, with $\sigma_\delta^2 = 1$, $\sigma_s^2 = 0.4$ (thus again synchrony $I_s = 0.71$ for all species). The intercept β_s is 1 for all species except for species 1, for which we vary it from 1 (same value as the others) to -1.5. A typical data set for $\beta_1 = -1.5$, the most extreme case considered, is shown in Figure 4-5.

We then analyse these data sets with the synchrony model. The procedure is repeated for 50 simulations for each value of β_1. The results (bias and RMSE; Figure 4-6) show no effect of one species having a different intercept from the others, indicating that the estimation of synchrony is robust to such differences.

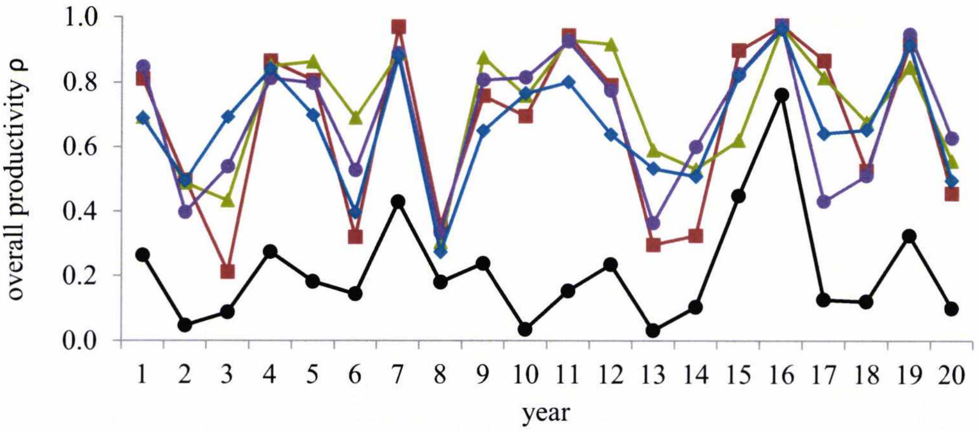


Figure 4-5 Example of overall productivity ρ values produced for 5 species and $T = 20$ years with the following parameter values: intercepts $\beta_s = [-1.5, 1, 1, 1, 1]$, $\sigma_\delta^2 = 1$, $\sigma_s^2 = [0.4, 0.4, 0.4, 0.4, 0.4]$ (and consequently, $I_s = [0.71, 0.71, 0.71, 0.71, 0.71]$). The black line represents species 1.

4.1.4 A species' variance limiting the amount of common variation

We note in section 2.2 that the concept of synchrony as defined here encompasses the magnitude of the variations. We could expect that the amount of synchronous variation in a set of species would be limited if one or several of the species considered have little year-to-year variation in the parameter for which we want to estimate synchrony. We conduct a simulation study to verify whether a species of low overall variance can limit the amount of synchrony in the set.

Using variances $\sigma_\delta^2 = 0.6$ and $\sigma_s^2 = 0.2$, we simulate common and species-specific random terms for $S = 3$ species and $T = 30$ years. These variances would imply a priori a synchrony index of 0.75. For all species except the first one, we derived productivity values and simulate productivity data based on these year random terms. Then for species 1 we calculate the productivity values $\rho_1(t)$ with a dampening of the 'common terms', based on the following equation:

$$\text{logit}(\rho_1(t)) = \beta_1 + \sqrt{k} \cdot \delta(t) + 0.5 \cdot \varepsilon_1(t),$$

where k is a scaling factor that we vary from 1 (no scaling) to 0.2 (strong scaling).

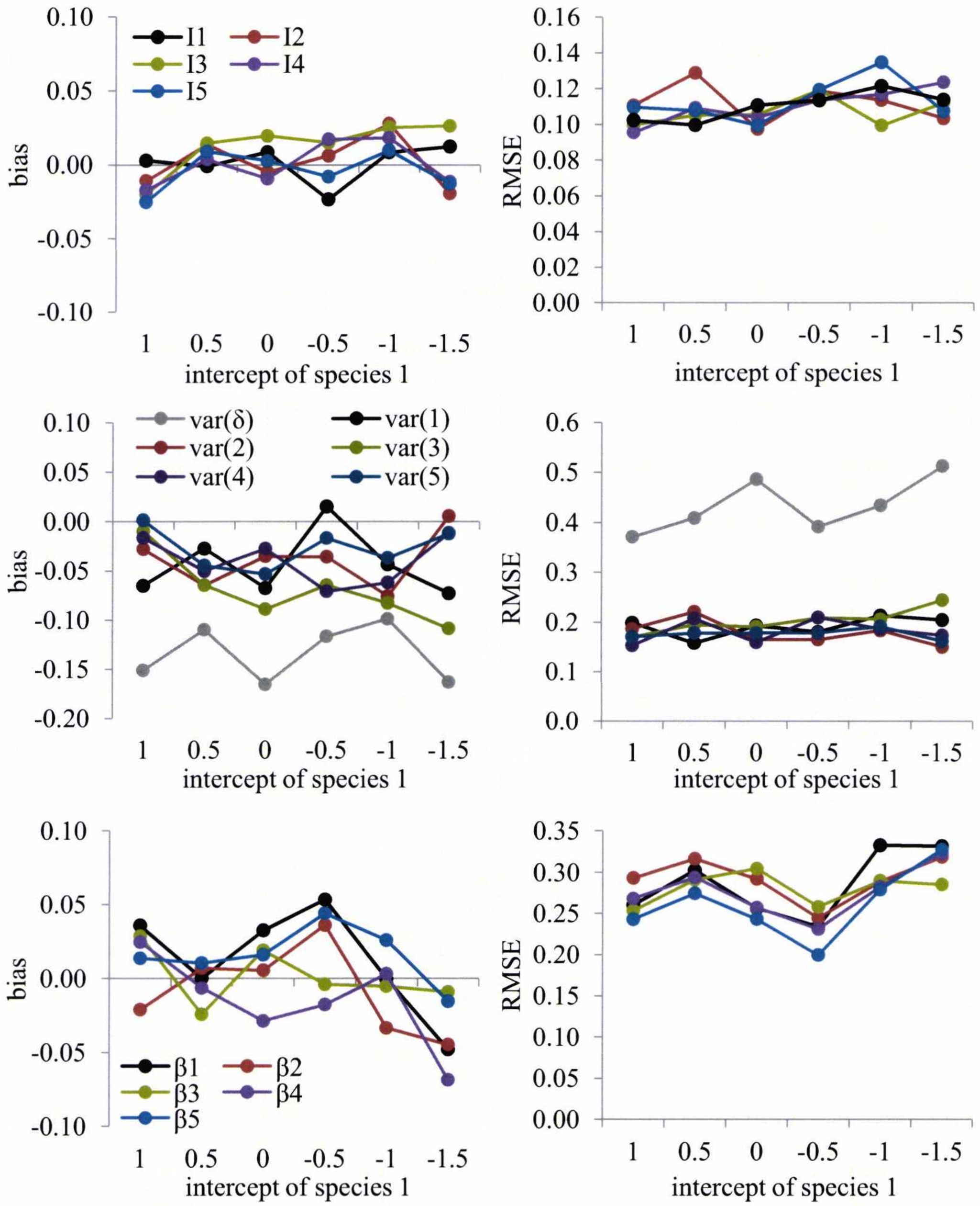


Figure 4-6 Bias (left panels) and RMSE (right panels) of the indices of synchrony (I_s), common (σ_δ^2) and species-specific (σ_s^2) variances, and regression intercepts (β_s), calculated for 50 simulations, 5 species and $T = 20$ years, and the intercept of species 1 (β_1) ranging from 1 (equal to the other species) to -1.5.

Such data sets emulate scenarios in which one of the species in the set has some degree of synchrony with the other species (ensured by design via the presence of the $\delta(t)$ random terms) but lower overall variation (which we control with the scaling factor k). We also apply a constant scaling of 0.5 to the species-specific terms $\varepsilon_1(t)$, so that species 1 has little year-to-year variation in ρ overall. Figure 4-7 displays a typical example of productivity values generated for $k = 0.2$, the most extreme case considered.

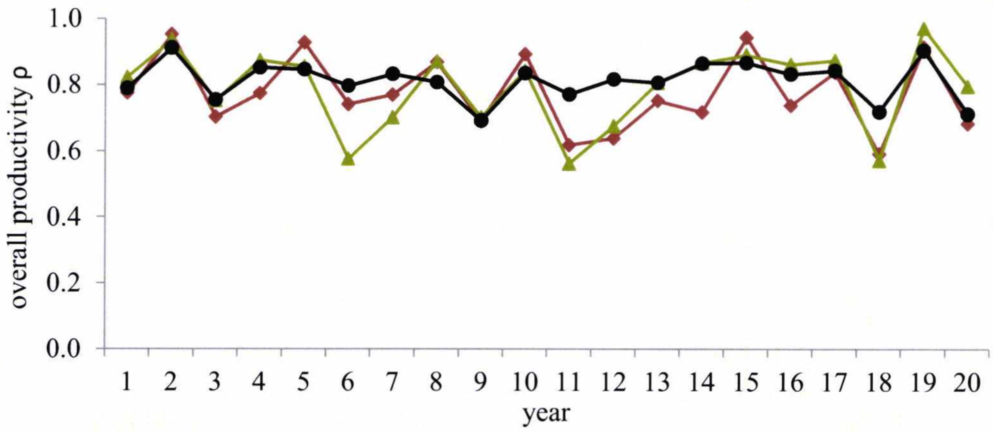


Figure 4-7 Example of overall productivity ρ values produced for 3 species and $T = 20$ years with the following parameter values: intercepts $\beta_s = 1.5$, $\sigma_\delta^2 = 0.6$, $\sigma_s^2 = [0.1, 0.4, 0.4]$, and applying a scaling factor $k = 0.2$ to the common terms of species 1 (whose resulting productivity is represented by the black line).

When $k = 1$ (no scaling of the common terms for species 1), the indices of synchrony would be 0.92 for species 1 (due to the 0.5 scaling applied to $\boldsymbol{\varepsilon_1}$) and 0.75 for the rest of the species. We would expect the synchrony indices to decrease with the amount of scaling k, as the new common signal is in principle limited by the scaling applied to the common terms in species 1.

For each value of k, we analyse 50 simulated data sets using the synchrony model structure. Figure 4-8 shows the resulting mean and variance of the point estimates (the median of the marginal posterior distributions) calculated over the 50 simulations. As expected, the estimated synchronous variance $\hat{\sigma}_\delta^2$ decreases as the amplitude of the common terms of species 1 is dampened (scenarios with lower k). Consequently, in species 2 and 3 the asynchronous variances ($\hat{\sigma}_2^2$ and $\hat{\sigma}_3^2$) are boosted, as their species-specific random terms absorb the diminishing variation that was previously common. The species that limits the common variation (species 1) retains a high and slowly increasing index of synchrony I_1 while both I_2 and I_3 decrease. The estimation of the intercepts β_s remains largely unaffected.

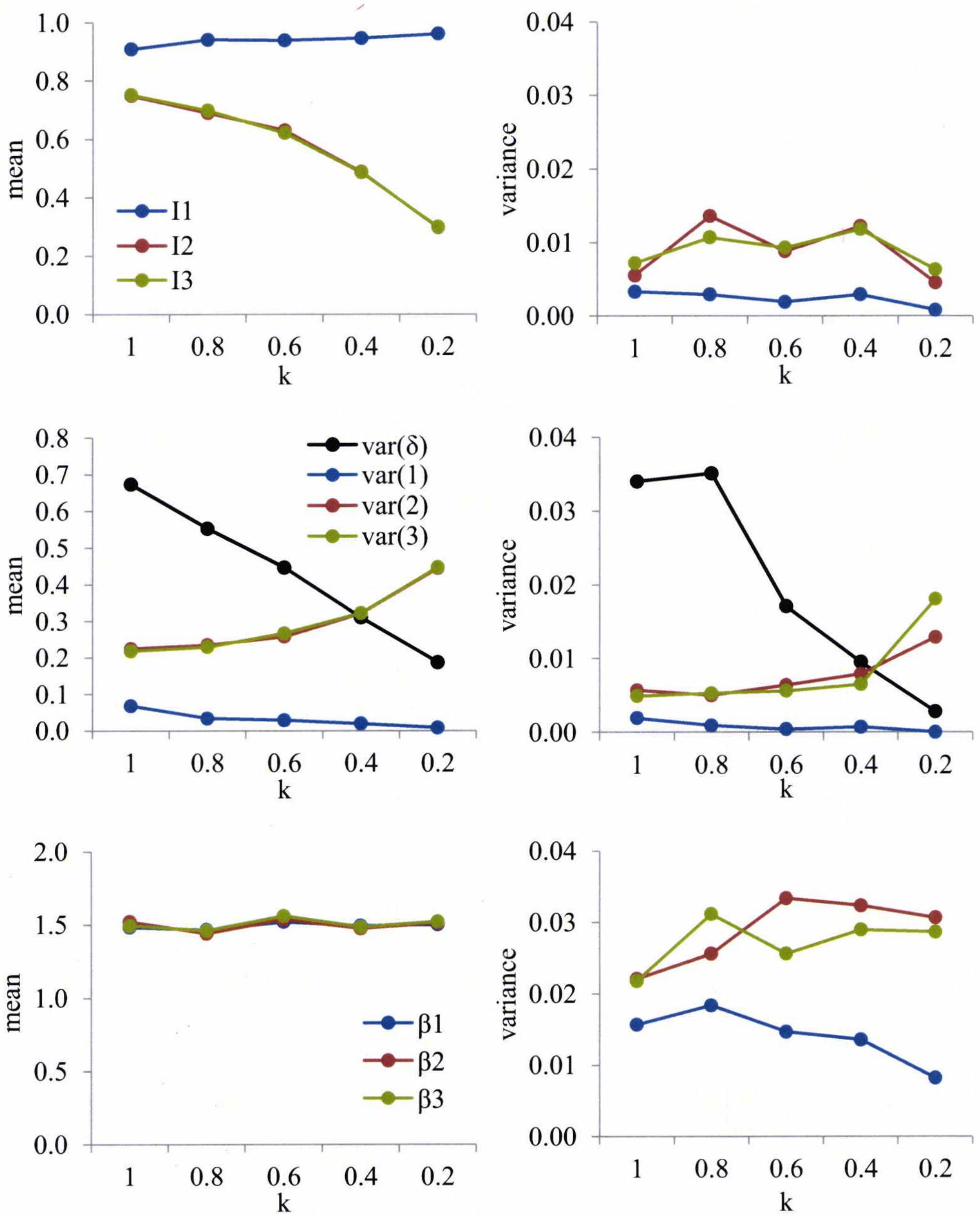


Figure 4-8 Mean (left panels) and corresponding variance (right panels) of the point estimates (median of the marginal posterior distributions) of 50 simulated data sets, for the indices of synchrony (I_s), common (σ_δ^2) and species-specific (σ_s^2) variances, and regression intercepts (β_s). The variance reduction coefficient k for species 1 varies from 1 (no reduction) to 0.2 (very little common variation). Study period length is $T = 30$ years.

4.1.5 *A test for spurious synchrony*

We have shown that the synchrony framework is capable of estimating synchrony when it is present. This section explores the opposite situation: we investigate the robustness of the model to spurious estimation of synchrony when there is none by design. We would expect that in analyses of short time series, where the estimation of the random effects variances is challenging, the model may estimate some degree of synchrony even when in reality no mechanisms synchronise the species. This aspect is relevant to ensure that when the model is applied to a real data set, we can be confident that, when some level of synchrony is estimated, such an effect really exists.

We simulate productivity data for a varying number of species (from $S = 2$ to 5) and years (from $T = 5$ to 25). In all cases, the data sets are completely asynchronous ($\sigma_\delta^2 = 0$, $\sigma_s^2 = 0.4$), that is, their productivities are independent as there are no common random terms. The indices of synchrony should be zero for all species. For each combination of S and T, 50 data sets are created and analysed with the synchrony model, allowing the model to estimate spurious synchrony. The mean and variance of the point estimates (median of marginal posterior distributions) are calculated for each combination (S, T).

The results (Figure 4-9) show that for short time series, the model estimates a substantial amount of spurious synchrony (25-35%) with a large variance, which corresponds to a non-zero estimate of the synchronous variance $\hat{\sigma}_\delta^2$. Adding species to the set does reduce the amount of spurious synchrony, and the difference is particularly noticeable when we move from only two to more than two species. The amount of spurious synchrony reduces substantially as the number of years increases.

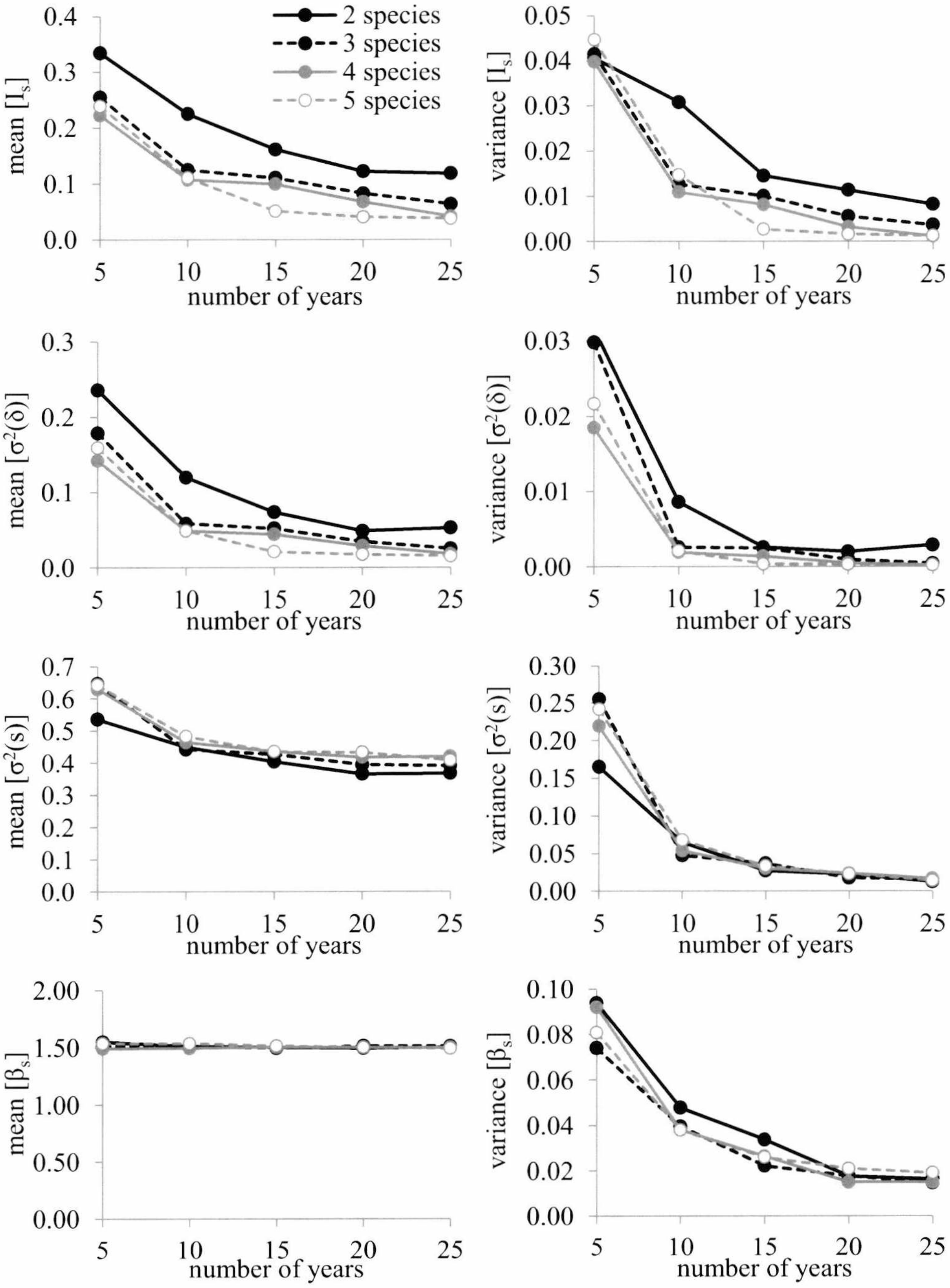


Figure 4-9 Mean (left panels) and corresponding variance (right panels) of the point estimates (median of the marginal posterior distributions) of 50 simulated data sets, for the parameters of interest (indices of synchrony (I_S), common (σ_δ^2) and species-specific (σ_S^2) variances, and regression intercepts (β_S)), a varying number of species and years. The values shown for I_S, σ_S^2 and β_S are the means or variances averaged over all species considered in that particular combination.

These results indicate that it is preferable to work with longer time series, particularly when few species are studied. A general recommendation (at least for these values) would be to analyse at least 20 years if there are only two species in the set, or at least 10 years if there are more than two species. We note that this is largely fulfilled in our analyses of synchrony for the Isle of May seabird community: $S = 3$ species and $T = 23$ years for adult survival (section 2.3); $S = 5$ and $T = 24$ for overall productivity (section 3.1) and components of productivity (section 3.2). The analysis of synchrony in clutch size underdispersion parameters (section 3.3) has only $S = 2$ and $T = 12$, but note the estimated synchrony indices are large (>0.4) in all cases, although rather imprecise. These results are also relevant to single-species multi-colony analyses; we note that in Grosbois *et al.* (2009), multi-population synchrony is estimated for $S = 4$ populations and $T = 11$ years.

One important aspect to note is that the model estimates the amount of 'synchrony' there is in the system independently of whether that synchrony has a 'mechanistic' or 'stochastic' origin; the former corresponds to species that respond similarly and thus have $\sigma_\delta^2 \neq 0$, the latter is created by chance from independently varying species.

With our simulations, we estimate the level of synchrony for a given configuration that may correspond to the purely stochastic part (as we know by design that the time series are created independently); this is the level of synchrony which is therefore not interesting for ecological inference. Our interest lies in synchrony that has been generated mechanistically (i.e. the species are responding synchronously to some aspect of their biotic or abiotic environment). As expected, the stochastic element of synchrony is reduced as the time series analysed become longer and also as more species are included in the set.

This type of simulation can form the basis for a test of the level of 'stochastic' or spurious synchrony that the model may estimate for the amount of data and parameter values of a real data set. Such a test can be performed after analysing the real data set to determine whether the estimated synchrony indices differ from that expected under the null hypothesis of lack of synchrony, an important aspect of the study of synchrony (Buonaccorsi *et al.* 2001).

We explain here the approach in more detail using as an example the 5-species productivity data set of the Isle of May (analysed in section 3.1):

(i) We first analyse the real data set with a model that does not include common terms, so that $\text{logit}(\rho_s(t)) = \beta_s + \varepsilon_s(t)$. Such a model estimates the species-specific variances σ_s^2 assuming that all the variation in each species is asynchronous. It also estimates the species-specific intercepts.

(ii) The posterior medians of these parameters are then used to simulate matched data sets with $S = 5$ species and $T = 24$ years, which have a level of asynchronous year-to-year variation equivalent to that of the real species in the Isle of May data set.

(iii) We analyse the simulated data sets (in which we know by design that there is no synchrony) with the synchrony model and calculate the mean and variance of the point estimates (medians of marginal posterior distributions) of the indices of synchrony I_S over 100 simulations (using WinBUGS with 100000 MCMC samples after 100000 samples burn-in).

(iv) Finally, these means are compared (Table 4-1) to the estimates of synchrony obtained from the synchrony analysis of the Isle of May productivity data set (Table 3-1).

(v) Despite the inherent imprecision of the estimates of the indices of synchrony, their 95% CI clearly do not include the values obtained from the simulation of asynchronous data sets, which would represent the spurious level of synchrony estimated from a system with $S = 5$ species, $T = 24$ years and the amount of year-to-year variation that characterises the real data set. We can therefore conclude that the Isle of May estimates of productivity synchrony do not represent stochastically-generated synchrony, but are an expression of a synchronous response of the species to variations in their environment.

Table 4-1 Mean and variance of the point estimates of the indices of synchrony I_s obtained for each species from 100 data sets with completely asynchronous productivity ('Simulation study'), and the estimates (median and 95% CI) obtained from the analysis of the real Isle of May data set.

	Simulation study		Isle of May estimates
	mean	variance	median [95% CI]
I_1	0.028	0.0005	0.295 [0.097, 0.636]
I_2	0.029	0.0005	0.292 [0.102, 0.594]
I_3	0.169	0.0200	0.870 [0.448,1.000]
I_4	0.011	0.0001	0.092 [0.030, 0.234]
I_5	0.019	0.0002	0.120 [0.044, 0.276]

4.1.6 Covariance and common terms

The common random terms in the synchrony model and the existence of covariance between species are related concepts. Completely uncorrelated (i.e. independent) responses have by definition no common component, and we already mentioned (section 2.2.2) that negatively-correlated variations are not seen as 'common' in our synchrony models, so some degree of positive correlation is therefore required for a set of species to be synchronous in a demographic parameter.

We present first two simple cases of overall positive correlation and negative correlation. Let us define $x_s(t)$ as the overall year-to-year variation on the logit scale for a demographic parameter (such as productivity), for species s and year t:

$$\operatorname{logit}(\rho_s(t)) = \beta_{0s} + x_s(t),$$

where we let in general the $x_s(t)$ terms be distributed as a multivariate normal $\boldsymbol{x}(t) \sim \mathrm{MVN}(\mathbf{0}, \boldsymbol{\Sigma})$, with variance-covariance matrix

$$\boldsymbol{\Sigma} = \begin{bmatrix} \sigma_{x1}^2 & \sigma_{12} & \cdots & \sigma_{1S} \\ \sigma_{12} & \sigma_{x2}^2 & & \sigma_{2S} \\ \vdots & & \ddots & \vdots \\ \sigma_{1S} & \sigma_{2S} & \cdots & \sigma_{xS}^2 \end{bmatrix}.$$

Here σ_{xs}^2 is the variance of $\boldsymbol{x}_s$ and σ_{sr} the covariance between species s and r. In practice, instead of covariance, we may specify pairwise correlations between species

s and r as $r_{sr} = \sigma_{sr}/(\sigma_{xs}\sigma_{xr})$. When all $r_{sr} = 0$, the species are independent. Figure 4-10 shows two examples of overall year-to-year variation $x_s(t)$ generated using a multivariate normal distribution with means 0, variances $\sigma_x^2 = 0.4$ for all species and strong covariances between all pairwise combinations of species, either positive (0.3; top panel, three species) or negative (-0.3; bottom panel, two species). In these simple cases, a visual inspection suggests that the $x_s(t)$ terms appear rather 'synchronous' in the case of positive covariance (that is, a large part of their year-to-year variation could be explained by 'synchronous terms' $\boldsymbol{\delta}$), but that this is not so in the case of negative correlation. Indeed, when we generate a productivity data set based on these random terms and analyse it with the multi-species synchrony model, we obtain high indices of synchrony in the first case ($\hat{I}_s = [0.91, 0.76, 0.80]$) but not in the second one (very low estimate of the common variance: $\hat{\sigma}_\delta^2 = 0.009$).

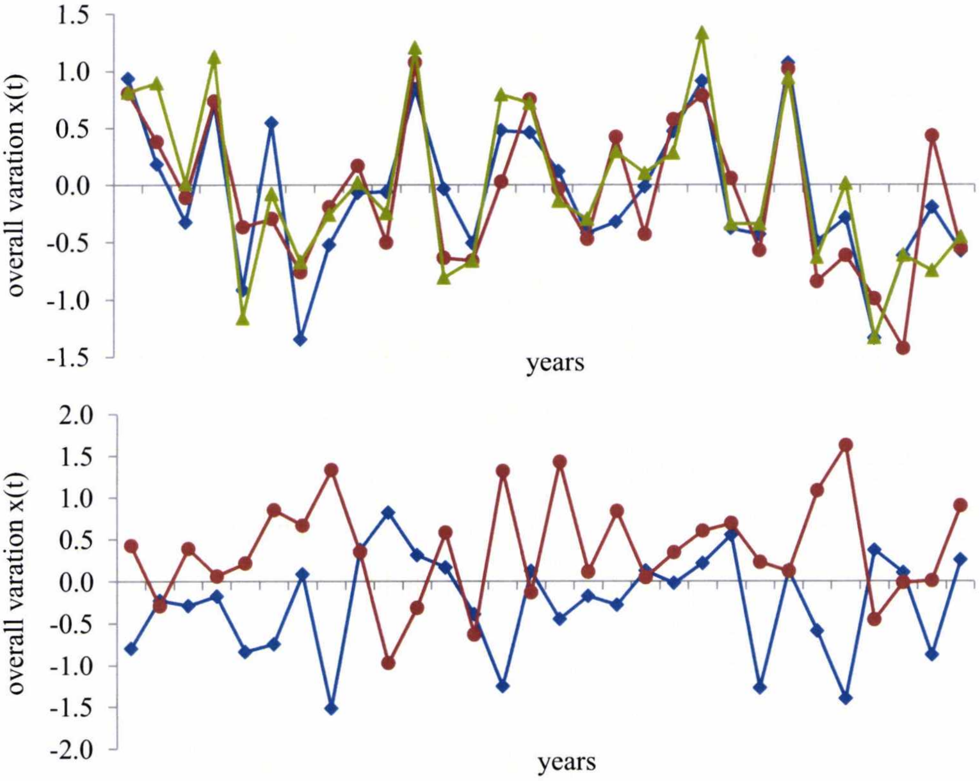


Figure 4-10 Examples of overall variation $x_s(t)$ generated with pairwise covariance between species. Top panel: three species with positive pairwise covariance 0.3; bottom panel: two species with negative covariance -0.3. $T = 30$ years.

We explore now in more detail how positive covariance in a set of species can be interpreted as synchrony when using the multi-species synchrony model. Let us assume a set of $S = 3$ species with correlation in their year-to-year variation so that $r_{12} = 0.8$, $r_{13} = 0.7$, $r_{23} = 0.9$, and $\sigma_{xs}^2 = 0.8, \forall s$. We randomly generate the values of $x_s(t)$ from a multivariate normal distribution with these parameters for $T = 200$ years, using function *mvnrnd* in MATLAB. The corresponding values of productivity ρ are calculated using intercepts $\beta_{0s} = [-0.2, 2, 1]$, as

$$\rho_s(t) = \{1 + \exp(-\beta_{0s} - x_s(t))\}^{-1}.$$

A data set of breeding success is generated randomly from these values of productivity, consisting of the number of chicks $F_s(t)$ that fledge from 2000 eggs per species per year. We estimate synchrony using the multi-species synchrony model,

$$\text{logit}(\rho_s(t)) = \beta_{0s} + \delta(t) + \varepsilon_s(t),$$

$$\delta(t) \sim \text{N}(0, \sigma_\delta^2), \qquad \varepsilon_s(t) \sim \text{N}(0, \sigma_s^2),$$

Figure 4-11 (top panels) shows the marginal posterior distributions of the estimated common ($\hat{\sigma}_\delta^2$) and species-specific ($\hat{\sigma}_s^2$) variances and related indices of synchrony I_s. The common variation created by the high positive correlation between the species is absorbed by the common δ terms ($\hat{\sigma}_\delta^2 = 0.91$), and the species with highest combined correlation with the two others (species 2) ends up with practically no species-specific variation ($\hat{\sigma}_2^2 = 0.02$). Slightly higher variances are estimated for the two other species (0.35 and 0.15 respectively).

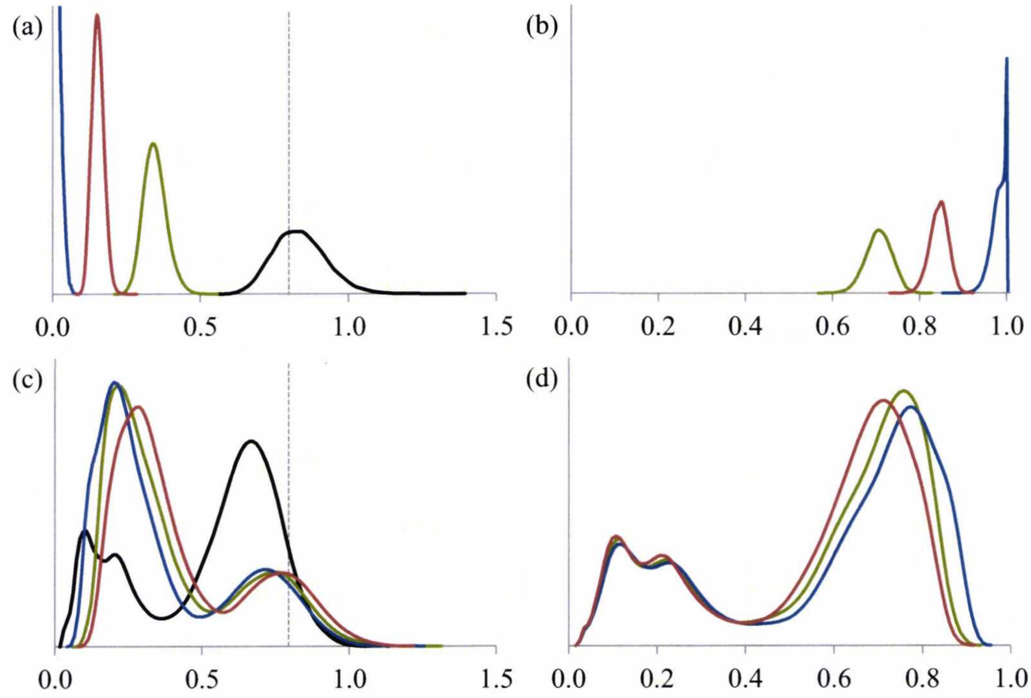


Figure 4-11 Kernel density estimates (calculated with MATLAB function *ksdensity*) of the marginal posterior distributions of variances (a & c) and indices of synchrony (b & d), obtained with the usual synchrony model (a & b) or when allowing the model to estimate both common terms and correlation between species-specific terms using a multivariate normal distribution (c & d). Green = species 1, blue = species 2, red = species 3, black = common terms $\boldsymbol{\delta}$. Data generated with $\sigma_x^2 = [0.8, 0.8, 0.8]$ (marked by a vertical dotted line) and correlations: $r_{12} = 0.8,\ r_{13} = 0.7,\ r_{23} = 0.9$.

In Chapter 3 (see Figure 3-6) we note that the estimated common terms $\boldsymbol{\delta}$ from the productivity synchrony analysis show correlation with the 'seabird index' calculated following the method in Frederiksen, Mavor & Wanless (2007), based on Principal Component Analysis (Jolliffe 1986) performed directly on productivity on the probability scale. Here we perform PCA on $\boldsymbol{x}_s$, the overall year-to-year variations on the logit scale (after standardising each of these by subtracting the mean and dividing by the SD). The calculation is based on the known values of $\boldsymbol{x}_s$, from which the data set was simulated. A scatterplot of the first principal component '**PC1**' versus the estimated common terms $\boldsymbol{\delta}$ (Figure 4-12) suggests that, despite the differences in amplitudes, the concept of 'common variation' comes close to that of explaining as much as possible of the variation in the data set.

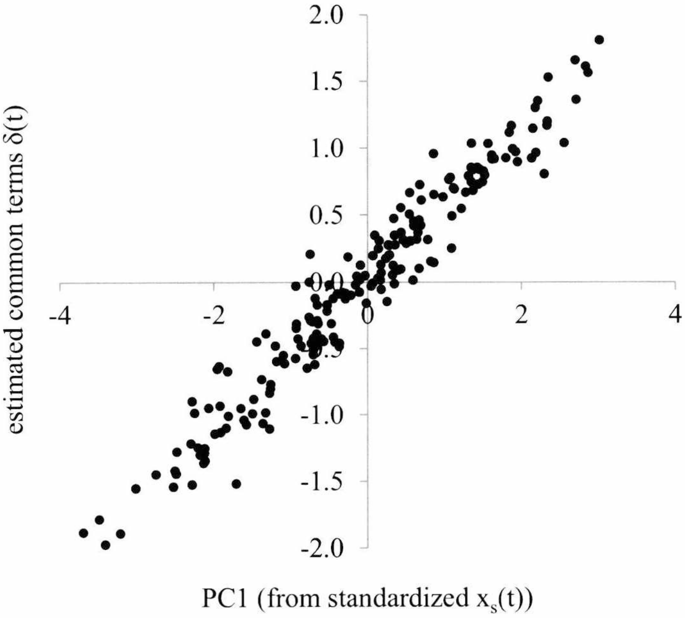


Figure 4-12 Scatterplot of the estimated common terms $\delta(t)$ and the first principal component obtained from applying PCA to the (known) overall year-to-year variation $x_s(t)$ of the set of species (after standardising).

In some studies, one may want to estimate the variance-covariance matrix of the overall variation $x_s(t)$, as an alternative to the synchrony model:

$$\text{logit}(\rho_s(t)) = \beta_{0s} + x_s(t),$$

$$\boldsymbol{x}(t) \sim \text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}), \qquad \text{with } \boldsymbol{\Sigma} = \begin{bmatrix} \sigma_{x1}^2 & r_{12}\sigma_{x1}\sigma_{x2} & r_{13}\sigma_{x1}\sigma_{x3} \\ r_{12}\sigma_{x1}\sigma_{x2} & \sigma_{x2}^2 & r_{23}\sigma_{x2}\sigma_{x3} \\ r_{13}\sigma_{x1}\sigma_{x3} & r_{23}\sigma_{x2}\sigma_{x3} & \sigma_{x3}^2 \end{bmatrix}.$$

Fitting this model to the simulated productivity data set, we can estimate pairwise correlations for all combinations of species but, as we note in section 2.2.2, such a model does not involve synchrony with respect to the complete set of species. We fit this model in WinBUGS using the multivariate normal distribution $dmnorm$, parameterised with the vector of means ($mu[\,]$, zero in our case) and the precision matrix, $\boldsymbol{\Omega} = \boldsymbol{\Sigma}^{-1}$. We specify the prior of $\boldsymbol{\Omega}$ as a Wishart distribution: $\boldsymbol{\Omega} \sim \text{Wishart}_\text{d}(\boldsymbol{R}, \nu_0)$, where the scale matrix $\boldsymbol{R}$ (d x d symmetric non-singular matrix; here $d = S$, the number of species) represents our prior belief regarding the precision of $\boldsymbol{\Sigma}$, and ν_0 are the degrees of freedom of the distribution (Spiegelhalter *et al.*

1996). We choose $\nu_0 = S = 3$ to specify an uninformative prior (McCarthy 2007, p.275) and a diagonal matrix of ones for R. The analysis (involving 100000 MCMC samples after a burn-in of 100000) is able to estimate the correlation structure well, with medians (and 95% CIs): $\hat{r}_{12} = 0.79\ (0.73, 0.83)$, $\hat{r}_{13} = 0.70\ (0.62, 0.76)$, $\hat{r}_{23} = 0.91\ (0.88, 0.93)$.

One may ask what happens if we attempt to fit a model that estimates simultaneously common terms $\boldsymbol{\delta}$ and a covariance structure in the residual (species-specific) terms $\boldsymbol{\varepsilon}_s$. Such a model would have

$$\text{logit}\big(p_s(t)\big) = \beta_{0s} + \delta(t) + \varepsilon_s(t),$$

$$\delta(t) \sim \text{N}\big(0, \sigma_\delta^2\big),$$

$$\varepsilon(t) \sim \text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}), \qquad \boldsymbol{\Sigma} = \begin{bmatrix} \sigma_1^2 & r_{12}\sigma_1\sigma_2 & r_{13}\sigma_1\sigma_3 \\ r_{12}\sigma_1\sigma_2 & \sigma_2^2 & r_{23}\sigma_2\sigma_3 \\ r_{13}\sigma_1\sigma_3 & r_{23}\sigma_2\sigma_3 & \sigma_3^2 \end{bmatrix}.$$

The results (Figure 4-11, bottom panels) show that the model finds two possible explanations for the evident common signal: it is either created by common terms $\delta(t)$ (higher σ_δ^2, lower σ_s^2 and r_{sr}), or high positive covariance (low σ_δ^2 and high r_{sr}). This is evident in the bimodal nature of the marginal posteriors or in the joint posterior of e.g. σ_δ^2 and the correlation coefficients (Figure 4-13 shows an example with r_{12}). Common terms and positive covariance offer alternative explanations for the same data, and are thus in a way confounded. In this case, posterior summaries such as the mean or median may not be very informative, given the bimodality.

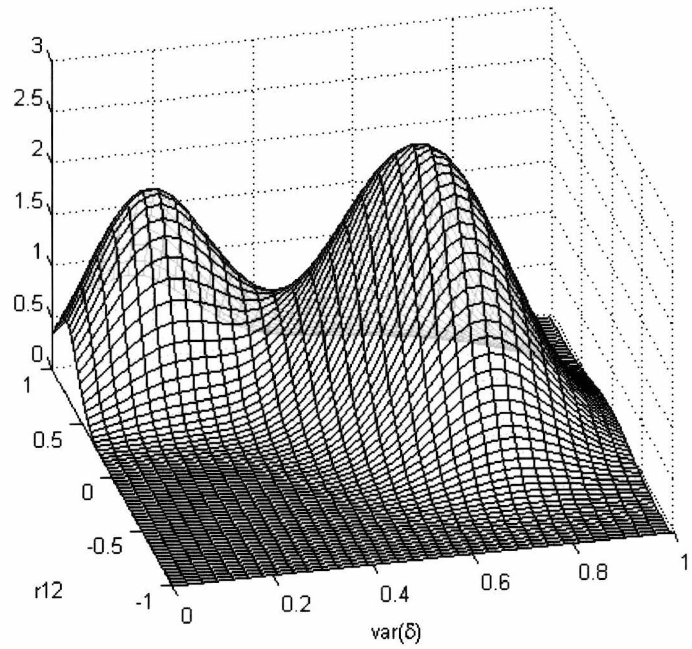


Figure 4-13 Joint posterior distribution (2D-kernel density estimate) of σ_δ^2 ('var(δ)') and r_{12}.

4.2 *Extensions of the synchrony modelling framework*

In the following sections we propose several possible extensions of the multi-species synchrony modelling framework, and suggest potential applications of the framework beyond the multi-species case. Again, we use overall productivity ρ as an example, but the ideas are generally applicable to any demographic parameter of interest.

4.2.1 Detrended synchrony

In all models considered so far, synchrony is defined for the year-to-year variations over a species-specific constant value, the intercept of the logistic regression. This concept can be expanded to defining synchrony on the year-to-year variations over a linear trend with time on the logit scale, with $Y(t)$ = standardised years (subtracting the mean and dividing the difference by the standard deviation), so that

$$\text{logit}\big(\rho_s(t)\big) = \{\alpha_s + \beta_s Y(t)\} + \delta(t) + \varepsilon_s(t). \tag{4.1}$$

This detrended synchrony model is conceptually different from the estimation of the common trend proposed in section 3.1.6: in (4.1) each species has its own linear relationship with time (intercept and slope), while in the 'common trend mode' the slope parameter is common to all species, as its estimation is the focus of the analysis.

We simulate 50 data sets for three species and an increasing number of years (from 5 to 25), with regression parameters $\alpha_s = [1, 1.5, 2.5]$, $\beta_s = [-1, -0.8, -1.5]$, and the same variances for all species: $\sigma_\delta^2 = 1$, $\sigma_\varepsilon^2 = 0.4$ (and thus $I_s = 0.71$). Figure 4-14 plots an example data set generated with such values.

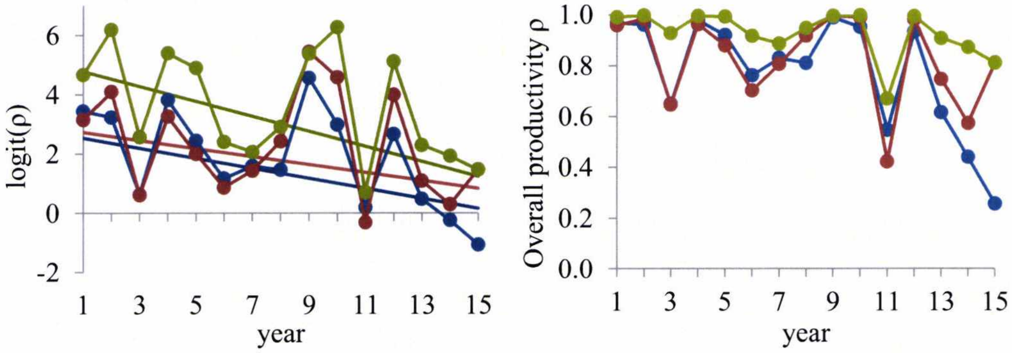


Figure 4-14 Example of 3-species data set ($T = 15$ years) with linear trends (on the logit scale) and synchrony. Left panel: values of logit(ρ) and linear trends. Right panel: productivity ρ on the probability scale. Linear trend parameters: $\alpha_s = [1,1.5,2.5], \beta_s = [-1,-0.8,-1.5]$; random effects variances: $\sigma_\delta^2 = 1, \sigma_\varepsilon^2 = 0.4$.

The results of the simulations (Figure 4-15) show that the model is able to estimate all parameters, including the regression coefficients and the indices of synchrony, with the expected effect of longer time series giving a smaller bias and RMSE.

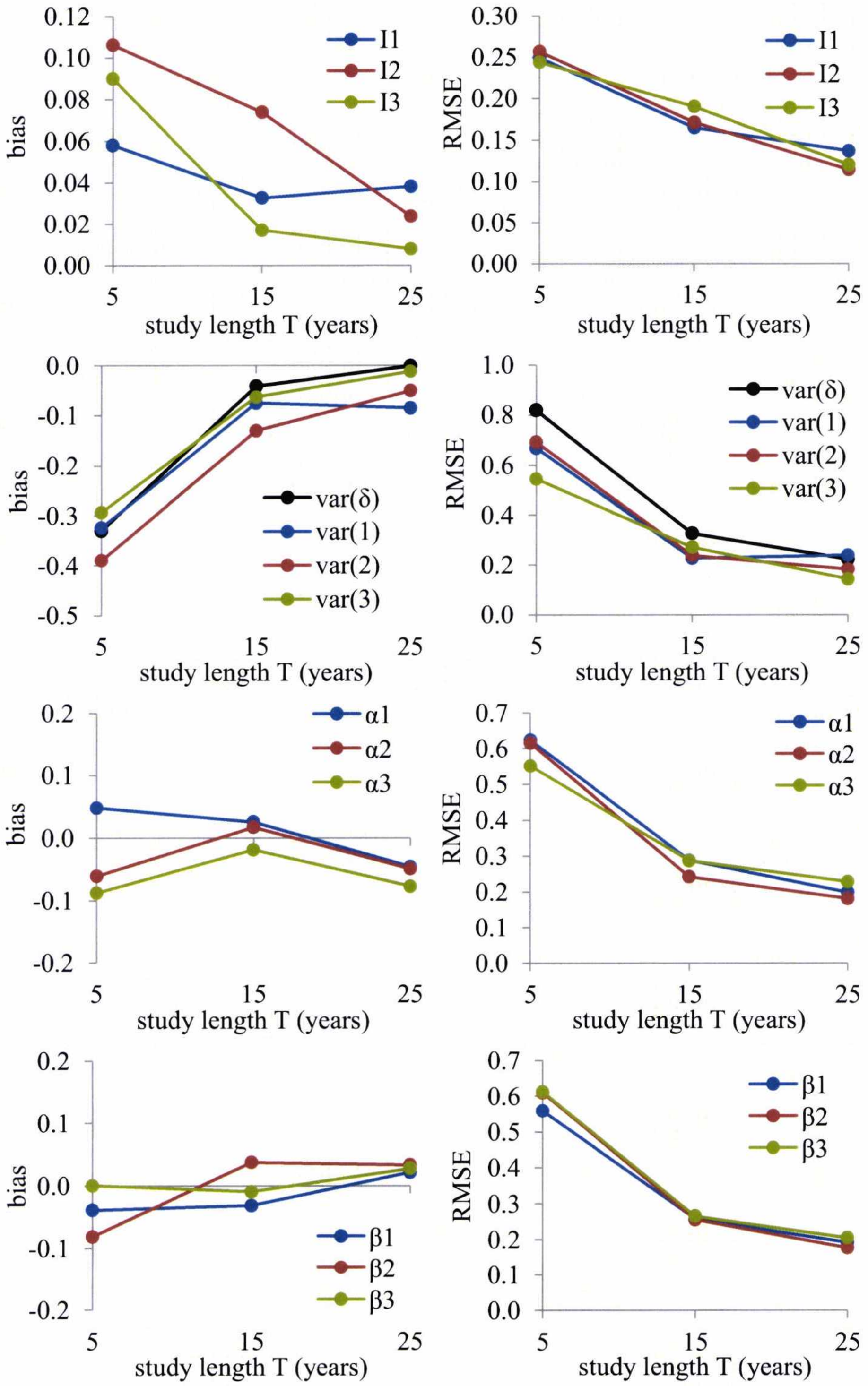


Figure 4-15 Bias (left panels) and RMSE (right panels) of the indices of synchrony (I_s), common (σ_δ^2, denoted 'var(δ)') and species-specific (σ_s^2, denoted 'var(s)') variances, and regression intercepts (α_s) and slopes (β_s) for the detrended synchrony model (50 simulations, 3 species, study length $T = \{5,15,25\}$ years.

The choice of modelling synchrony in the variation over a constant value or over a trend in time is a subjective one that depends on the interest of the study. We also note that more complex relationships with time can alternatively be modelled instead of a linear trend on the logistic scale.

4.2.2 Autocorrelation in the random terms

When a strong temporal autocorrelation is anticipated in the random variation (as in e.g. Ripa & Lundberg 1996), it can be accounted for using a multivariate normal distribution to model the common and/or species-specific random terms, with the covariance structure representing correlation between successive years. We describe here as an example the model for an AR1 structure (1-year autocorrelation) in the common random terms $\delta(t)$ of overall productivity ρ, but the approach can easily be extended to other random terms as well as to longer time-dependence. For each species s and year t, the binomial model and logistic regression with random terms is as previously defined for independent terms

$$F_s(t) \sim Bin\left(E_s(t),\ \rho_s(t)\right),$$

$$\text{logit}\left(\rho_s(t)\right) = \beta_s + \delta(t) + \varepsilon_s(t).$$

In this example, we assume the species-specific random terms to be independent

$$\varepsilon_s(t) \sim N(0, \sigma_s^2).$$

The main difference arises for the common terms, which are now defined as a multivariate normal (MVN) distribution

$$\{\delta(1), \delta(2), \dots, \delta(T)\} \sim \text{MVN}(\mathbf{0}, \mathbf{\Sigma}),$$

$$\mathbf{\Sigma} = \begin{bmatrix} \tilde{\sigma}_\delta^2 & \sigma_t & 0 & \dots & 0 & 0 \\ \sigma_t & \tilde{\sigma}_\delta^2 & \sigma_t & \dots & 0 & 0 \\ 0 & \sigma_t & \tilde{\sigma}_\delta^2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & \tilde{\sigma}_\delta^2 & \sigma_t \\ 0 & 0 & 0 & \dots & \sigma_t & \tilde{\sigma}_\delta^2 \end{bmatrix}.$$

Here $\tilde{\sigma}_\delta^2$ represents the variance of the common terms when the autocorrelation has been taken into account, and σ_t is the covariance between the common terms in consecutive years, $\delta(t)$ and $\delta(t+1), \forall t$. The indices of synchrony can now be defined using the variance of the common terms $\tilde{\sigma}_\delta^2$ as

$$I_s' = \frac{\tilde{\sigma}_\delta^2}{\tilde{\sigma}_\delta^2 + \sigma_s^2}.$$

4.2.3 *Scaled common terms*

An interesting variation on the multi-species synchrony framework presented in previous chapters is to let the common random terms have different variance for each species, unlike in the models shown so far where the $\delta(t)$ terms were exactly the same in all species. In order to achieve this, we define 'species-specific common random terms' $\delta_s(t) = \sigma_{\delta s}\bar{\delta}(t)$, where $\bar{\delta}(t) \sim \mathrm{N}(0,1)$ are common to all species, and $\sigma_{\delta s}^2$ is the species-specific 'variance of the common terms'. For instance for productivity ρ, with species s and year t

$$\mathrm{logit}\big(\rho_s(t)\big) = \beta_{0s} + \delta_s(t) + \varepsilon_s(t) = \beta_{0s} + \sigma_{\delta s}\bar{\delta}(t) + \varepsilon_s(t), \qquad (4.2)$$

where the asynchronous terms are defined as previously, $\varepsilon_s(t) \sim \mathrm{N}(0, \sigma_s^2)$. The indices of synchrony will now be

$$I_s = \frac{\sigma_{\delta s}^2}{\sigma_{\delta s}^2 + \sigma_s^2}.$$

Such a model could find a set of species synchronous even when one species in the set has much lower overall year-to-year variation, unlike when the common random terms are 'common' to all species in the strict sense (as discussed in section 2.2.2).

An alternative formulation of the model is based directly on the total variance of each species (v_s^2) and the indices of synchrony

$$\mathrm{logit}\big(\rho_s(t)\big) = \beta_{0s} + v_s\sqrt{I_s}\bar{\delta}(t) + v_s\sqrt{1 - I_s}\bar{\varepsilon}_s(t),$$

with $\bar{\delta}(t), \bar{\varepsilon}_s(t) \sim \mathrm{N}(0,1)$. This equation is mathematically equivalent to (4.2) and was suggested by Grosbois *et al.* (2009) for the multi-population situation. We note that this model has more parameters to estimate than the synchrony model used in this thesis, for the same amount of data.

4.2.4 Adding a further level of random effects

In cases where species within the set can be classified into groups on the basis of shared ecological traits that might be reflected in the demographic parameter of interest, a further level of random effects could be added to the synchrony model. One way of looking at this 'group-level effect' is to think that the species-specific random terms of the species within the group are positively correlated with a stronger correlation than with species outside the group. The group-level random terms will absorb the variation that is common within that group of species but not to the rest of the set. That is, we effectively partition the overall variation into a hierarchy of levels: 'community' effect (with variance σ_δ^2; for all species in the set), a 'group' effect (with variance σ_γ^2; only for the species that belong to the group) and 'species-specific' effect (with variance σ_s^2 for each species s). The group may be defined for example by a feeding guild, with more closely related variations in productivity, or by the species overwintering in similar geographical areas (and therefore sharing similar variations in mortality).

As an illustration, if we have a community with five species, and species 1, 2 and 3 can be classed as belonging to a common group (e.g. a feeding guild), we can add guild-specific random terms $\gamma_{123}(t)$, only shared between the species that belong to the group, so that productivity can be modelled as

$$\operatorname{logit}\big(\rho_s(t)\big) = \begin{cases} \beta_s + \delta(t) + \gamma_{123}(t) + \varepsilon_s(t), & s \in \{1,2,3\} \\ \beta_s + \delta(t) + \varepsilon_s(t), & s \in \{4,5\} \end{cases}$$

where $\gamma_{123}(t) \sim N\big(0, \sigma_\gamma^2\big)$. The indices of synchrony have to be defined taking into account the estimated variance σ_γ^2, so that for species within the group, the total variance is the sum of community, guild-level and species-specific variances, but only community and species-specific variances are summed for species outside the group:

$$I_s = \begin{cases} \dfrac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_\gamma^2 + \hat{\sigma}_s^2} & s \in \{1,2,3\} \\ \dfrac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2} & s \in \{4,5\} \end{cases}$$

4.2.5 *Multi-species multi-population synchrony*

Few studies address simultaneously spatial and species synchrony (but see Swanson & Johnson 1999). Such a situation could be tackled with a multi-species multi-population framework, combining the multi-population model proposed by Grosbois *et al.* (2009) with the multi-species model presented in this thesis:

$$\operatorname{logit}\left(\rho_{sp}(t)\right) = \beta_{sp} + \delta(t) + \lambda_s(t) + \gamma_p(t) + \varepsilon_{sp}(t). \tag{4.3}$$

Productivity $\rho_{sp}(t)$ for species s in site (or 'population') p and year t would be related to a species-and-site-specific baseline β_{sp} and random effects which would include overall common terms δ, terms specific to species (λ_s) and sites (γ_p), and finally a residual that represent species-and-site-specific terms (ε_{sp}). As in previous models, we assume all random terms to be independent, normally-distributed with zero mean and variances given by

$$\delta(t) \sim \mathrm{N}\left(0, \sigma_\delta^2\right), \forall t$$

$$\lambda_s(t) \sim \mathrm{N}\left(0, \sigma_s^2\right), \forall s, t$$

$$\gamma_p(t) \sim \mathrm{N}\left(0, \sigma_p^2\right), \forall p, t$$

$$\varepsilon_{sp}(t) \sim \mathrm{N}\left(0, \sigma_{sp}^2\right), \forall s, p, t$$

A series of indices of synchrony can be defined for each species s and site p, based on the estimated variances of the random terms

$$I_{sp} = \frac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \left(\hat{\sigma}_s^2 + \hat{\sigma}_p^2 + \hat{\sigma}_{sp}^2\right)}.$$

Such indices represent the percentage of the total year-to-year variation in productivity of the species s at site p that is common to all sites and species.

Alternatively, one could define the indices with respect to the variation in productivity that is specific to that species s at that site p

$$I_{(sp)} = \frac{\left(\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2 + \hat{\sigma}_p^2\right)}{\left(\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2 + \hat{\sigma}_p^2\right) + \hat{\sigma}_{sp}^2}.$$

Note that multi-species-only and multi-population-only synchrony indices could also be derived, conditional on a given site p or species s respectively, and are akin to those presented in this thesis and in Grosbois *et al.* (2009)

$$I_s(p) = \frac{\left(\hat{\sigma}_\delta^2 + \hat{\sigma}_p^2\right)}{\left(\hat{\sigma}_\delta^2 + \hat{\sigma}_p^2\right) + \left(\hat{\sigma}_s^2 + \hat{\sigma}_{sp}^2\right)},$$

$$I_p(s) = \frac{\left(\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2\right)}{\left(\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2\right) + \left(\hat{\sigma}_p^2 + \hat{\sigma}_{sp}^2\right)}.$$

With more parameters to be estimated compared to the multi-species or multi-colony cases, we can expect the requirements in terms of amount of data needed to be able to estimate them to increase.

4.2.6 Multi-parameter synchrony

Estimating the relationship between demographic parameters is of interest in evolutionary ecology and may have implications for conservation management (Wintrebert *et al.* 2005). Positive correlation has been found e.g. between breeding probability and adult survival in the kittiwake (Cam *et al.* 2002). The multi-species synchrony framework can be extended to estimate synchrony in the year-to-year variations of a set of demographic parameters, for a single species. For instance, with the data sets available for the Isle of May guillemots, one could look at synchrony between adult survival (s_a) and productivity (ρ). As we will see in Chapter 5, data are also available to estimate guillemot first-year survival (s_1), and this third parameter could be included in the set. In this case, for each demographic parameter $\theta = \{s_a, s_1, \rho\}$ and year t, we would define common (δ) and parameter-specific (ε_θ) random terms in the three parameters as follows

$$\mathrm{logit}\big(s_1(t)\big) = \beta_{s1} + \delta(t) + \varepsilon_{s1}(t),$$

$$\mathrm{logit}\big(s_a(t)\big) = \beta_{sa} + \delta(t) + \varepsilon_{sa}(t),$$

$$\mathrm{logit}\big(\rho(t)\big) = \beta_\rho + \delta(t) + \varepsilon_\rho(t),$$

where $\delta(t) \sim \mathrm{N}(0, \sigma_\delta^2)$ and $\varepsilon_\theta(t) \sim \mathrm{N}(0, \sigma_\theta^2)$, $\forall t, \forall \theta$, are independent random terms. As defined for multi-species synchrony, the estimated variances of the random terms can be used to calculate indices of synchrony that represent, for each parameter θ, the fraction of the year-to-year variation (on the logit scale) that is common to all parameters in the set

$$I_\theta = \frac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_\theta^2}.$$

In this multi-parameter synchrony model, each demographic parameter can be estimated from an independent data set, with common terms $\delta(t)$ bringing the different likelihood components into a single model. A more robust estimation may be obtained thanks to the integration of demography and population counts with the use of an integrated population model (IPM; introduced in section 5.4).

As an alternative, when it is ecologically reasonable to expect the variations in the different demographic parameters to be of different magnitude, it is worth considering the model with scaled common terms described in section 4.2.3.

4.2.7 Beyond demographic rates: synchrony in site-occupancy

The application of random effects to study multi-species synchrony could be explored for other types of parameters beyond demographic rates. One such example is provided by occupancy models (MacKenzie *et al.* 2006) where detection/non-detection data of an unmarked species collected over repeated visits to a series of sites are used to estimate the proportion of sampled sites where the species is present, taking into account imperfect detection of the species. With constant occupancy ψ and detection probability p, the hierarchical formulation of the basic occupancy model (Royle & Dorazio 2008) consists of a state variable z_i (the true state of site i: occupied or not) and an observation process that models the actual detection/non-detection (coded as 1 or 0) in replicate survey k at site i, $h_{i,k}$:

$$z_i \sim \text{Bernoulli}(\psi),$$

$$h_{i,k} \sim \text{Bernoulli}(pz_i).$$

Covariates can be introduced in both ψ and p through a logit link function.

Occupancy probably fluctuates over time, possibly around a mean value. If we have detection/non-detection data for several species at several sites over a number of years T, and we can assume that the year-to-year variation in site occupancy ψ corresponds to a normally-distributed variation around a mean value on the logit scale, we could model its fluctuations using random terms, as shown in previous chapters for demographic parameters. For species s and year t, occupancy could be modelled as:

$$\text{logit}(\psi_S(t)) = \beta_s + \delta(t) + \varepsilon_s(t), \tag{4.4}$$

where β_s are species-specific baseline values (occupancy may be different for different species), around which the year-to-year variation is partitioned between common (δ) and species-specific (ε_s) year random terms. Year-specific covariates could also be included in the equation above. Also, it is often the case that occupancy varies depending on spatial covariates, characteristics of the sampled sites that influence the probability of the species occupying the site. This dependency could be introduced using site-specific covariates. Overall, a general model that includes residual synchrony could be, for species s, year t and site i:

$$\text{logit}(\psi_S(t,i)) = \beta_{0s} + \sum_{j=1}^{J}\{\beta_{js}c_j(i)\} + \sum_{k=1}^{K}\{\beta'_{ks}c'_k(t)\} + \delta(t) + \varepsilon_s(t). \tag{4.5}$$

In this case, $\psi_s(t, i)$ (the probability of site i being occupied by species s in year t) depends on a set of J site-specific covariates c_j, a set of K year-specific covariates c'_k and two random terms. The variance of the common terms $\delta(t)$ represents the variation of occupancy over time that is synchronous to all species considered, while the variances of the species-specific terms $\varepsilon_s(t)$ correspond to the asynchronous components. The derivation of indices of synchrony and the contribution of the year-specific covariates in synchronising and desynchronising occupancy over time is then straightforward. We note that in (4.5), the random terms represent residual variation after the spatial variation and part of the temporal variation have been accounted for by the spatial and temporal covariates; the derived indices therefore represent synchrony in such residual terms.

Finally, we note that multispecies occupancy models have already been proposed to study communities (e.g. Russell *et al.* 2009) although not specifically targeted to investigate synchrony in occupancy.

4.3 Discussion

This chapter presents the first exploration of the performance and properties of the concept of synchrony defined with respect to the common variation, as used in this thesis for multi-species and multi-parameter analyses, and in Grosbois *et al.* (2009) for single-species multi-population analyses.

We use simulated data to verify that bias in the estimation of synchrony reduces as the number of years of the study increases, noting e.g. that for three species the estimation of synchrony based on fewer than about 10 years appear positively biased and rather imprecise. We highlight again the fact that these synchrony models take into account the magnitude of the variations, and that a species with small variance may limit the amount of common variation. Also, as expected, the estimation of the species-specific baselines (the intercepts in the logistic regressions) appears more robust than that of variances. Although specific recommendations should be based on targeted simulations constructed for the system of interest, it is clear that to estimate random effect variances, and therefore synchrony, long (> 10 years) time series of demographic data have to be collected, especially when the set consist of few species. This point highlights the importance of long-term monitoring programs like that at the Isle of May.

For a given configuration (number of species, number of years, variances), we propose a Monte Carlo test to determine the level of spurious synchrony that may be estimated stochastically from independent species: estimates of synchrony that are above that level are indicative of a synchronous response of the species to variations in their environment. In the case of the Isle of May 5-species productivity analysis, we show that all estimated synchrony indices are above the spurious levels obtained from simulation of independent data sets, suggesting that such indices do not represent stochastically-generated synchrony.

We also demonstrate that there is a relationship between the existence of the common random terms (necessary for synchrony) and correlation of the year-to-year variations in the demographic parameter of interest. As common terms and covariance are related, we caution against estimating a full covariance structure and the common terms simultaneously, as the resulting model could be overparameterised. We recall here that negative correlation is not estimated as synchrony in this modelling framework. We show that the variance-covariance structure of the overall variation can be estimated with a valid model, but that such a model does not shed light into synchrony as defined in this thesis (i.e. with respect to the common variation in the community under study). We end the section noting an interesting relationship with the first principal component of PCA.

In the second part of the chapter, we propose several model extensions that may be of interest in different circumstances, from detrended synchrony to the addition of intermediate grouping levels in the random effects to reflect e.g. feeding guilds. Some indications are also given regarding how the synchrony modelling framework could be extended beyond the multi-species demography scenario. We nevertheless caution that the properties of these models should be studied more carefully before they are applied in practice.

5 BRINGING IT ALL TOGETHER: INTEGRATED POPULATION MODELLING OF THE ISLE OF MAY SEABIRD COMMUNITY

The modelling so far has concentrated on multi-species synchrony of one single demographic aspect at a time, either adult survival (Chapter 2) or breeding-success related parameters (Chapter 3). In this chapter we proceed to integrate data not only for several species but also for several demographic parameters together with population counts, into a single 'integrated population model' (IPM) that jointly models abundance and the demographic parameters that drive its fluctuations, in a single likelihood. The concept and context of integrated population models (IPM) have been introduced in Chapter 1. Here we start by describing the structure of independent integrated population models for each of the three auk species at the Isle of May: the Atlantic puffin, the common guillemot and the razorbill. These three species are then modelled jointly, estimating multi-species synchrony in adult survival and overall productivity, in what to our knowledge constitutes the first 'multi-species' integrated population model (msIPM).

5.1 Single-species Integrated Population Models (ssIPM)

Three sources of data are available for puffins, guillemots and razorbills at the Isle of May. Two of these have already been mentioned in previous chapters: mark-resight data of individuals marked as breeding adults of unknown age (Chapter 2) and total counts of fledged chicks out of a number of monitored nests (Chapter 3). A third type consists of colony counts of breeding pairs, conducted annually for guillemots and razorbills and less frequently for puffins. In the particular case of guillemots, two extra data sets are also available: mark-resight-recovery data from individuals ringed as chicks and proportions of breeding pairs that skipped breeding in different years. Although some of these data sets exist for different time periods for the 3 species considered, we restrict the modelling to the common years (1984-2009), so that when the multi-species IPM is constructed using random terms for estimating synchrony in adult survival and in productivity, such terms can be defined across species. We denote the $T = 26$ years of data by $t = 1, \ldots, T$. The individual data sets and corresponding 'single-species' IPMs (ssIPM) models are described in more detail in the next sections.

In all three ssIPMs, a state-space model (Buckland *et al.* 2004; King *et al.* 2009, p.307) is used to model population counts, which consists of two linked models: a system process and an observation process. First of all, a system process model describes the true population abundance $\boldsymbol{N}(t+1)$ for the different age classes at year $t+1$, as a function of the previous year's abundance, incorporating the values of relevant demographic parameters. We will describe the structure of the population model for each species in a compact way using a Leslie matrix (Caswell 2001). The degree of complexity (and realism) of the ssIPM for each species obviously depends on the data sets available and the ecology of the species.

The general structure of the population models for the three auks is described in Figure 5-1. The abundance of breeding adults $\boldsymbol{N_a}$ actually refers to that of breeding females, which is equivalent to the number of breeding pairs as the three species considered are monogamous (Gaston & Jones 1998). A number $N_a(t)$ of breeding females in year t will produce a single egg. Each egg has a probability $\rho(t)$ (overall productivity in year t) of hatching and the chick surviving until fledging. A factor 0.5 is included to take into account that on average only half of the chicks will be females (balanced sex ratio at fledging). The number of female fledglings in year t will therefore be

$$G(t) \sim \mathrm{Bin}(N_a(t), \rho(t)/2).$$

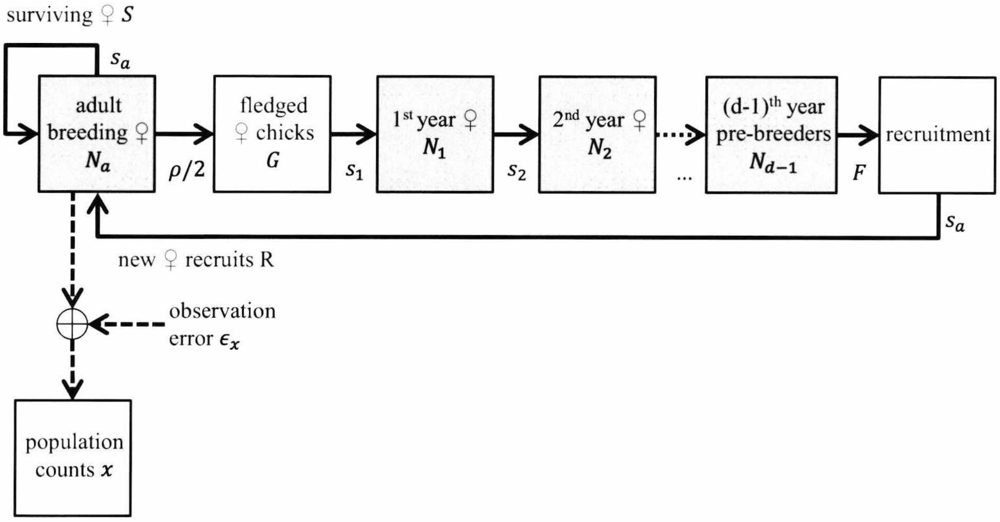


Figure 5-1 Generic structure of the integrated population model for an auk species at the Isle of May. Shaded boxes represent the abundance of the different age-classes (1st year to (d-1)th year, and 'adult'). Dashed lines represent the observation process. Age of first breeding: d. Other model parameters are described in the text.

Only a fraction of these fledglings will survive their first winter, so that the number of 'age 1' females at time $t + 1$will be:

$$N_1(t+1) \sim \mathrm{Bin}\big(G(t), s_1(t)\big),$$

where $s_1(t)$ is the survival probability over the first year of life. The number of immature females of increasing age can be modelled in the same way using binomial distributions with the corresponding age-specific survival probabilities. Although age at first breeding will vary between individuals of the same species, we model recruitment using the median value of age at first breeding, denoted d_s for species s. Pre-breeders $N_{d-1}(t)$ represent the number of females in the year before first breeding. A non-negligible fraction of the puffins and guillemots born at the Isle of May permanently emigrate and recruit to other colonies (Harris, Halley & Wanless 1996; Harris & Wanless 2011). Although pre-breeder emigration has not been studied in Isle of May razorbills, we assume that a substantial minority of Isle of May immature razorbills recruit to other colonies, based on results from Skokholm (Lloyd 1974). We define fidelity F (1- probability of permanent emigration) as the probability of an individual female recruiting into the Isle of May breeding population, which we assume constant for simplicity. We also assume that survival over the winter immediately before recruiting is equal to that of adult birds, s_a, so that the number of new recruits $R(t)$ in the female adult population in year t will be

$$R(t) \sim \mathrm{Bin}\big(N_{d-1}(t-1), Fs_a(t-1)\big).$$

In practice, we do not have enough data directly related to immature razorbills and puffins that would allow us to separate pre-breeder emigration from mortality, or to estimate age-dependent survival probabilities, so for these species we use a 'combined survival' parameter ϕ_c which includes survival since fledging to the year before recruitment, as well as fidelity. Note that since permanent emigration and mortality are in this case confounded, we sould rather talk about 'apparent survival' (which we denote by letter ϕ) than 'true survival' s; we follow this common naming convention (White & Burnham 1999) throughout this chapter. With this simplification, the number of new recruits for razorbills and puffins can be modelled as

$$R(t) \sim \mathrm{Bin}\left(N_a(t-d), \rho(t-d)\frac{1}{2}\phi_c s_a(t-1)\right).$$

From the already existing female adult population at time $t-1$, individuals will survive to year t with probability s_a: $S(t) \sim \mathrm{Bin}\big(N_a(t-1), s_a(t-1)\big)$. The total number of adult breeding females at year t will therefore be the sum of the surviving adults and the new female recruits, that is, $N_a(t) = S(t) + R(t)$. Established breeding adults of the three species rarely move to other colonies (Gaston & Jones 1998) so we assume adult emigration is very low and therefore set adult fidelity $F_a = 1$ in the IPMs. Although a minority of birds born in other colonies is expected to immigrate and recruit into the Isle of May population (razorbills in Skokholm, Lloyd 1974; Halley & Harris 1993; Harris & Wanless 2011), our models assume that there is no immigration as we do not have data to estimate it.

Figure 5-2 shows the parameters involved in a generic population model for a species with an age of first breeding of $d = 5$, with a clarification on how we define year indices for adult survival $\boldsymbol{s}$, population abundance $\boldsymbol{N_a}$ and productivity $\boldsymbol{\rho}$, as well as age.

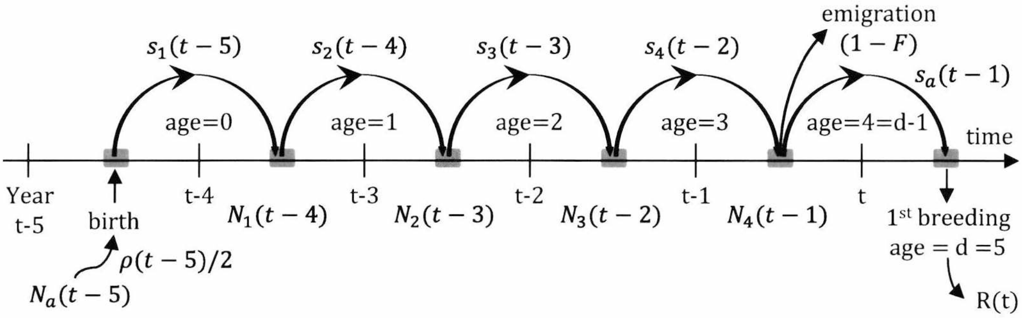


Figure 5-2 Diagram of the different parameters involved in the population model of a species with age of first breeding of $d = 5$ (e.g. razorbills). The year mark indicates the start of the calendar year and we assume that the breeding season happens roughly in the middle of the year. Age is defined for the interval between breeding seasons.

An observation model relates an imperfect observation of abundance to the true state of the system: the abundance of female breeders $N_a(t)$. The imperfect observation consists of population counts $x(t)$ of adult breeding pairs over the whole Isle of May between $t = 1$ and $t = T$. Island-wide counts have been carried out annually for guillemots and razorbills and less frequently for puffins. We model these counts with a normally distributed observation error with variance σ_x^2:

$$x(t) \sim \mathrm{N}(N_a(t), \sigma_x^2), \qquad t \in \{d+1, \dots, T\}.$$

We only model counts starting in year $d + 1$: as only the adult age class is counted in the Isle of May monitoring, there is no direct source of information about the abundance of the younger age classes for the first d years modelled and thus the counts for the first d years cannot be related to N_a abundance modelled as a function of parameters and immature abundance. We use the counts for the first d years to initialise the population model for that period $t \in \{1, \dots, d\}$, by setting informative normal priors for the adult population, assuming the same variance as for the observation error:

$$N_a(t) \sim \mathrm{N}(x(t), \sigma_x^2), \qquad t \in \{1, \dots, d\}.$$

In practice, the value obtained from the normal distribution is rounded to the nearest integer. We note that alternative initialisation methods have been proposed for the Kalman filter in the frequentist approach (Besbeas, Borysiewicz & Morgan 2009; Besbeas & Morgan 2012a) although their application in the Bayesian approach has not been investigated.

The following sections describe the specific data sets and ssIPMs for razorbills, puffins and guillemots, with a more detailed account of the parameters involved and their relationship through the integrated population model. We note that in the ssIPMs, the random effects used in the estimation of synchrony are not present. They will be added to the model when jointly modelling the three auk species (section 5.5). In the following sections, we use parameter subscripts (or superscripts in likelihood functions) for simplicity to identify the species, with razorbills denoted by 'R', puffins by 'P' and guillemots by 'G'.

5.2 *Razorbill IPM*

5.2.1 *Adult mark-resight data set*

Between 1984 and 2009, 163 razorbills were marked as breeding adults at the Isle of May. A total of 3620 live resightings were collected from 1985 to 2009, and the MR data summarised as an m-array $\boldsymbol{m_R}$. We model this data set according to the standard open-population Cormack-Jolly-Seber (CSJ) model as explained in section 2.3.3, assuming no adult emigration (so that estimated parameters are true survival: $\phi_a = s_a$) and fully year-dependent survival probabilities, $\boldsymbol{s_{aR}} = \{s_{aR}(t): t = 1, \dots, T-1\}$. Adults are marked using a combination of colours in three colour-rings and a uniquely numbered metal ring, and we assume that adults remain identifiable through their life (M. P. Harris, *personal communication*). Resight probability is also year-dependent and includes trap-dependence so that, for each individual, its value depends on the year (with a year-dependent variable $\boldsymbol{p_R^*} = \{p_R^*(t): t = 1, \dots, T-1\}$) and on whether the individual was resighted or not the year before (with a constant a_R; see section

2.3.4). Full details of the MR model and the expression of the likelihood $L^R_{MR(A)}(\boldsymbol{m_R}|\boldsymbol{s_{aR}}, \boldsymbol{p^*_R}, a_R)$ can be found in sections 2.3.1 and 2.3.4.

5.2.2 Breeding success data set

As described in section 3.1.2, breeding success data consist of a series of yearly counts of razorbill chicks $C_R(t)$ that fledge from a number of monitored adult pairs $E_R(t)$ that make a breeding attempt. $E_R(t)$ ranged from 73 to 194 depending on the year, with a mean of 135 pairs. As razorbills lay a single egg, data can be modelled as a binomial variable $C_R(t) \sim \text{Bin}\big(E_R(t), \rho_R(t)\big)$, where $\rho_R(t)$ is the overall productivity of razorbills in year t. We represent the data using vectors $\boldsymbol{C_R} = \{C_R(t): t \in (1, \dots, T)\}$ and $\boldsymbol{E_R} = \{E_R(t): t \in (1, \dots, T)\}$, and the full data set as $\boldsymbol{P_R} = \{\boldsymbol{C_R}, \boldsymbol{E_R}\}$. Letting $\boldsymbol{\rho_R} = \{\rho_R(t): t \in (1, \dots, T)\}$ be the set of overall productivity parameters, the likelihood corresponding to the binomial model for the razorbill breeding success data set is

$$L^R_{BS}(\boldsymbol{P_R}|\boldsymbol{\rho_R}) = \prod_{t=1}^{T} \binom{E_R(t)}{C_R(t)} \rho_R(t)^{C_R(t)} \{1 - \rho_R(t)\}^{E_R(t) - C_R(t)}. \tag{5.1}$$

5.2.3 Breeding population counts data set

We model the time-series of counts of adult female razorbill breeding pairs $N_a(t)$ using a state-space model. There are not enough data from ringed razorbill chicks to attempt modelling the resighting and ring-recoveries for these individuals at the Isle of May. As a consequence of the lack of direct data on immature survival, the IPM assumes a constant 'combined immature survival' ϕ_{cR} which combines survival from fledging to the year before first breeding, as well as pre-breeder fidelity (and thus represents apparent survival). We use an age of first breeding $d_R = 5$ years, the median value ($n = 20$) obtained from razorbills at Skokholm Island in Wales (Lloyd & Perrins 1977). Due to lack of detailed data on razorbills skipping breeding in a particular year, the model assumes that all breeding birds breed every year. The resulting matrix population model and Leslie matrix $\boldsymbol{M^R_t}$ for the razorbill system process model are:

$$\begin{pmatrix} N_{1\mathrm{R}} \\ N_{2\mathrm{R}} \\ N_{3\mathrm{R}} \\ N_{4\mathrm{R}} \\ N_{aR} \end{pmatrix}_{\mathrm{t+1}} = \mathbf{M}_{\mathbf{t}}^{\mathbf{R}} \cdot \begin{pmatrix} N_{1\mathrm{R}} \\ N_{2\mathrm{R}} \\ N_{3\mathrm{R}} \\ N_{4\mathrm{R}} \\ N_{aR} \end{pmatrix}_{t} + \begin{pmatrix} \eta_{1\mathrm{R}} \\ \eta_{2\mathrm{R}} \\ \eta_{3\mathrm{R}} \\ \eta_{4\mathrm{R}} \\ \eta_{aR} \end{pmatrix}_{t},$$

$$\boldsymbol{M_t^R} = \begin{pmatrix} 0 & 0 & 0 & 0 & \rho_R(t)\frac{1}{2}\phi_{cR}^{*} \\ \phi_{cR}^{*} & 0 & 0 & 0 & 0 \\ 0 & \phi_{cR}^{*} & 0 & 0 & 0 \\ 0 & 0 & \phi_{cR}^{*} & 0 & 0 \\ 0 & 0 & 0 & F_R s_{aR}(t) & s_{aR}(t) \end{pmatrix},$$

where $\phi_{cR} = (\phi_{cR}^{*})^4 F_R$ and the η_{xR} represent additive binomial error terms that account for the fact that the model is stochastic. The number of new razorbill recruits $\boldsymbol{R_R} = \{R_R(t)\colon t = 6, \dots, T\}$, surviving adult females $\boldsymbol{S_R} = \{S_R(t)\colon t = 6, \dots, T\}$ and total adult breeding female razorbills $\boldsymbol{N_{aR}} = \{N_{aR}(t)\colon t = 6, \dots, T\}$ can be modelled as

$$R_R(t) \sim \mathrm{Bin}\left(N_{aR}(t-5), \rho_R(t-5)\frac{1}{2}\phi_{cR}s_{aR}(t-1)\right),$$

$$S_R(t) \sim \mathrm{Bin}\big(N_{aR}(t-1), s_{aR}(t-1)\big),$$

$$N_{aR}(t) = R_R(t) + S_R(t).$$

Letting $\rho_R(t-5)\frac{1}{2}\phi_{cR} = \tau_R(t-5)$ for notational simplicity, the 'likelihood' of the system process model can be written as

$$\begin{aligned} &L_N^R(\boldsymbol{R_R}, \boldsymbol{S_R} | \phi_{cR}, \boldsymbol{s_{aR}}, \boldsymbol{\rho_R}) \\ &\quad = \prod_{t=6}^{T} \Bigg[\binom{N_{aR}(t-5)}{R_R(t)} \{\tau_R(t-5)s_{aR}(t-1)\}^{R_R(t)} \\ &\quad \cdot \{1-\tau_R(t-5)s_{aR}(t-1)\}^{N_{aR}(t-5)-R_R(t)} \\ &\quad \cdot \binom{N_{aR}(t-1)}{S_R(t)} \{s_{aR}(t-1)\}^{S_R(t)}\{1-s_{aR}(t-1)\}^{N_{aR}(t-1)-S_R(t)}\Bigg]. \end{aligned}$$

Note that L_N^R is not a true likelihood strictly speaking (it does not involve the observed data) but rather a description of the unobserved underlying population changes; it can also be thought as a prior of the true population abundance (King *et al.* 2009, p.313).

Given the razorbill population counts $\boldsymbol{x_R} = \{x_R(t): t = 6, \dots, T\}$, the likelihood of the observation process can be written as

$$L_{OBS}^R(\boldsymbol{x_R}|\boldsymbol{N}_{aR}, \sigma_{xR}^2) = \prod_{t=6}^{T} \left[\frac{1}{\sigma_{xR}\sqrt{2\pi}} \cdot \exp\left(-\frac{\{x_R(t) - N_{aR}(t)\}^2}{2\sigma_{xR}^2} \right) \right].$$

Finally, the likelihood of the razorbill state-space population model (L_{POP}^R) is the product of the likelihood of the observation model (L_{OBS}^R) and the system process model (L_N^R):

$$\begin{aligned} &L_{POP}^R(\boldsymbol{x_R}|\boldsymbol{R_R}, \boldsymbol{S_R}, \phi_{cR}, \boldsymbol{s_{aR}}, \boldsymbol{\rho_R}, \sigma_{xR}^2) \\ &\qquad = L_{OBS}^R(\boldsymbol{x_R}|\boldsymbol{R_R}, \boldsymbol{S_R}, \sigma_{xR}^2) \times L_N^R(\boldsymbol{R_R}, \boldsymbol{S_R}|\phi_{cR}, \boldsymbol{s_{aR}}, \boldsymbol{\rho_R}). \end{aligned}$$

5.2.4 Joint likelihood: razorbill ssIPM

Assuming independence between the different data sets involved, the joint likelihood of the razorbill ssIPM model over the parameters and unobserved population abundance can be found by multiplying the likelihoods of the different components of the model:

$$\begin{aligned} &L_{IPM}^R(\boldsymbol{x_R}, \boldsymbol{m_R}, \boldsymbol{P_R}|\boldsymbol{R}_R, \boldsymbol{S_R}, \phi_{cR}, \boldsymbol{s_{aR}}, \boldsymbol{p_R^*}, a_R, \boldsymbol{\rho_R}) \\ &\qquad = L_{POP}^R(\boldsymbol{x_R}|\boldsymbol{R}_R, \boldsymbol{S_R}, \phi_{cR}, \boldsymbol{s_{aR}}, \boldsymbol{\rho_R}, \sigma_{xR}^2) \times L_{MR(A)}^R(\boldsymbol{m_R}|\boldsymbol{s_{aR}}, \boldsymbol{p_R^*}, a_R) \\ &\qquad \times L_{BS}^R(\boldsymbol{P_R}|\boldsymbol{\rho_R}). \end{aligned}$$

Table 5-1 (in page 162) shows the parameters that are shared between different ssIPM components.

5.3 *Atlantic puffin IPM*

5.3.1 *Adult mark-resight data set*

A total of 578 puffins were ringed as breeding adults at the Isle of May between 1984 and 2008, with 3620 live resightings obtained from 1985 to 2009 summarised in the form of a summary m-array $\boldsymbol{m_P}$. We model this MR data set using the standard open-population Cormack-Jolly-Seber (CSJ) model as explained in section 2.3.3, assuming no adult emigration and fully year-dependent survival probabilities $\boldsymbol{s_{aP}} = \{s_{aP}(t): t = 1, \dots, T-1\}$. Resight probability is also year-dependent and includes trap-dependence; the related parameters involved in the likelihood are the year-dependent $\boldsymbol{p_P^*} = \{p_P^*(t): t = 1, \dots, T-1\}$ and a trap-dependence constant a_P. Full details of the MR model and the expression of the likelihood $L_{MR(A)}^{P}(\boldsymbol{m_P} | \boldsymbol{s_{aP}}, \boldsymbol{p_P^*}, a_P)$ can be found in sections 2.3.1 and 2.3.4.

5.3.2 *Breeding success data set*

In the case of puffins, the number of monitored breeding pairs ranged from 32 to 196, with a mean of 159 pairs (only 1984 and 1985 had fewer than 100 burrows monitored). We model puffin breeding success data with the same binomial model structure as described for razorbills in section 5.2.2:

$$L_{BS}^{P}(\boldsymbol{P_P} | \boldsymbol{\rho_P}) = \prod_{t=1}^{T} \binom{E_P(t)}{C_P(t)} \rho_P(t)^{C_P(t)} \{1 - \rho_P(t)\}^{E_P(t) - C_P(t)},$$

where $\boldsymbol{\rho_P} = \{\rho_P(t): t \in (1, \dots, T)\}$ is the set of puffin overall productivity parameters and $\boldsymbol{P_P} = \{\boldsymbol{C_P}, \boldsymbol{E_P}\}$ represents the full breeding success data set, with $\boldsymbol{C_P} = \{C_P(t): t \in (1, \dots, T)\}$ being the number of fledglings and $\boldsymbol{E_P} = \{E_P(t): t \in (1, \dots, T)\}$ the number of monitored pairs.

5.3.3 *Breeding population counts data set*

As for razorbills, we do not incorporate into the puffin ssIPM any data directly related to immature survival (e.g. data from puffins marked as chicks). Consequently, we assume an apparent ‘combined immature survival’ ϕ_{cP} which incorporates the survival probabilities of all stages between fledging to recruiting into the Isle of May population. The model also assumes that adult breeding females breed every year as we do not have data to model individuals skipping breeding. We use $d_P = 7$ as age of first breeding (obtained from $n = 108$ chicks at the Isle of May; M. P. Harris, *personal communication*). In the case of puffins, population counts are only available for seven years within the study period. Years 1984 and 1989 are used to create the priors for initialising the population model (missing years between 1984 and 1990 are interpolated linearly). Only the counts of years 1992, 1998, 2003, 2008 and 2009 fall within the period in which the population model is already initialised. The model is fitted only to the observations of these years, but is able to obtain marginal posterior distributions for the true adult population for all years.

The system process model is described with the following equation and Leslie matrix $\boldsymbol{M}_t^P$:

$$\begin{pmatrix} N_{1\mathrm{P}} \\ N_{2\mathrm{P}} \\ N_{3\mathrm{P}} \\ N_{4\mathrm{P}} \\ N_{5\mathrm{P}} \\ N_{6\mathrm{P}} \\ N_{a\mathrm{P}} \end{pmatrix}_{\mathrm{t+1}} = \boldsymbol{M}_t^P \cdot \begin{pmatrix} N_{1\mathrm{P}} \\ N_{2\mathrm{P}} \\ N_{3\mathrm{P}} \\ N_{4\mathrm{P}} \\ N_{5\mathrm{P}} \\ N_{6\mathrm{P}} \\ N_{a\mathrm{P}} \end{pmatrix}_{\mathrm{t}} + \begin{pmatrix} \eta_{1\mathrm{P}} \\ \eta_{2\mathrm{P}} \\ \eta_{3\mathrm{P}} \\ \eta_{4\mathrm{P}} \\ \eta_{5\mathrm{P}} \\ \eta_{6\mathrm{P}} \\ \eta_{a\mathrm{P}} \end{pmatrix}_{t},$$

$$\boldsymbol{M}_t^P = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \frac{\rho_P(t)}{2}\phi_{cP}^* \\ \phi_{cP}^* & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_{cP}^* & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_{cP}^* & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_{cP}^* & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_{cP}^* & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & F_P s_{aP}(t) & s_{aP}(t) \end{pmatrix},$$

where $\phi_{cP} = (\phi_{cP}^*)^6 F_P$ and the η_{xP} are additive binomial error terms that account for the model stochasticity. According to this model, the number of new puffin recruits $\boldsymbol{R_P} = \{R_P(t)\colon t = 8, \dots, T\}$, surviving adult females $\boldsymbol{S_P} = \{S_P(t)\colon t = 8, \dots, T\}$ and total adult breeding female puffins $\boldsymbol{N_{aP}} = \{N_{aP}(t)\colon t = 8, \dots, T\}$ can be modelled as

$$R_P(t) \sim \mathrm{Bin}\left(N_{aP}(t-7), \rho_P(t-7)\frac{1}{2}\phi_{cP} s_{aP}(t-1)\right),$$

$$S_P(t) \sim \text{Bin}\big(N_{aP}(t-1), s_{aP}(t-1)\big),$$

$$N_{aP}(t) = R_P(t) + S_P(t).$$

Letting $\rho_P(t-7)\frac{1}{2}\phi_{cP} = \tau_P(t-7)$, the likelihood of the system process model is

$$\begin{aligned} & L_N^P(\boldsymbol{R_P}, \boldsymbol{S_P} | \phi_{cP}, \boldsymbol{s_{aP}}, \boldsymbol{\rho_P}) \\ & \quad = \prod_{t=8}^{T} \Bigg[\binom{N_{aP}(t-7)}{R_P(t)} \{\tau_P(t-7) s_{aP}(t-1)\}^{R_P(t)} \\ & \quad \cdot \{1 - \tau_P(t-7) s_{aP}(t-1)\}^{N_{aP}(t-7) - R_P(t)} \\ & \quad \cdot \binom{N_{aP}(t-1)}{S_P(t)} \{s_{aP}(t-1)\}^{S_P(t)} \{1 - s_{aP}(t-1)\}^{N_{aP}(t-1) - S_P(t)} \Bigg]. \end{aligned}$$

Given the puffin population counts $\boldsymbol{x_P} = \{x_P(t) \colon t \in \boldsymbol{\theta_t}\}$, available in years $\boldsymbol{\theta_t} = \{9, 15, 20, 25, 26\}$, the likelihood of the observation process can be written as

$$L_{OBS}^P(\boldsymbol{x_P} | \boldsymbol{N}_{aP}, \sigma_{xP}^2) = \prod_{t \in \theta_t} \left[\frac{1}{\sigma_{xP}\sqrt{2\pi}} \cdot \exp\left(-\frac{\{x_P(t) - N_{aP}(t)\}^2}{2\sigma_{xP}^2} \right) \right].$$

We obtain the likelihood of the state-space population model (L_{POP}^P) as the product of the likelihood of the observation (L_{OBS}^P) and system (L_N^P) process models:

$$\begin{aligned} & L_{POP}^P(\boldsymbol{x_P} | \boldsymbol{R_P}, \boldsymbol{S_P}, \phi_{cP}, \boldsymbol{s_{aP}}, \boldsymbol{\rho_P}, \sigma_{xP}^2) \\ & \qquad = L_{OBS}^P(\boldsymbol{x_P} | \boldsymbol{R_P}, \boldsymbol{S_P}, \sigma_{xP}^2) \times L_N^P(\boldsymbol{R_P}, \boldsymbol{S_P} | \phi_{cP}, \boldsymbol{s_{aP}}, \boldsymbol{\rho_P}). \end{aligned}$$

5.3.4 Joint likelihood: puffin ssIPM

Assuming independence between the data sets, the joint likelihood of the IPM model can be found by multiplying the likelihoods of the different components of the model:

$$\begin{aligned} & L_{IPM}^P(\boldsymbol{x_P}, \boldsymbol{m_P}, \boldsymbol{P_P} | \boldsymbol{R_P}, \boldsymbol{S_P}, \phi_{cP}, \boldsymbol{s_{aP}}, \boldsymbol{p_P^*}, a_P, \boldsymbol{\rho_P}) \\ & \qquad = L_{POP}^P(\boldsymbol{x_P} | \boldsymbol{R}_P, \boldsymbol{S_P}, \phi_{cP}, \boldsymbol{s_{aP}}, \boldsymbol{\rho_P}, \sigma_{xP}^2) \times L_{MR(A)}^P(\boldsymbol{m_P} | \boldsymbol{s_{aP}}, \boldsymbol{p_P^*}, a_P) \\ & \qquad \times L_{BS}^P(\boldsymbol{P_P} | \boldsymbol{\rho_P}). \end{aligned}$$

Table 5-1 (in page 162) shows the parameters that are shared between different ssIPM components.

5.4 *Common guillemot IPM*

The common guillemot ssIPM is substantially different from those of puffin and razorbill as more data sets are available: data on birds skipping breeding in a particular year, and mark-resight-recovery data from guillemots ringed as chicks, which contributes valuable information regarding immature survival and emigration.

5.4.1 *Adult mark-resight data set*

A total of 837 guillemots were ringed as breeding adults at the Isle of May between 1984 and 2008, and live resightings collected between 1985 and 2009 were summarised as an m-array $\boldsymbol{m_G}$. We model this data set with the standard open-population Cormack-Jolly-Seber (CSJ) model, as described in section 2.3.3. We assume no adult emigration and fully year-dependent survival $\boldsymbol{s_{aG}} = \{s_{aG}(t): t = 1, \dots, T-1\}$. Resight probability depends on the year and on whether the individual was resighted the season before (controlled by parameters $\boldsymbol{p_G^*} = \{p_G^*(t): t = 1, \dots, T-1\}$ and a_G respectively). Sections 2.3.1 and 2.3.4 provide more details of the model as well as the expression of the corresponding likelihood $L_{MR(A)}^{G}(\boldsymbol{m_G} | \boldsymbol{s_{aG}}, \boldsymbol{p_G^*}, a_G)$.

5.4.2 *Chick mark-resight-recovery data set*

A total of 6569 common guillemot chicks were ringed at the colony on the Isle of May between 1984 and 2009 (annual totals ringed ranged from 113 to 325, with mean 253). Each chick was given a unique colour ring on one leg (inscribed with an individual code) and a numbered metal ring on the other. Two areas were used: a 400-m length of cliff ('area A') and a nearby skerry ('area B') of lesser visibility; chicks were only ringed in the latter area up until 1997 (1356 chicks in total). Full details about the field methods are given in Harris, Frederiksen & Wanless (2007). From 1985 to 2010, regular searches were made during the breeding season for ringed birds that had returned to the Isle of May. This resulted in 11388 individual resightings (excluding the initial capture) which translated into 4738 detections in the mark-resight history (as the raw resightings include individuals seen more than once in a breeding season). An additional 248 ring recoveries from dead guillemots found on the Isle of May and elsewhere were collected up to 2009. All resightings occurred at the Isle of May, but with the inclusion of data on rings recovered outside the breeding colony the model is able to estimate true survival and fidelity separately, as opposed to apparent survival (the combined effect of both) in mark-recapture studies (Burnham 1993).

We start by describing the likelihood corresponding to the guillemot chick mark-resight-recovery data ('MRR(C)') with a generic age and year-dependence structure, based on a computationally-efficient multi-state approach that uses sufficient statistic matrices (McCrea 2012). For this we define two mutually-exclusive states, which allow the modelling of emigration:

(i) State 1 ('Isle of May'): the individual has not permanently emigrated and recruited to another population outside the Isle of May;

(ii) State 0 ('Emigrated'): the individual has taken the decision of permanently emigrating and recruiting into another breeding colony. Such birds do not contribute to population abundance at the Isle of May. The state is unobserved although rings can still be recovered from dead birds in this state.

We note that state 1 obviously does not imply that the bird lives permanently at the Isle of May (none of the auks do) but that it visits the Isle of May during the breeding season (either as an immature that has not recruited yet or as a breeding adult that has recruited into the Isle of May breeding population). Supposing that resightings happen for guillemots aged $a = 1, \dots, A$ during years $t = 1, \dots, T$ (with no recoveries after $t = T$), we can define the following model parameters:

(i) $\phi_{a,t}(r)$: probability that a bird in state $r = \{0,1\}$ aged a at year t survives until age $a + 1$. In our system, we assume survival probability is the same for birds that recruit into the Isle of May and elsewhere, so that $\phi_{a,t}(1) = \phi_{a,t}(0) = \phi_{a,t}$;

(ii) $\psi_{a,t}(r,s)$: probability that a bird in state $r = \{0,1\}$ aged a in year t, moves to state $s = \{0,1\}$ by age $a+1$, given that it is alive at this age. Fidelity is $\psi_{a,t}(1,1) = F_{a,t}$ and permanent emigration is $\psi_{a,t}(1,0) = 1 - F_{a,t}$. The transition from state 0 to 1 is by definition impossible, so $\psi_{a,t}(0,1) = 0$, $\psi_{a,t}(0,0) = 1$;

(iii) $p_{a,t}(r)$: probability that a bird alive in state $r = \{0,1\}$ aged a at year t is resighted at this age. As birds that emigrate permanently cannot be resighted, $p_{a,t}(0) = 0$. We denote resightings at the Isle of May as $p_{a,t}(1) = p_{a,t}$;

(iv) $\lambda_{a,t}(r)$: 'reporting' or 'recovery' probability, i.e. probability that a bird in state $r = \{0,1\}$ aged a at year t that dies before age $a+1$ is recovered dead and its numbered metal ring reported (before age $a+1$). We assume it is equal for birds in both states: $\lambda_{a,t}(1) = \lambda_{a,t}(0) = \lambda_{a,t}$.

We define the following set of probabilities, and derive their values for our particular case of states 1 and 0, from the expressions in McCrea (2012):

(i) $Q_{a,b,t}(r,s)$: probability that a bird migrates from state $r = \{0,1\}$ aged a at year t, to state $s = \{0,1\}$ at age $b+1$ and is unobserved between these ages:

$$Q_{a,b,t}(1,0) = \begin{cases} \phi_{a,t}(1 - F_{a,t}), & a = b \\ \phi_{a,t}\{(1 - F_{a,t})Q_{a+1,b,t+1}(0,0) + F_{a,t}(1 - p_{a+1,t+1})Q_{a+1,b,t+1}(1,0)\}, & a < b \end{cases}$$

$$Q_{a,b,t}(1,1) = \begin{cases} \phi_{a,t}F_{a,t}, & a = b \\ \phi_{a,t}F_{a,t}(1 - p_{a+1,t+1})Q_{a+1,b,t+1}(1,1), & a < b \end{cases}$$

$$Q_{a,b,t}(0,0) = \begin{cases} \phi_{a,t}, & a = b \\ \phi_{a,t}Q_{a+1,b,t+1}(0,0), & a < b \end{cases}$$

$$Q_{a,b,t}(0,1) = 0.$$

(ii) $O_{a,b,t}(r,s)$: probability that a bird in state $r = \{0,1\}$ aged a at year t, remains unobserved until it is resighted at age $b+1$ in state $s = \{0,1\}$:

$$O_{a,b,t}(1,1) = Q_{a,b,t}(1,1)p_{b+1,t+b-a+1}$$

$$O_{a,b,t}(1,0) = O_{a,b,t}(0,1) = O_{a,b,t}(0,0) = 0.$$

(iii) $D_{a,b,t}(r)$: probability that a bird is recovered dead between ages b and $b+1$, given that it was last observed alive in state $r = \{0,1\}$ aged a at time t:

$$D_{a,b,t}(1) = \begin{cases} (1-\phi_{a,t})\lambda_{a,t}, & a = b \\ (1-\phi_{b,t+b-a})\lambda_{b,t+b-a}\{Q_{a,b-1,t}(1,0) + (1-p_{b,t+b-a})Q_{a,b-1,t}(1,1)\}, & a < b \end{cases}$$

$$D_{a,b,t}(0) = 0.$$

(iv) $\chi_{a,t}(r)$: probability that a bird alive in state $r = \{0,1\}$ at age a at year t is not seen again alive or dead during the rest of study:

$$\chi_{a,t}(0) = \begin{cases} 1, & t = T \\ (1-\lambda_{a,t})(1-\phi_{a,t}) + \phi_{a,t}\chi_{a+1,t+1}(0), & t < T \end{cases}$$

$$\chi_{a,t}(1) = \begin{cases} 1, & t = T \\ (1-\lambda_{a,t})(1-\phi_{a,t}) + \phi_{a,t}\{(1-F_{a,t})\chi_{a+1,t+1}(0) + F_{a,t}(1-p_{a+1,t+1})\chi_{a+1,t+1}(1)\}, & t < T \end{cases}$$

The MRR data set can be summarized using a set of sufficient statistics as follows:

(i) $n_{a,b,t}(r,s)$: number of birds observed in state $r = \{0,1\}$ at age a in year t and next seen alive in state $s = \{0,1\}$ aged $b+1$;

(ii) $d_{a,b,t}(r)$: number of birds recovered dead at age b that were last observed alive in state $r = \{0,1\}$ aged a in year t;

(iii) $v_{a,t}(r)$: number of birds seen alive (including initial release) for the last time in state $r = \{0,1\}$ aged a in year t, and not recovered dead at a later encounter occasion.

Given that no guillemots are ever captured or resighted in state 0, only the following terms are non-zero: $n_{a,b,t}(1,1)$, $d_{a,b,t}(1)$ and $v_{a,t}(1)$.

Based on the three sufficient statistics matrices $\boldsymbol{n}$, $\boldsymbol{d}$ and $\boldsymbol{v}$, and the parameters and probabilities defined above, we can proceed to write the full age- and year-dependent likelihood of the guillemot mark-resight-recovery data set. Taking into account restrictions in the relationships of the indices,

$$L(\boldsymbol{n}, \boldsymbol{d}, \boldsymbol{v} | \boldsymbol{\phi}, \boldsymbol{\psi}, \boldsymbol{p}, \boldsymbol{\lambda}) = \prod_{a=1}^{A-1} \prod_{b=a}^{A-1} \prod_{t=a}^{(T-1+a-b)} \left\{ O_{a,b,t}(1,1)^{n_{a,b,t}(1,1)} \times D_{a,b,t}(1)^{d_{a,b,t}(1)} \right\} \times \prod_{a=1}^{A} \prod_{t=a}^{T-1} \chi_{a,t}(1)^{v_{a,t}(1)}. \tag{5.2}$$

Note that also the terms $\chi_{a,t}(0)$, $Q_{a,b,t}(0,0)$, $Q_{a,b,t}(1,0)$ and $Q_{a,b,t}(1,1)$ must be calculated as they are indirectly involved in the expressions above.

The generic fully age- and time-dependent likelihood (5.2) may be simplified for our particular data set, considering that some ages will have very similar parameter values (e.g. adult survival, irrespective of actual age), that parameters with small variations over time will be modelled more parsimoniously with constant parameters, and that in some cases we might not have enough data to estimate fully year-dependent parameters. The age- and year-dependency model structure we use for the guillemot chick data is similar to that in Harris, Frederiksen & Wanless (2007) and Reynolds *et al.* (2009), with a few differences supported by preliminary investigations of model structure carried out in the frequentist framework using program MARK (White & Burnham 1999) with the 'combined live-dead encounter' model (Burnham 1993); more details are given in section 6.1.2. The guillemot MRR(C) model has the following structure:

(i) Year-dependent first-year survival $s_1(t)$, but constant survival for birds in their 2nd and 3rd-to-5th years of life (s_2 and s_{35} respectively, with $s_{35} = s_3 = s_4 = s_5$). Adult survival (for birds aged 5 years or more) is also fully year-dependent: $s_a(t)$;

(ii) Year-dependent resight probabilities, separately for three age classes ($p_2(t), p_3(t)$ and $p_{45}(t)$ for 2, 3 and '4-to-5' year old birds), and then for adults ($p_a(t)$, for $a > 5$ years). We fix $p_1 = 0$ as young guillemots do not return to their natal colony in their first year of life. Note that parameters $s_1(t)$ and $s_2(.)$ are nevertheless not confounded (see Example 6 in Cole & McCrea 2012). All resight probabilities are estimated independently for each ringing area (A or B, indicated by superscripts), as guillemots tend to come back to the general area where they were born and resight probabilities are known to be different for these two ringing areas (Harris, Frederiksen & Wanless 2007);

(iii) We let the model estimate fidelity in the two years before recruitment (F_5 and F_6 respectively, for age classes '5', '6' years of life). Fidelity is fixed to one for younger birds ($F_{1-4} = 1$), as a preliminary exploration of the data set revealed boundary estimates of one for these parameters and that recruitment at that early age is uncommon. We also assume that fidelity is one for adults ($F_a = 1$);

(iv) When immature guillemots start recruiting into the breeding population, the numbered colour-rings used for their individual identification during resightings start wearing and may eventually be lost. Also, a bird may recruit to a part of the colony that is not visible during resighting searches. These two processes (colour-ring loss/wear and recruitment into an area of low visibility) are in principle confounded with emigration, as for monitoring purposes, individuals become unobservable alive (i.e. no resighting possible) but the metal rings may still be recovered once the bird dies. Reynolds *et al.* (2009) noted that these two processes can be separated from 'true' fidelity with the help of an IPM, as they impact very differently on population counts (more on this in section 5.4.6). In our model, we define ψ as the probability that an adult guillemot (marked with a colour-ring as chick) retains a readable ring, and recruits (or continues breeding) at a visible location. As we assume 'true' fidelity is 1 for adults, and that ψ only applies to birds that have started breeding (and are therefore adults), in the likelihood (5.2) we can model the 'retention of colour rings and recruitment to a visible location' using the 'fidelity' parameter $\psi_{a,t}(1,1) = F_{a>6,t} = \psi$ for $a > 6$;

(v) A general trend of decreasing reporting probabilities has been noticed in several species ringed in the UK (Robinson, Grantham & Clark 2009), so we fit a linear trend with time (on the logit scale) in $r(t) = \lambda_{a,t}$, common to all ages: $\text{logit}\big(r(t)\big) = \alpha_0 + \alpha_1 \tau$, where τ denotes the standardised years (from 1 to $T - 1$).

For notational simplicity, we define for area A: $\boldsymbol{p}_2^A = \{p_2^A(t): t = 3, \dots, T\}$, $\boldsymbol{p}_3^A = \{p_3^A(t): t = 4, \dots, T\}$, $\boldsymbol{p}_{45}^A = \{p_{45}^A(t): t = 5, \dots, T\}$, $\boldsymbol{p}_{\boldsymbol{a}}^A = \{p_a^A(t): t = 7, \dots, T\}$; and equivalently for guillemots ringed in area B: $\boldsymbol{p}_2^B = \{p_2^B(t): t = 3, \dots, 17\}$, $\boldsymbol{p}_3^B = \{p_3^B(t): t = 4, \dots, 18\}$, $\boldsymbol{p}_{45}^B = \{p_{45}^B(t): t = 5, \dots, 20\}$, $\boldsymbol{p}_{\boldsymbol{a}}^B = \{p_a^B(t): t = 7, \dots, T\}$. We denote also the complete set of resight-probability parameters for the data set collected from guillemots ringed as chicks as $\boldsymbol{p}_G^C = \{\boldsymbol{p}_2^A, \boldsymbol{p}_3^A, \boldsymbol{p}_{45}^A, \boldsymbol{p}_a^A, \boldsymbol{p}_2^B, \boldsymbol{p}_3^B, \boldsymbol{p}_{45}^B, \boldsymbol{p}_a^B\}$, fidelity parameters $\boldsymbol{F}_G = \{F_5, F_6\}$, immature survival $\boldsymbol{s}_{iG} = \{\boldsymbol{s}_1, s_2, s_{35}\}$.

Given their different resight probabilities, we can treat data from areas A and B as two distinct data sets, $\{\boldsymbol{n}_A, \boldsymbol{d}_A, \boldsymbol{v}_A\}$ and $\{\boldsymbol{n}_B, \boldsymbol{d}_B, \boldsymbol{v}_B\}$, and apply likelihood (5.2) to both areas, obtaining L_A^G and L_B^G respectively. The overall likelihood of the complete MRR(C) data set can be constructed by multiplying both:

$$\begin{aligned} L_{MRR(C)}^G\big(\boldsymbol{n}_G, \boldsymbol{d}_G, \boldsymbol{v}_G \,|\, \boldsymbol{s}_{iG}, \boldsymbol{s}_{aG}, \boldsymbol{p}_G^C, \alpha_0, \alpha_1, \boldsymbol{F}_G, \psi\big) \\ = L_A^G(\boldsymbol{n}_A, \boldsymbol{d}_A, \boldsymbol{v}_A \,|\, \boldsymbol{s}_{iG}, \boldsymbol{s}_{aG}, \boldsymbol{p}^A, \alpha_0, \alpha_1, \boldsymbol{F}_G, \psi) \\ \times L_B^G(\boldsymbol{n}_B, \boldsymbol{d}_B, \boldsymbol{v}_B \,|\, \boldsymbol{s}_{iG}, \boldsymbol{s}_{aG}, \boldsymbol{p}^B, \alpha_0, \alpha_1, \boldsymbol{F}_G, \psi). \end{aligned}$$

5.4.3 *Efficient implementation of the MRR likelihood*

The likelihood in (5.2) can be implemented in WinBUGS/JAGS using the ‘zero-trick’ (as explained in section 3.3.4). An alternative approach is based on the realization that the likelihood (5.2) is product-multinomial (McCrea 2012). This fact eases the implementation in WinBUGS/JAGS in practice, as the more efficient in-built *dmulti* multinomial distribution can be used instead of a bespoke likelihood description through the ‘zero-trick’. For releases of guillemots aged a in year t in state 1 (Isle of May; no releases in state 0), the multinomial cell probabilities are:

$$\{O_{a,a,t}(1,1),\dots,O_{a,A,t}(1,1),D_{a,a,t}(1),\dots,D_{a,A,t}(1),\chi_{a,t}(1)\},$$

with corresponding observed cell numbers:

$$\{n_{a,a,t}(1,1),\dots,n_{a,A,t}(1,1),d_{a,a,t}(1),\dots,d_{a,A,t}(1),v_{a,t}(1)\}.$$

A preliminary analysis in WinBUGS indicated that the product-multinomial approach was about 2.6 times faster than the more inefficient direct likelihood construction. The analysis in JAGS gave a further speed improvement of x7.9 compared to using WinBUGS, for this particular model structure.

5.4.4 *Breeding success data set*

The number of monitored guillemot pairs ranged from 656 to 1014, with a mean of 828 pairs, a substantially larger value than for razorbills and puffins. We model guillemot breeding success data as a binomial distribution as described for razorbills in section 5.2.2:

$$C_G(t) \sim \mathrm{Bin}\big(E_G(t),\rho_G(t)\big), \qquad t = 1,\dots,T.$$

The corresponding likelihood is

$$L_{BS}^{G}(\boldsymbol{P}_{\boldsymbol{G}}|\boldsymbol{\rho}_{\boldsymbol{G}}) = \prod_{t=1}^{T}\binom{E_G(t)}{C_G(t)}\rho_G(t)^{C_G(t)}\{1-\rho_G(t)\}^{E_G(t)-C_G(t)},$$

where $\boldsymbol{\rho_G} = \{\rho_G(t) : t \in (1, \dots, T)\}$ is the set of guillemot overall productivity parameters and $\boldsymbol{P_G} = \{\boldsymbol{C_G}, \boldsymbol{E_G}\}$ represents the full breeding success data set, with $\boldsymbol{C_G} = \{C_G(t) : t \in (1, \dots, T)\}$ being the number of guillemot fledglings and $\boldsymbol{E_G} = \{E_G(t) : t \in (1, \dots, T)\}$ the number of monitored pairs.

5.4.5 Data on non-breeders

Every year, a small proportion of guillemot pairs (typically below 10%) do not attempt breeding during the breeding season. Data have been collected at the Isle of May about non-breeding by counting the number of pairs $\xi_{bG}(t)$ that do not skip breeding at any particular year t, out of a number of monitored pairs $\xi_{mG}(t)$, which ranged between 155 and 389 (mean=310 pairs/year). Given this data set $\boldsymbol{\xi_G} = \{\xi_{bG}(t), \xi_{mG}(t) : t = 1, \dots, T\}$, the non-breeding process can be modelled with a binomial distribution, $\xi_{bG}(t) \sim \text{Bin}(\xi_{mG}(t), B_G(t))$, where $B_G(t)$ is the probability of a guillemot pair breeding in year t (and therefore $1 - B_G(t)$ is the probability that a pair skips the breeding process). Given the set of breeding probabilities $\boldsymbol{B_G} = \{B_G(t) : t = 1, \dots, T\}$, the likelihood for this 'non-breeding' model is

$$L_{NB}^{G}(\boldsymbol{\xi_G} | \boldsymbol{B_G}) = \prod_{t=1}^{T} \binom{\xi_{mG}(t)}{\xi_{bG}(t)} B_G(t)^{\xi_{bG}(t)} \{1 - B_G(t)\}^{\xi_{mG}(t) - \xi_{bG}(t)}.$$

5.4.6 Breeding population counts data set

We model yearly counts of guillemot breeding females using a population model which assumes that guillemots start breeding at age $d_G = 6$ (median value from observations at the Isle of May (Harris, Halley & Swann 1994), $n = 42$). In the case of guillemots, we have direct information regarding immature survival (MRR(C) data set) so we incorporate the immature survival and fidelity structure defined in section 5.4.2 into the population model. The system process model that relates the true population abundance to the demographic rates through a Leslie matrix $\boldsymbol{M_t^G}$ can be written as

$$\begin{pmatrix} N_{1G} \\ N_{2G} \\ N_{3G} \\ N_{4G} \\ N_{5G} \\ N_{aG} \end{pmatrix}_{\mathrm{t+1}} = \boldsymbol{M}_t^G \cdot \begin{pmatrix} N_{1G} \\ N_{2G} \\ N_{3G} \\ N_{4G} \\ N_{5G} \\ N_{aG} \end{pmatrix}_{\mathrm{t}} + \begin{pmatrix} \eta_{1G} \\ \eta_{2G} \\ \eta_{3G} \\ \eta_{4G} \\ \eta_{5G} \\ \eta_{aG} \end{pmatrix},$$

$$\boldsymbol{M}_t^G = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & \mathrm{B_G(t)}\dfrac{\rho_G(t)}{2}s_1(t) \\ s_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{35} & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{35} & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{35}F_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{aG}(t)F_6 & s_{aG}(t) \end{pmatrix},$$

where η_{xG} are additive binomial error terms to account for the model stochasticity. As we noted in section 5.4.2, the usually confounded effects of birds emigrating and becoming unidentifiable/unobservable at the colony (mainly due to loss and wear of colour-rings and recruitment to a location within the colony that is not visible to an observer), can be separated in this model. Note that parameter ψ ('retention of colour-ring and recruitment to a visible location') does not appear in the Leslie matrix $\boldsymbol{M}_t^G$ as, although the mentioned processes prevent further resightings, these individuals still contribute to population abundance and growth at the Isle of May, unlike in the case of true emigration for pre-breeders (Figure 5-3). Note also that, independently of permanent emigration and/or 'ring loss', all individuals are available for dead-recovery, which is based on finding the metal ring which we assume is never lost nor becomes unreadable even if the colour-rings used for live resightings have been lost.

According to this model, the number of new guillemot recruits $\boldsymbol{R_G} = \{R_G(t): t = 7, \dots, T\}$, surviving adult females $\boldsymbol{S_G} = \{S_G(t): t = 7, \dots, T\}$ and total adult breeding female guillemots $\boldsymbol{N_{aG}} = \{N_{aG}(t): t = 7, \dots, T\}$ can be modelled as

$$R_G(t) \sim \mathrm{Bin}\left(N_{aG}(t-6), B_G(t-6)\rho_G(t-6)\frac{1}{2}s_1(t-6)s_2 s_{35}^3 F_5 F_6 s_{aG}(t-1)\right),$$

$$S_G(t) \sim \mathrm{Bin}\big(N_{aG}(t-1), s_{aG}(t-1)\big),$$

$$N_{aG}(t) = R_G(t) + S_G(t).$$

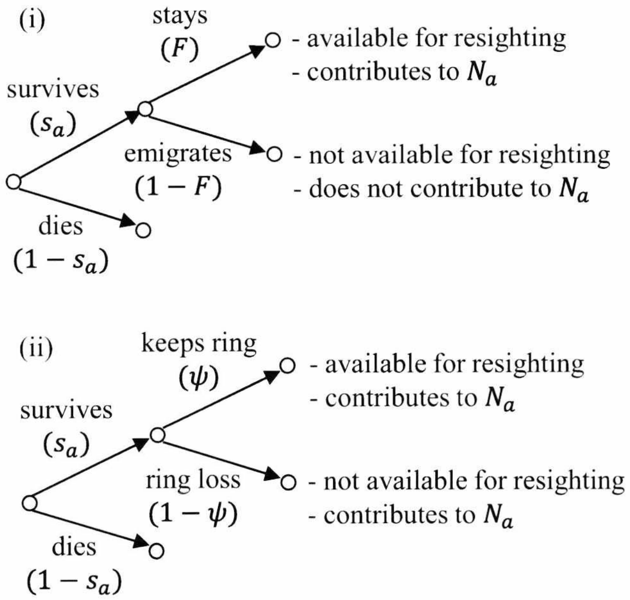


Figure 5-3 Diagram of the steps involved during recruitment (i) and 'retention of colour-ring and recruitment to a visible location' (ii), denoted here as 'keeps ring' for simplicity. The former process may happen in the two years before recruitment (with probabilities F_5 and F_6 respectively), the latter after recruitment. 'Emigration' refers to permanent emigration, i.e. recruitment into a different population. Despite superficial similarity between processes (i) and (ii), a critical difference is that individuals that suffer 'ring loss' still contribute to adult population abundance and future growth at the Isle of May, while individuals that permanently emigrate do not.

Letting $B_G(t-6)\rho_G(t-6)\frac{1}{2}s_1(t-6)s_2s_{35}^3F_5F_6 = \tau_G(t-6)$, the likelihood of the system process model is

$$L_N^G(\boldsymbol{R_G}, \boldsymbol{S_G} | \boldsymbol{s_G}, \boldsymbol{F_G}, \boldsymbol{s_{aG}}, \boldsymbol{\rho_G})$$

$$= \prod_{t=7}^{T} \left[\binom{N_{aG}(t-6)}{R_G(t)} \{\tau_G(t-6)s_{aG}(t-1)\}^{R_G(t)} \right.$$

$$\cdot \{1-\tau_G(t-6)s_{aG}(t-1)\}^{N_{aG}(t-6)-R_G(t)}$$

$$\left. \cdot \binom{N_{aG}(t-1)}{S_G(t)} \{s_{aG}(t-1)\}^{S_G(t)} \{1-s_{aG}(t-1)\}^{N_{aG}(t-1)-S_G(t)} \right].$$

Given the guillemot population counts $\boldsymbol{x_G} = \{x_G(t): t = 7, \dots, T\}$, the likelihood of the observation process can be written as

$$L_{OBS}^G(\boldsymbol{x_G} | \boldsymbol{N_{aG}}, \sigma_{xG}^2) = \prod_{t=7}^{T} \left[\frac{1}{\sigma_{xG}\sqrt{2\pi}} \cdot \exp\left(-\frac{\{x_G(t) - N_{aG}(t)\}^2}{2\sigma_{xG}^2} \right) \right].$$

The likelihood of the state-space population model (L_{POP}^{G}) can be constructed as the product of the likelihood of the observation (L_{OBS}^{G}) and the system (L_{N}^{G}) process models:

$$\begin{aligned} L_{POP}^{G}(\boldsymbol{x}_{\boldsymbol{G}} | \boldsymbol{R}_{\boldsymbol{G}}, \boldsymbol{S}_{\boldsymbol{G}}, \boldsymbol{s}_{\boldsymbol{G}}, \boldsymbol{F}_{\boldsymbol{G}}, \boldsymbol{s}_{\boldsymbol{aG}}, \boldsymbol{\rho}_{\boldsymbol{G}}, \sigma_{xG}^{2}) \\ = L_{OBS}^{G}(\boldsymbol{x}_{\boldsymbol{G}} | \boldsymbol{R}_{\boldsymbol{G}}, \boldsymbol{S}_{\boldsymbol{G}}, \sigma_{xG}^{2}) \times L_{N}^{G}(\boldsymbol{R}_{\boldsymbol{G}}, \boldsymbol{S}_{\boldsymbol{G}} | \boldsymbol{s}_{\boldsymbol{G}}, \boldsymbol{F}_{\boldsymbol{G}}, \boldsymbol{s}_{\boldsymbol{aG}}, \boldsymbol{\rho}_{\boldsymbol{G}}), \end{aligned}$$

with immature survival parameters $\boldsymbol{s}_{\boldsymbol{G}} = \{\boldsymbol{s}_{\boldsymbol{1}}, s_2, s_{35}\}$ and pre-breeder fidelity parameters $\boldsymbol{F}_{\boldsymbol{G}} = \{F_5, F_6\}$.

5.4.7 Joint likelihood: guillemot ssIPM

The joint likelihood of the guillemot IPM model is constructed by multiplying the likelihoods of the different components of the model, assuming independence between the data sets

$$\begin{aligned} L_{IPM}^{G}\big(\boldsymbol{x}_{\boldsymbol{G}}, \boldsymbol{m}_{\boldsymbol{G}}, \boldsymbol{n}_{\boldsymbol{G}}, \boldsymbol{d}_{\boldsymbol{G}}, \boldsymbol{v}_{\boldsymbol{G}}, \boldsymbol{P}_{\boldsymbol{G}}, \boldsymbol{\xi}_{\boldsymbol{G}} | \boldsymbol{N}_{\boldsymbol{G}}, \boldsymbol{s}_{\boldsymbol{aG}}, \boldsymbol{\rho}_{\boldsymbol{G}}, \sigma_{xG}^{2}, \boldsymbol{p}_{\boldsymbol{G}}^{*}, a_G, \boldsymbol{s}_{\boldsymbol{G}}, \boldsymbol{p}_{\boldsymbol{G}}^{\boldsymbol{C}}, \alpha_0, \alpha_1, \boldsymbol{F}_{\boldsymbol{G}}, \psi, \boldsymbol{B}_{\boldsymbol{G}}\big) \\ = L_{POP}^{G}(\boldsymbol{x}_{\boldsymbol{G}} | \boldsymbol{R}_{\boldsymbol{G}}, \boldsymbol{S}_{\boldsymbol{G}}, \boldsymbol{s}_{\boldsymbol{G}}, \boldsymbol{F}_{\boldsymbol{G}}, \boldsymbol{s}_{\boldsymbol{aG}}, \boldsymbol{\rho}_{\boldsymbol{G}}, \sigma_{xG}^{2}) \times L_{MR(A)}^{G}(\boldsymbol{m}_{\boldsymbol{G}} | \boldsymbol{s}_{\boldsymbol{aG}}, \boldsymbol{p}_{\boldsymbol{G}}^{*}, a_G) \\ \times L_{MRR(C)}^{G}\big(\boldsymbol{n}_{\boldsymbol{G}}, \boldsymbol{d}_{\boldsymbol{G}}, \boldsymbol{v}_{\boldsymbol{G}} | \boldsymbol{s}_{\boldsymbol{iG}}, \boldsymbol{s}_{\boldsymbol{aG}}, \boldsymbol{p}_{\boldsymbol{G}}^{\boldsymbol{C}}, \alpha_0, \alpha_1, \boldsymbol{F}_{\boldsymbol{G}}, \psi\big) \times L_{BS}^{G}(\boldsymbol{P}_{\boldsymbol{G}} | \boldsymbol{\rho}_{\boldsymbol{G}}) \\ \times L_{NB}^{G}(\boldsymbol{\xi}_{\boldsymbol{G}} | \boldsymbol{B}_{\boldsymbol{G}}). \end{aligned}$$

Table 5-1 (in page 162) shows the parameters that are shared between different IPM components. Note that we use different adult resight probabilities for guillemots marked as chicks ($\boldsymbol{p}_{\boldsymbol{G}}^{\boldsymbol{C}}$) than for birds marked as adults ($\boldsymbol{p}_{\boldsymbol{G}}$, derived from $\boldsymbol{p}_{\boldsymbol{G}}^{*}$ and $\boldsymbol{a}_{\boldsymbol{G}}$), as high resight probabilities are expected for the latter, given a higher resight effort and that they are highly likely to return to the same breeding spot where they were ringed. On the contrary, adult survival $\boldsymbol{s}_{\boldsymbol{aG}}$ is a common parameter for the adult MR likelihood $L_{MR(A)}^{G}$ and the chick MRR likelihood $L_{MRR(C)}^{G}$.

5.5 Multi-species Integrated Population Model (msIPM)

5.5.1 Bringing all the information together

The single-species integrated models (ssIPMs) in the previous sections bring together data sets and model components that relate to each species independently. We now model jointly the ssIPMs for the three auks in a single multi-species integrated model (msIPM). Here the effect of the community is modelled as shared year random terms, estimated independently in adult survival and in overall productivity. The general idea and random effects structure is as described in sections 2.3.2 and 3.1.2 respectively. In summary, we add year random effects on the logistic scale that are either common to all species ($\delta_\phi(t), \delta_\rho(t)$) or species-specific ($\varepsilon_{\phi s}(t), \varepsilon_{\rho s}(t)$, for species s), with subscripts 'ϕ' and 'ρ' denoting adult survival and overall productivity

$$\begin{aligned}\text{logit}(\rho_s(t)) &= \beta_{\rho s} + \delta_\rho(t) + \varepsilon_{\rho s}(t), \quad t \in \{1,..,T\}, \quad s \in \{1,2,3\},\\ \text{logit}(s_{as}(t)) &= \beta_{\phi s} + \delta_\phi(t) + \varepsilon_{\phi s}(t), \quad t \in \{1,..,T-1\}, \quad s \in \{1,2,3\}.\end{aligned}$$

The random effects are considered independent (across years and species) and normally distributed as follows

$$\begin{aligned}\delta_\phi(t) &\sim N(0, \sigma^2_{\delta\phi}), \quad t \in \{1,..,T-1\},\\ \varepsilon_{\phi s}(t) &\sim N(0, \sigma^2_{\varepsilon\phi s}), \quad t \in \{1,..,T-1\}, \quad s \in \{1,2,3\},\\ \delta_\rho(t) &\sim N(0, \sigma^2_{\delta\rho}), \quad t \in \{1,..,T\},\\ \varepsilon_{\rho s}(t) &\sim N(0, \sigma^2_{\varepsilon\rho s}), \quad t \in \{1,..,T\} \quad s \in \{1,2,3\}.\end{aligned}$$

From a hierarchical point of view, the new parameters to estimate are the random effects terms and their variances, and the logistic regression intercepts; overall productivity and adult survival are now derived parameters. For the three auk species, the likelihoods corresponding to the adult MR and breeding success data sets, as well as the population model, now depend on the random effects parameters $\boldsymbol{\delta}_{\boldsymbol{\rho}}, \boldsymbol{\varepsilon}_{\boldsymbol{\rho s}}, \sigma^2_{\delta\rho}, \sigma^2_{\varepsilon\rho s}, \boldsymbol{\delta}_{\boldsymbol{\phi}}, \boldsymbol{\varepsilon}_{\boldsymbol{\phi s}}, \sigma^2_{\delta\phi}, \sigma^2_{\varepsilon\phi s}$ and intercepts $\beta_{\rho s}$ and $\beta_{\phi s}$. For instance, for razorbill breeding success data we have

$$L^R_{BS}(\boldsymbol{P_R}|\boldsymbol{\delta_\rho}, \boldsymbol{\varepsilon_{\rho R}}, \sigma^2_{\delta\rho}, \sigma^2_{\varepsilon\rho R}, \beta_{\rho s}) = f^R_{BS}(\boldsymbol{P_R}|\boldsymbol{\delta_\rho}, \boldsymbol{\varepsilon_{\rho R}}, \beta_{\rho s}) f_{\delta\rho}(\boldsymbol{\delta_\rho}|\sigma^2_{\delta\rho}) f^R_{\varepsilon\rho}(\boldsymbol{\varepsilon_{\rho R}}|\sigma^2_{\varepsilon\rho R}),$$

where $f(.)$ denotes pdf or pmf (for continuous or discrete data respectively). Defining in the same way the pdfs for the adult survival random terms, $f_{\delta\phi}(\boldsymbol{\delta_\phi}|\sigma^2_{\delta\phi})$ and $f^R_{\varepsilon\phi}(\boldsymbol{\varepsilon_{\phi R}}|\sigma^2_{\varepsilon\phi R})$, the part of the msIPM likelihood that corresponds to the complete razorbill data set is a joint distribution over the model parameters, the random terms and the unobserved population abundance

$$
\begin{aligned}
f_{IPM}^{R}&\left(\boldsymbol{x_R}, \boldsymbol{m_R}, \boldsymbol{P_R} \middle| \boldsymbol{R}_R, \boldsymbol{S_R}, \phi_{cR}, \boldsymbol{\delta_\phi}, \boldsymbol{\varepsilon_{\phi s}}, \sigma_{\delta\phi}^2, \sigma_{\epsilon\phi s}^2, \beta_{\phi s}, \boldsymbol{p_R^*}, a_R, \boldsymbol{\delta_\rho}, \boldsymbol{\varepsilon_{\rho R}}, \sigma_{\delta\rho}^2, \sigma_{\epsilon\rho R}^2, \beta_{\rho s}\right) \\
&= f_{POP}^{R}\left(\boldsymbol{x_R} \middle| \boldsymbol{R}_R, \boldsymbol{S_R}, \phi_{cR}, \boldsymbol{\delta_\phi}, \boldsymbol{\varepsilon_{\phi s}}, \beta_{\phi s}, \boldsymbol{\delta_\rho}, \boldsymbol{\varepsilon_{\rho R}}, \beta_{\rho s}, \sigma_{xR}^2\right) \\
&\times f_{MR(A)}^{R}\left(\boldsymbol{m_R} \middle| \boldsymbol{\delta_\phi}, \boldsymbol{\varepsilon_{\phi s}}, \beta_{\phi s}, \boldsymbol{p_R^*}, a_R\right) f_{BS}^{R}\left(\boldsymbol{P_R} \middle| \boldsymbol{\delta_\rho}, \boldsymbol{\varepsilon_{\rho R}}, \beta_{\rho s}\right) \\
&\times f_{\delta\phi}\left(\boldsymbol{\delta_\phi} \middle| \sigma_{\delta\phi}^2\right) f_{\varepsilon\phi}^{R}\left(\boldsymbol{\varepsilon_{\phi R}} \middle| \sigma_{\varepsilon\phi R}^2\right) f_{\delta\rho}\left(\boldsymbol{\delta_\rho} \middle| \sigma_{\delta\rho}^2\right) f_{\varepsilon\rho}^{R}\left(\boldsymbol{\varepsilon_{\rho R}} \middle| \sigma_{\epsilon\rho R}^2\right).
\end{aligned}
$$

We can write the likelihood components for the puffin and guillemot data sets in the same way. Denoting for each species s its complete data set as $\boldsymbol{h_s}$ and all species-specific parameters and auxiliary variables as $\boldsymbol{\theta_s}$ (including species-specific random terms and variances), the msIPM joint likelihood can be written as a function of each species' IPM distribution conditional on the random terms, and the pdf of the random terms

$$
\begin{aligned}
L_{msIPM}\left(\boldsymbol{h_R}, \boldsymbol{h_P}, \boldsymbol{h_G} \middle| \boldsymbol{\theta_R}, \boldsymbol{\theta_P}, \boldsymbol{\theta_G}, \boldsymbol{\delta_\phi}, \sigma_{\delta\phi}^2, \boldsymbol{\delta_\rho}, \sigma_{\delta\rho}^2\right) &= f_{IPM}^{R}\left(\boldsymbol{h_R} \middle| \boldsymbol{\theta_R}, \boldsymbol{\delta_\phi}, \boldsymbol{\delta_\rho}\right) \\
&\times f_{IPM}^{P}\left(\boldsymbol{h_P} \middle| \boldsymbol{\theta_P}, \boldsymbol{\delta_\phi}, \boldsymbol{\delta_\rho}\right) \times f_{IPM}^{G}\left(\boldsymbol{h_G} \middle| \boldsymbol{\theta_G}, \boldsymbol{\delta_\phi}, \boldsymbol{\delta_\rho}\right) \\
&\times f_{\delta\phi}\left(\boldsymbol{\delta_\phi} \middle| \sigma_{\delta\phi}^2\right) f_{\delta\rho}\left(\boldsymbol{\delta_\rho} \middle| \sigma_{\delta\rho}^2\right).
\end{aligned}
$$

Note that the pdfs of the common random terms $f_{\delta\phi}\left(\boldsymbol{\delta_\phi} \middle| \sigma_{\delta\phi}^2\right)$ and $f_{\delta\rho}\left(\boldsymbol{\delta_\rho} \middle| \sigma_{\delta\rho}^2\right)$ only appear once in the msIPM likelihood. The indices of synchrony for each species s, which are derived parameters, are obtained from the MCMC chains of the random effects variances as

$$
I_{\phi s} = \frac{\hat{\sigma}_{\delta\phi}^2}{\hat{\sigma}_{\delta\phi}^2 + \hat{\sigma}_{\varepsilon\phi s}^2} \quad \text{and} \quad I_{\rho s} = \frac{\hat{\sigma}_{\delta\rho}^2}{\hat{\sigma}_{\delta\rho}^2 + \hat{\sigma}_{\varepsilon\rho s}^2}.
$$

Figures 5-4 and 5-5 show a DAG for the guillemot and razorbill/puffin components of the msIPM. Table 5-1 (in page 162) lists the estimated parameters for the three auk species, specifying in which likelihood components they appear. Note how species-specific parameters are shared between sub-models within each species' population model, while 'community-level' synchrony parameters (the common random terms and their variances) are also shared across species, rendering the model multi-species.

5.5.2 Bayesian analysis of the msIPM

To carry out Bayesian inference, the joint posterior density is constructed as the product of the likelihood and the prior density for the parameters involved in the model

$$\begin{aligned}&\pi_{msIPM}(\boldsymbol{\theta_R}, \boldsymbol{\theta_P}, \boldsymbol{\theta_G}, \boldsymbol{\delta_\phi}, \sigma^2_{\delta\phi}, \boldsymbol{\delta_\rho}, \sigma^2_{\delta\rho} | \boldsymbol{h_R}, \boldsymbol{h_P}, \boldsymbol{h_G})\\ &\qquad \propto L_{msIPM}(\boldsymbol{h_R}, \boldsymbol{h_P}, \boldsymbol{h_G} | \boldsymbol{\theta_R}, \boldsymbol{\theta_P}, \boldsymbol{\theta_G}, \boldsymbol{\delta_\phi}, \sigma^2_{\delta\phi}, \boldsymbol{\delta_\rho}, \sigma^2_{\delta\rho})\\ &\qquad \times \pi(\boldsymbol{\theta_R}, \boldsymbol{\theta_P}, \boldsymbol{\theta_G}, \boldsymbol{\delta_\phi}, \sigma^2_{\delta\phi}, \boldsymbol{\delta_\rho}, \sigma^2_{\delta\rho}).\end{aligned}$$

In the Bayesian framework, random effects and the unobserved population abundances are treated as auxiliary variables whose MCMC chains are updated at each step. The MCMC algorithm samples from the joint posterior distribution, averaging out the auxiliary variables and obtaining samples from the marginal posterior distributions for all parameters of interest. In line with analyses in previous chapters, we specify priors to be as uninformative as possible:

(i) Flat proper priors $\mathrm{U}(0,1)$ for probability parameters: combined immature survival ϕ_{Cs} for all three species; for guillemots, also fidelity F_5, F_6, 'ring retention' ψ, probability of breeding $\boldsymbol{B}$, resight probabilities for birds ringed as chicks $\boldsymbol{p^A}, \boldsymbol{p^B}$, and immature survival $\boldsymbol{s_1}, s_2, s_{35}$.

(ii) Flat proper priors $\mathrm{U}(-5,5)$ for: the intercepts of the logistic regressions of adult survival ($\beta_{\phi s}$) and overall productivity ($\beta_{\rho s}$); resight probability trap-dependence coefficients a_s; intercept α_0 and slope α_1 of the linear temporal trend in guillemot ring-recovery probability.

(iii) Normally-distributed low-information priors $N(0,10^4)$ for the year-specific component of resight probabilities for birds ringed as adults $\boldsymbol{p_s^*}$.

(iv) Flat proper priors $\mathrm{U}(0,3)$ for the standard deviations of the common and species-specific random terms for ϕ and ρ: $\sigma_{\delta\phi}, \sigma_{\delta\rho}, \sigma_{\varepsilon\phi s}, \sigma_{\varepsilon\rho s}$.

(v) Flat proper priors for the standard deviations σ_{xs} of the observation errors for all species: $\mathrm{U}(0,15000)$ for puffins, $\mathrm{U}(0,5000)$ for the other species.

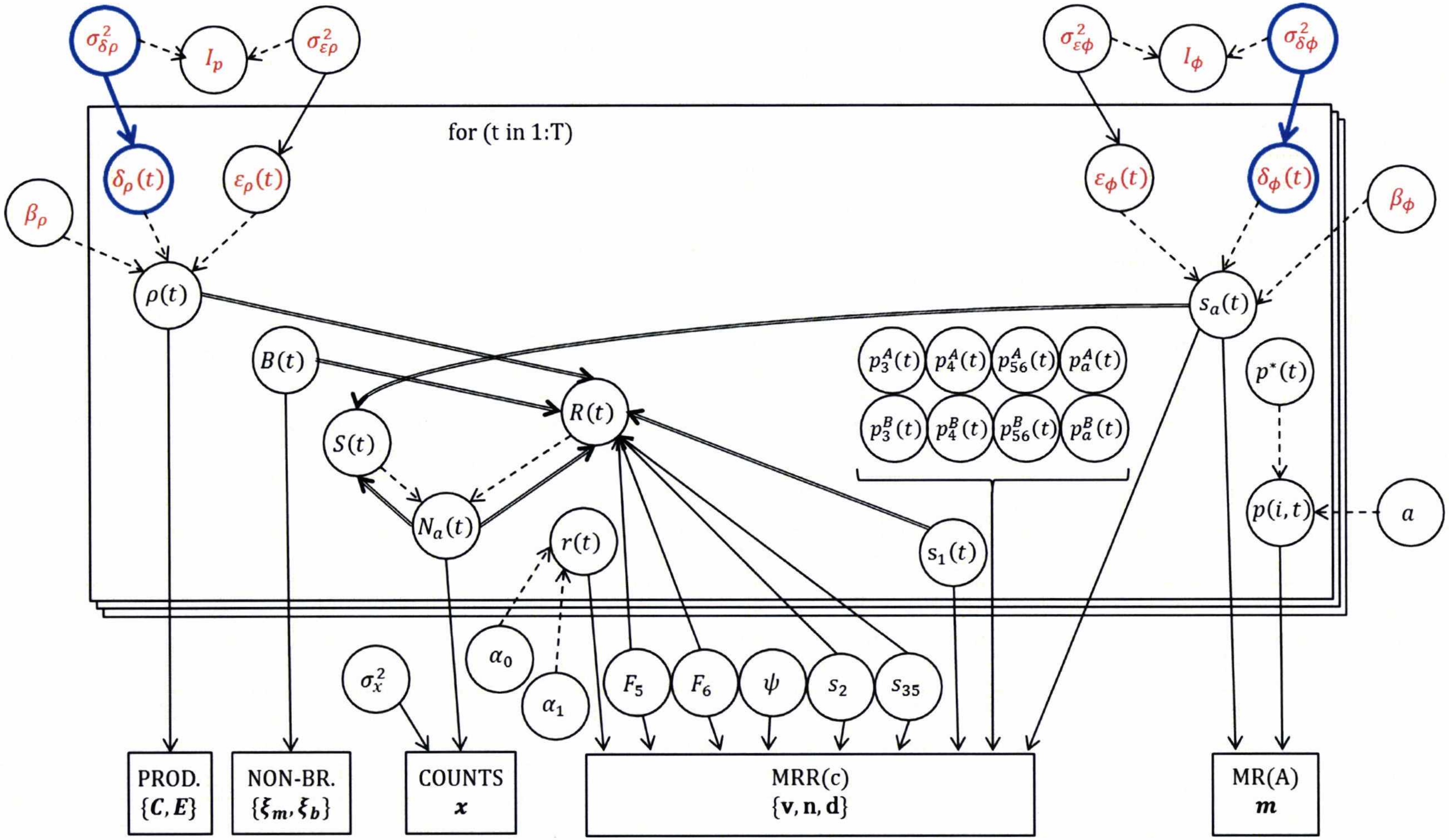


Figure 5-4 DAG of the guillemot IPM part. Variables are described in the text. Blue colour denotes parameters that are common with the other species. Variables in red are related to the calculation of synchrony indices. Double arrows indicate stochastic relationships with time-lags. Square=data set; solid line: stochastic relation. Dashed line: deterministic relation. Species subscripts have been omitted for clarity.

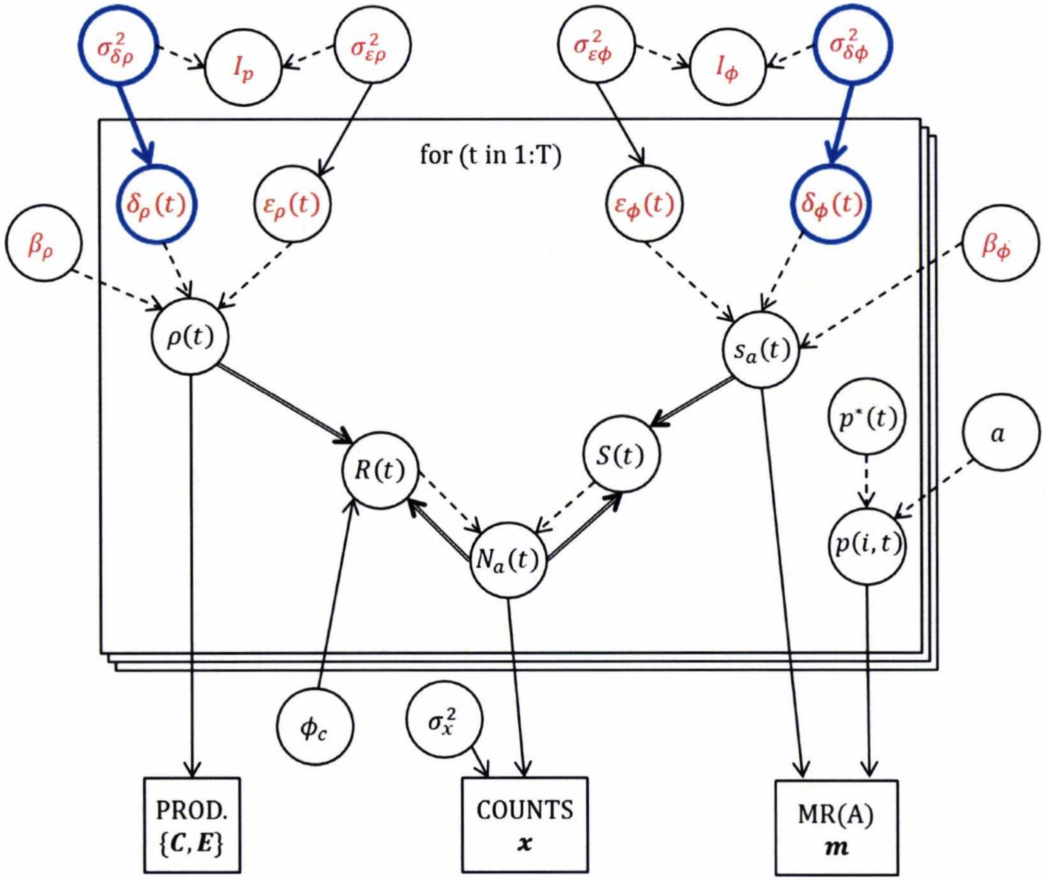


Figure 5-5 DAG of the razorbill and puffin IPM parts. Variables are described in the text. Blue colour denotes parameters that are common with the other species. Variables in red are related to the calculation of synchrony indices. Double arrows indicate stochastic relationships with time-lags. Square=data set; solid line: stochastic relation. Dashed line: deterministic relation. Species subscripts have been omitted for clarity.

Table 5-1 List of parameters involved in the msIPM, specifying in which model component for which species they appear. Column names refer to likelihood components names described in the ssIPM sections. 'R', 'P' and 'G' refer to razorbills, puffins and guillemots respectively. Year-specific parameters shown in bold. Synchrony-related parameters shown in blue; parameters related to all species in red.

Parameter	BS$_R$	MR(A)$_R$	POP$_R$	BS$_P$	MR(A)$_P$	POP$_P$	BS$_G$	NB$_G$	MR(A)$_G$	MRR(C)$_G$	POP$_G$
$\boldsymbol{\rho_R}$	✓		✓								
$\boldsymbol{\delta_\rho}, \sigma^2_{\delta\rho}$	✓		✓	✓		✓	✓				✓
$\beta_{\rho R}, \boldsymbol{\varepsilon_{\rho R}}, \sigma^2_{\varepsilon\rho R}$	✓		✓								
$\boldsymbol{s_{aR}}$		✓	✓								
$\boldsymbol{\delta_\phi}, \sigma^2_{\delta\phi}$		✓	✓		✓	✓			✓	✓	✓
$\beta_{\phi R}, \boldsymbol{\varepsilon_{\phi R}}, \sigma^2_{\varepsilon\phi R}$		✓	✓								
$\boldsymbol{p^*_R}, a_R, \boldsymbol{p_R}, \boldsymbol{\bar{p}_R}$		✓	✓								
ϕ_{cR}			✓								
σ^2_{xR}			✓								
R_R, S_R, N_R			✓								
$\boldsymbol{\rho_P}$				✓		✓					
$\beta_{\rho P}, \boldsymbol{\varepsilon_{\rho P}}, \sigma^2_{\varepsilon\rho P}$				✓		✓					
$\boldsymbol{s_{aP}}$					✓	✓					
$\beta_{\phi P}, \boldsymbol{\varepsilon_{\phi P}}, \sigma^2_{\varepsilon\phi P}$					✓	✓					
$\boldsymbol{p^*_P}, a_P, \boldsymbol{p_P}, \boldsymbol{\bar{p}_P}$					✓	✓					
ϕ_{cP}						✓					
σ^2_{xP}											
R_P, S_P, N_P						✓					
$\boldsymbol{\rho_G}$							✓				✓
$\beta_{\rho G}, \boldsymbol{\varepsilon_{\rho G}}, \sigma^2_{\varepsilon\rho G}$							✓				✓
$\boldsymbol{B}$								✓			✓
$\boldsymbol{s_{aG}}$									✓	✓	✓
$\beta_{\phi G}, \boldsymbol{\varepsilon_{\phi G}}, \sigma^2_{\varepsilon\phi G}$									✓	✓	✓
$\boldsymbol{p^*_G}, a_G, \boldsymbol{p_G}, \boldsymbol{\bar{p}_G}$									✓	✓	✓
$\boldsymbol{s_1}, s_2, s_{35}$										✓	✓
F_5, F_6, ψ										✓	✓
$\boldsymbol{r}, \alpha_0, \alpha_1$										✓	✓
$\boldsymbol{p^A_2}, \boldsymbol{p^A_3}, \boldsymbol{p^A_{45}}, \boldsymbol{p^A_a}$										✓	✓
$\boldsymbol{p^B_2}, \boldsymbol{p^B_3}, \boldsymbol{p^B_{45}}, \boldsymbol{p^B_a}$										✓	✓
ϕ_{cG}											✓
σ^2_{xG}											✓
R_G, S_G, N_G											✓

For uniform priors, the limits of the interval are selected based on preliminary analyses and we also check after analysis that the marginal posteriors are not limited by the priors. Gelman (2006) recommends the use of uniform priors for the standard deviation of normal distributions as a better alternative to inverse gamma priors on variances which appear rather informative, especially for small variances. This recommendation is echoed also in the context of mark-recapture (Royle 2008) and we also found this effect in our analysis of synchrony in adult survival (section 2.3.7). We therefore adopt uniform priors for the standard deviations of random terms and observation error.

The analysis of the msIPM is conducted with program JAGS v2.2.0 (Plummer 2003). We assess the convergence of the MCMC chains with the $\hat{R}$ Gelman–Rubin diagnostic (Gelman & Rubin 1992) calculated in the R package CODA (Plummer *et al.* 2006) for all variables from two chains started at different values. The statistic shows no evidence of lack of convergence after one million MCMC iterations ($\hat{R} \leq 1.03$, for most parameters < 1.02; the only $\hat{R} > 1.05$ is found for p_G^* for the last year (2009), which is estimated very imprecisely even in a MR-only analysis, and which has little impact on the population model).

5.5.3 Results of the multi-species IPM

The analysis consists of one million MCMC samples after a burn-in of one million samples. The samples are thinned to 1/40th to reduce memory requirements and avoid a large CODA file. In total, marginal posterior distributions are obtained using MCMC for 1031 model parameters. Of these, 390 are derived parameters (obtained deterministically from other parameters). Only six of the derived parameters (the indices of synchrony) could have been obtained a posteriori after the analysis, as they are not used in the likelihoods. For all marginal posteriors, we obtain the median and 95% CI. Figure 5-6 shows the estimated true adult female population abundance for the period 1984 to 2009 for the three auk species, comparing the estimated values to the population counts carried out at the Isle of May.

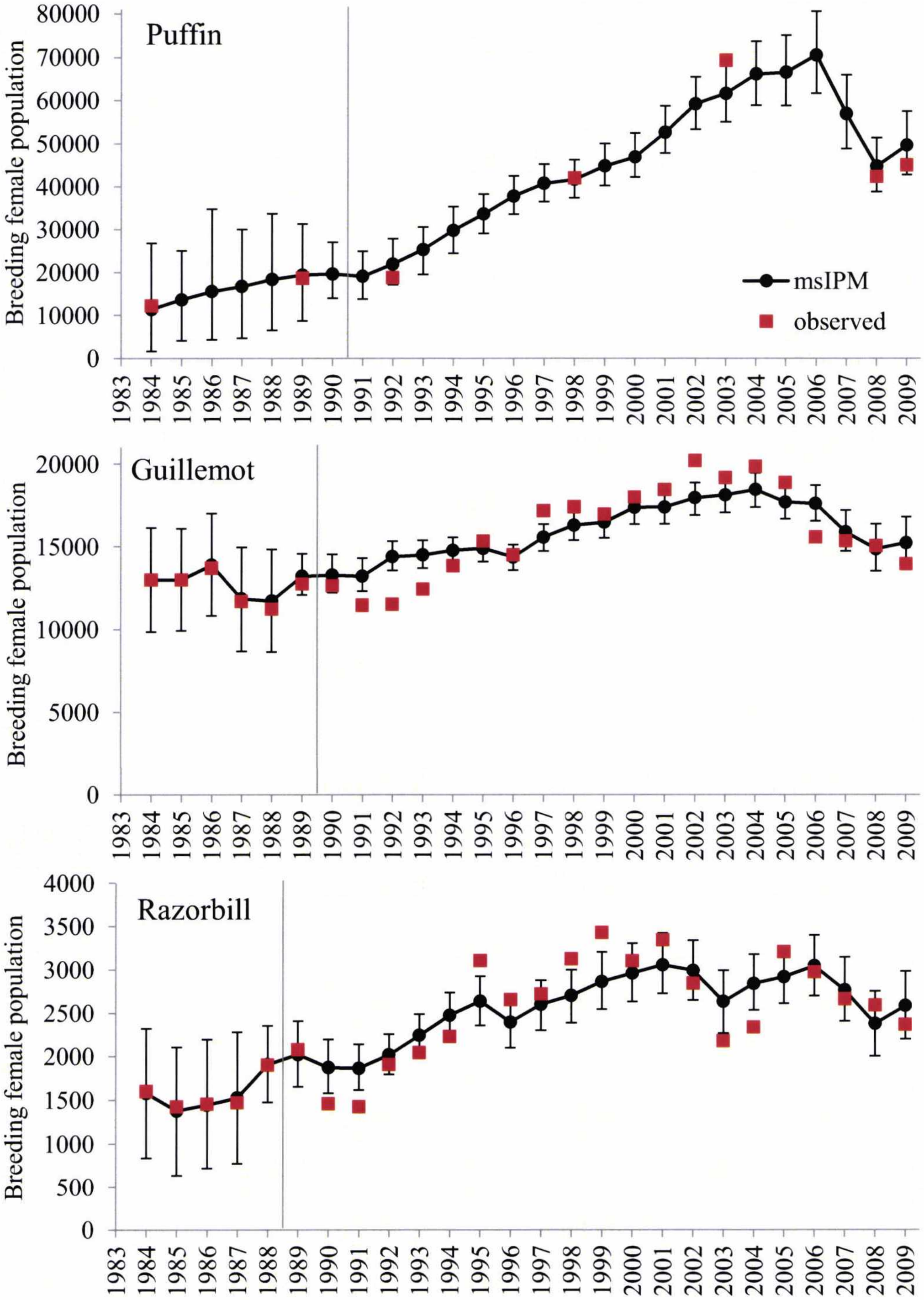


Figure 5-6 Estimates (median and 95% CI; black lines and circles) of the true breeding female population for puffins, guillemots and razorbills, obtained from the msIPM (solid circles). The population counts (red squares) are shown for comparison. Note that the scale is different for each species. The vertical line marks the end of the initialization period for each species' model component.

Puffins show the greatest change during this period, when population increased strongly from around 11390 in 1984 to 70540 in 2006. The latter number represents the highest puffin abundance at the Isle of May ever recorded, and the peak of a long period of increase since the 1950's when only a few pairs nested (Harris 1977). The estimates then show an unprecedented population crash to 44710 pairs two years after the peak (37% decline). Note that estimates are in line with the population counts: despite the counts only being available for five years after 1990, the IPM model is able to fit well the initial steady increase and then the population crash after 2007, estimating the peak of the population as taking place in 2006, despite the absence of a population count that year. The estimated observation error SD is $\hat{\sigma}_{xP} = 5551$ (Table 5-2).

Adult guillemot abundance shows less variation than that of puffins although the pattern is similar: abundance increases steadily for most of the period (from about 13000 to 18450 in 2004), then suffers a substantial decline in the last years of the study (to 14850 pairs in 2008; 19% decline). The estimates fit the counts reasonably well, although there is some discrepancy in 1991-93. We note that, despite having a more flexible model structure than the IPM parts related to puffins and razorbills, we still make some assumptions such as constant survival for immatures after their first year of life. The observation error SD is $\hat{\sigma}_{xG} = 1503$ pairs (Table 5-2).

The number of razorbills at the Isle of May is substantially smaller than those of guillemots and puffins. The pattern seen for the other two auks of a steady increase (roughly from 1500 to 3045 breeding pairs in 2006) followed by a population drop at the end of the period (down to 2377 pairs in 2008; 22% decline) is also present. The razorbill population appears to have suffered a drop also in 2003. The estimates fit the general trend in the population counts well, but note that these show greater annual variation. The model appears to have a slightly rigid structure, probably related to the fact that we impose a constant combined immature survival ϕ_{cR} due to the lack of direct information on immature survival. Attempts to fit more flexible models (e.g. allowing year-specific values of combined immature survival $\phi_{cR}(t)$) result in an overfit to the counts and very imprecise estimates of ϕ_{cR}. The model is nevertheless useful as it captures the general population trend, in agreement with the variations of demographic parameters. The estimated observation error SD is $\hat{\sigma}_{xR} = 358$ (Table 5-2).

Table 5-2 Estimates (median and 95% CI in brackets) of the msIPM constant parameters for puffins, guillemots and razorbills.

	Puffin	Guillemot	Razorbill
$\hat{\sigma}_{xs}$	5551 (2501, 11920)	1503 (1055, 2284)	358 (237, 550)
Trap-dependence $\hat{a}_s$	1.928 (1.633, 2.227)	3.240 (2.840, 3.618)	1.826 (1.234, 2.428)
Intercept $\hat{\beta}_{\phi s}$	2.436 (2.119, 2.823)	2.789 (2.548, 3.056)	2.319 (1.976, 2.721)
$\hat{\sigma}_{\varepsilon\phi s}$	0.625 (0.391, 0.970)	0.261 (0.019, 0.597)	0.519 (0.101, 0.961)
$\hat{\sigma}_{\delta\phi}$	0.493 (0.272, 0.748)		
$\hat{I}_{\phi s}$	0.383 (0.108, 0.697)	0.787 (0.270, 0.999)	0.477 (0.122, 0.968)
Intercept $\hat{\beta}_{\rho s}$	0.890 (0.627, 1.159)	1.002 (0.751, 1.250)	0.689 (0.518, 0.870)
$\hat{\sigma}_{\varepsilon\rho s}$	0.498 (0.300, 0.762)	0.491 (0.344, 0.702)	0.109 (0.006, 0.337)
$\hat{\sigma}_{\delta\rho}$	0.357 (0.237, 0.540)		
$\hat{I}_{\rho s}$	0.340 (0.127, 0.690)	0.344 (0.138, 0.651)	0.913 (0.545, 1.000)
$\hat{\alpha}_0$	NA	-3.084 (-3.225, -2.949)	NA
$\hat{\alpha}_1$	NA	-0.687 (-0.837, -0.540)	NA

Looking at the demographic parameters that underlie these population fluctuations for the three auk species, we first note that the estimates of adult survival and productivity (Figure 5-7) are similar to those obtained in analyses of each demographic parameter separately (Chapters 3 and 4 respectively); we therefore do not comment further on these results here but will do a formal comparison in section 5.5.4.

The estimated variances of the common and species-specific random terms of adult survival indicate that, for this set of species, the largest proportion of common year-to-year variation is found in guillemots ($\hat{I}_{\phi G} = 0.79$ versus $\hat{I}_{\phi P} = 0.38$ and $\hat{I}_{\phi R} = 0.48$; Table 5-2); these results are in line with those obtained in Chapter 3 (which did not include 2008 survival). In the case of overall productivity, most of the razorbill variation is estimated to be common while the proportion is much lower for the two other species ($\hat{I}_{\rho R} = 0.91$ versus $\hat{I}_{\rho P} = 0.34$ and $\hat{I}_{\rho G} = 0.34$; Table 5-2).

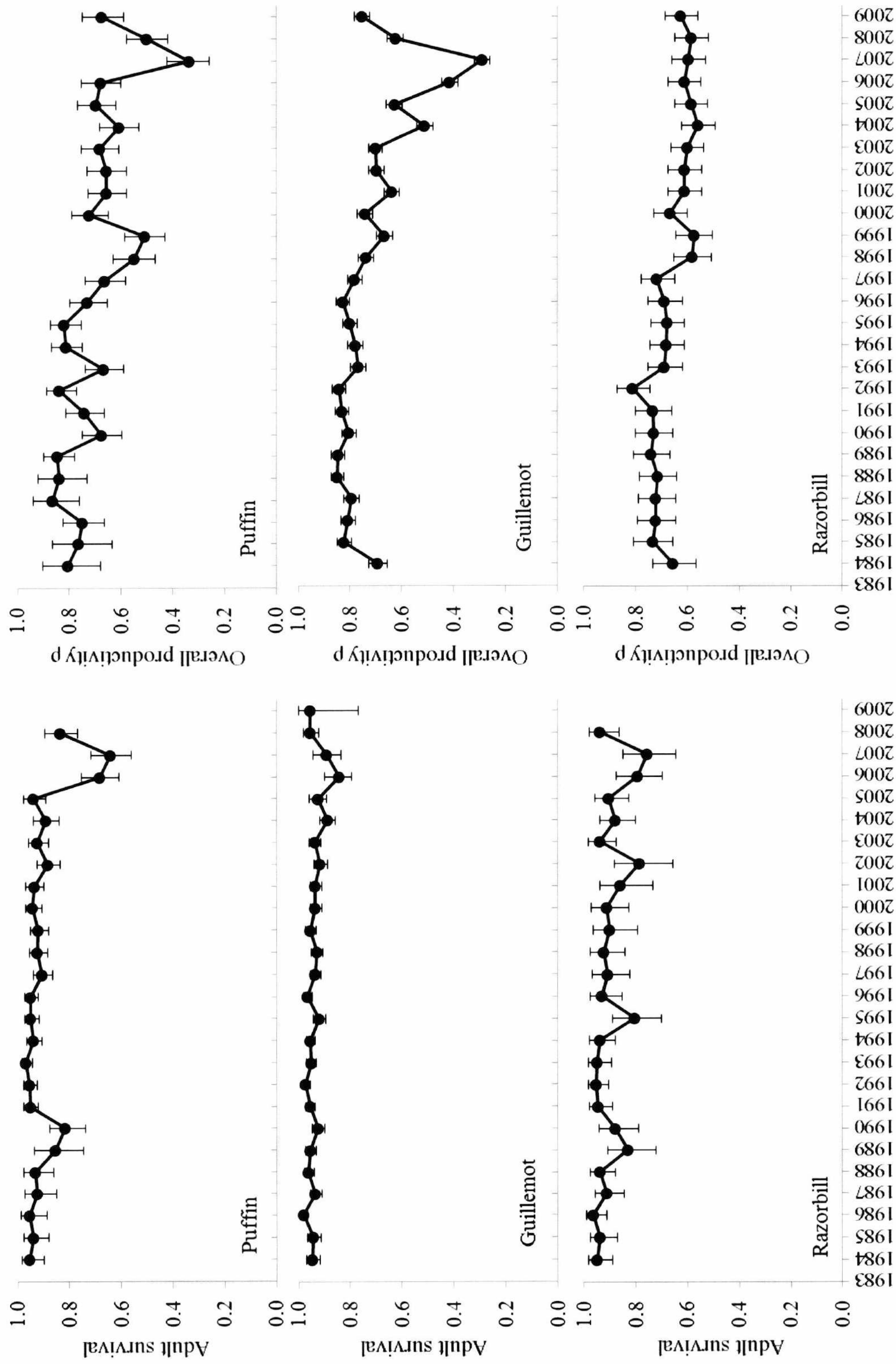


Figure 5-7 Estimates (median and 95% CI) of adult survival $s_{as}(t)$ and overall productivity $\rho_s(t)$ for puffins, guillemots and razorbills.

The combined survival probability (with 95% CIs) over the pre-breeding period is 0.761 (0.621, 0.905) for puffins and 0.501 (0.402, 0.614) for razorbills. These values are not directly comparable across species, as they represent combined survival over a different number of years. Taking the $(d_s - 1)^{\text{th}}$ root of these values, we obtain 0.955 and 0.841 respectively, which indicates a rather higher average (over age and years) survival for puffin immatures compared to razorbill immatures (but note that survival still has fidelity confounded).

For guillemots, the existence of the MRR dataset collected from birds marked as chicks provides a wealth of direct information on guillemot immature survival. The estimates of first-year survival for guillemots at the Isle of May show a very high year-to-year variability, with annual values ranging from 0.9 to almost 0, and an average value (geometric mean) of 0.338. A steady decline is clear from the late 1990s, reaching extremely low levels in 2004-2008 (Figure 5-8; note that the value of 2009 is estimated very imprecisely). Our results are comparable to those obtained in two previous analyses that included MRR data from guillemots ringed as chicks at the Isle of May, conducted up to years 2002 (Harris, Frederiksen & Wanless 2007) and 2005 (Reynolds *et al.* 2009), which did not include the population decline of the last years. Large variations in first-year survival are not uncommon in seabirds (e.g. in European shags at the Isle of May, as shown by Frederiksen *et al.* 2008a). The extremely low values in consecutive years are nevertheless worrying, and since guillemots do not recruit into the breeding population until they are around 6 years old, this feature is just starting to affect the Isle of May guillemot breeding population.

The survival estimates (and 95% CI) for the other age classes show an increasing progression towards the typically high values of adult survival (geometric mean for $s_{aG}(t)$: 0.936), with $\hat{s}_2 = 0.763\ (0.717, 0.809)$ over the 2nd winter and $\hat{s}_{35} = 0.898\ (0.876, 0.920)$ for older immatures. We note also that the decline in first-year survival in 2004-2008 coincides with a substantial drop in productivity, and that guillemot adult survival also suffered a reduction in 2006-2007 (Figure 5-7); such declines are also visible in the puffin estimates of adult survival and productivity.

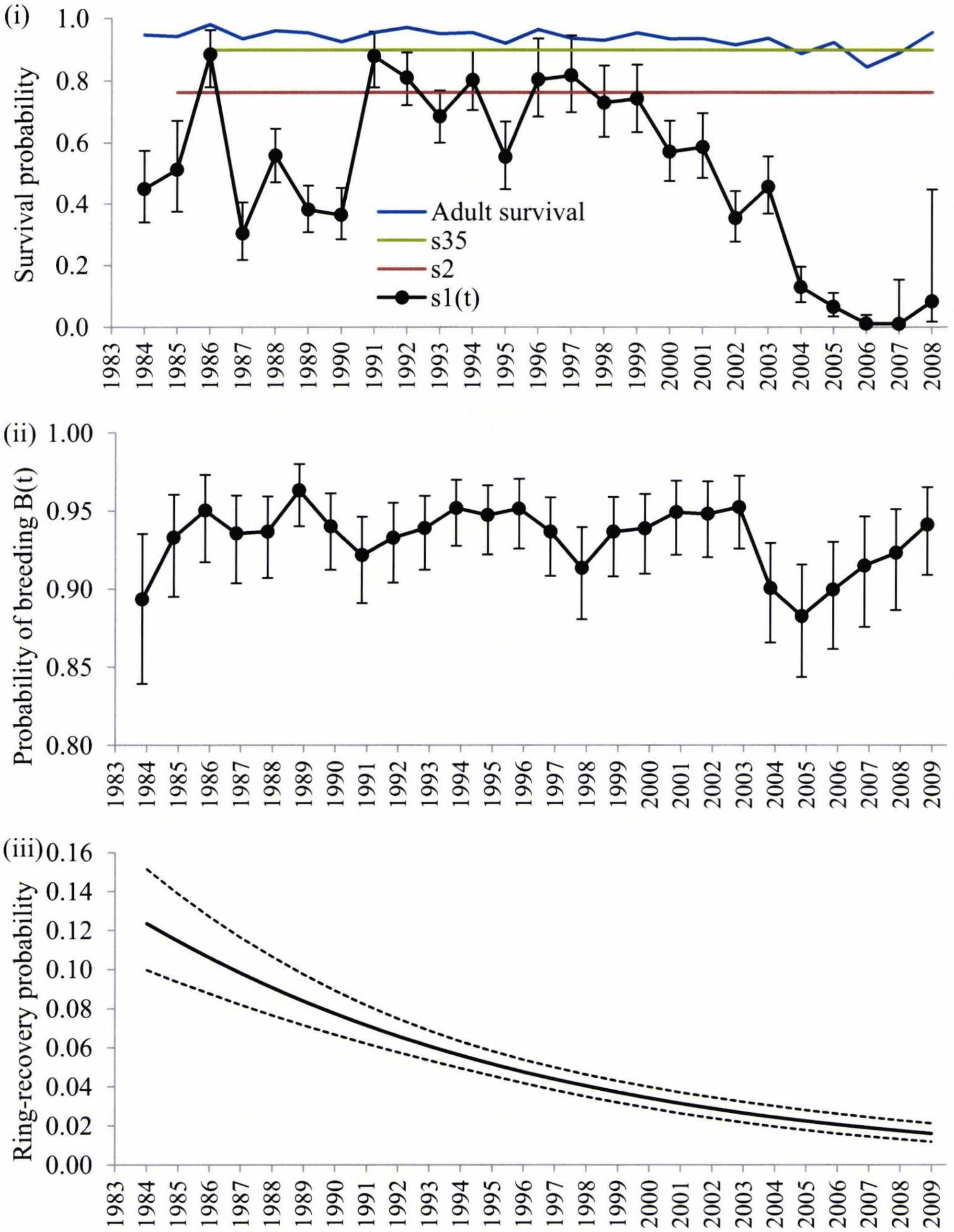


Figure 5-8 Estimates of demographic parameters for guillemots: (i) immature survival, with first-year survival $\hat{s}_1(t)$ (black line, with 95% CI; estimate for 2009 very imprecise and not shown), and $\hat{s}_2$ (red line), $\hat{s}_{35}$(green line) and adult survival $\hat{s}_{aG}(t)$ (blue line), shown for reference without CI; (ii) probability that an adult pair attempts breeding in a particular year, $\hat{B}(t)$ (with 95% CI; note the different scale); (iii) trend in ring-recovery probability $\hat{r}(t)$ over the study period (limits of the 95% CI shown as dashed lines).

Estimated resight probabilities for guillemots ringed as chicks are shown in Figure 5-9, separately for 2, 3 and 4-5 year old, and for adults. Note that resight probability for adults that have been ringed as chicks is substantially lower than that of guillemots ringed as breeding adults (see Figure 2-5 in Chapter 2). For guillemots ringed in both areas A and B, all age classes follow a similar pattern of increasing resight probabilities peaking at around 1991, followed by a sustained decline for ages 2, 3 and 4-5, more pronounced for younger birds (note that the imprecise estimates at the end of the series for $\boldsymbol{p}_2^A$, $\boldsymbol{p}_3^A$ and $\boldsymbol{p}_{45}^A$ are related to the few marked chicks that survived their first winter in the 2006 and 2007 cohorts). The 1985-1990 increase reflects a gradual increase in field effort (Harris, Frederiksen & Wanless 2007) but effort has since remained relatively constant so the subsequent declines in age-specific resight probabilities appear genuine. The observed declines in age-specific resight probabilities after 1991 may reflect a long-term behavioural change in immature guillemots. Within a year, resight probabilities tend to increase with age until adulthood, reflecting that as individuals age they are more likely to return to the colony during the breeding season and spend progressively longer there (Halley, Harris & Wanless 1995). However, immatures appear to have delayed their return to the colony until they are older as shown by a reducing resight probability for age 2 (strong decrease), that is carried over to resight probability for age 3 (medium decrease). Second-year birds have rarely been seen at the Isle of May in recent years (*unpublished data*). The decline is less evident in older immatures (age 4-5), which all return to the Isle of May within that age span. The fact that resighting probabilities increased until 1990 due to increased survey effort could mask an earlier decline. Moreover, the trend is not specifically associated with the last years of low survival and productivity at the Isle of May, and may have been happening for over 20 years. We currently have no clear hypothesis about the cause of this apparent change in prospecting behaviour, and we are not aware of such an effect having been observed in other colonies.

The probability of a ring being recovered and reported away from the Isle of May is estimated with a linear trend on the logit scale (Figure 5-8) which shows a significant decline: the estimated slope is $\hat{\alpha}_1 = -0.687\ (-0.837, -0.540)$. This trend concurs with that found for birds ringed in the UK from different bird species, including common guillemots (Robinson, Grantham & Clark 2009).

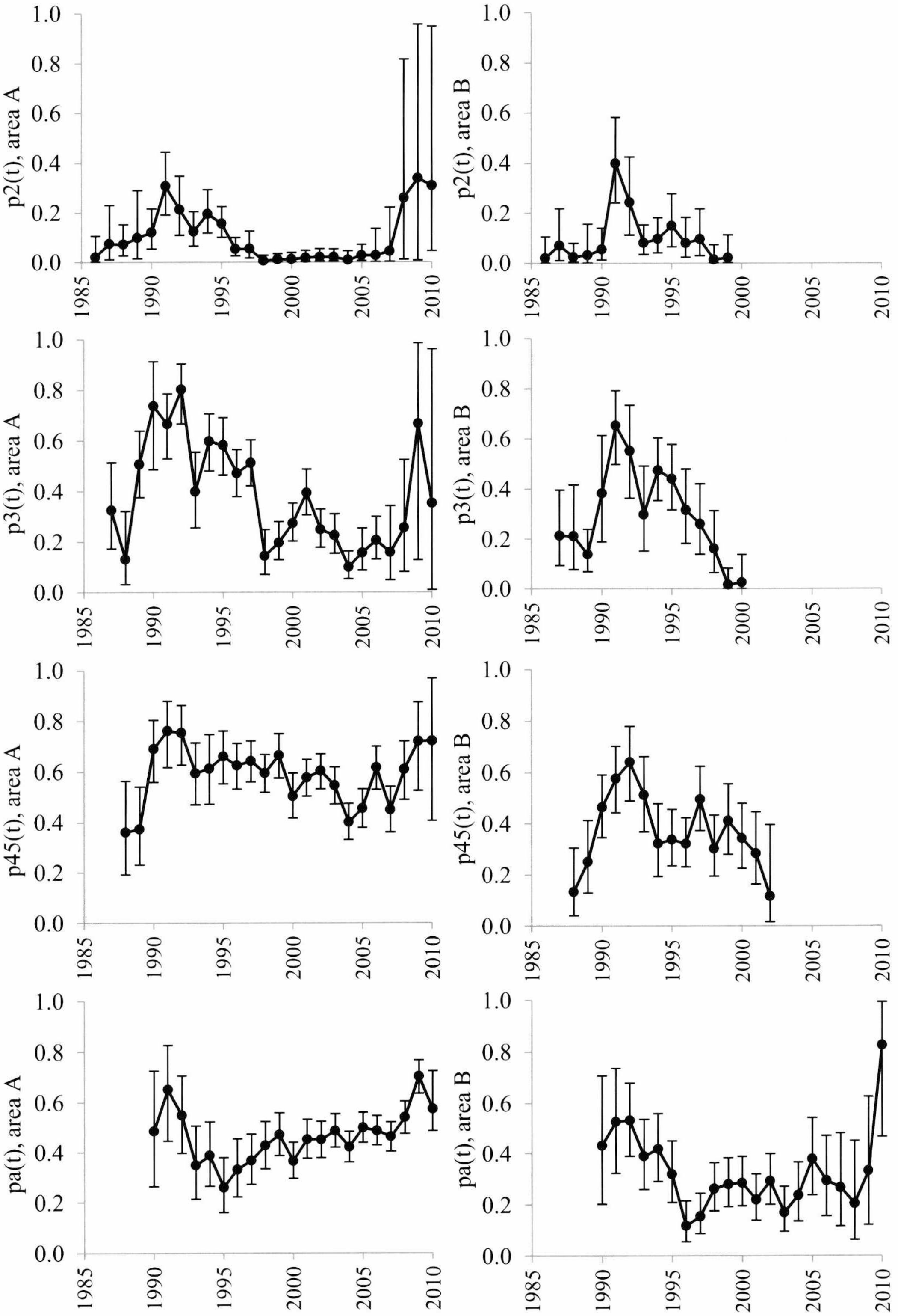


Figure 5-9 Resight probabilities for guillemots ringed as chicks in areas A (left panels) and area B (right panels). From top to bottom: estimated resight probabilities for guillemots in their 2nd ($\hat{p}_2$), 3rd ($\hat{p}_3$), 4th or 5th ($\hat{p}_{45}$) year of life, and adults ($\hat{p}_a$). Note that chicks were ringed in area B only until 1997.

We estimate that less than 20% of immature guillemots from the Isle of May permanently emigrate to other colonies before recruitment: $\hat{F}_5 = 0.865\ (0.820, 0.912)$ and $\hat{F}_6 = 0.834\ (0.786, 0.884)$. For guillemots ringed as chicks, once recruited into the Isle of May breeding population, the probability of staying identifiable (i.e. keeping the ring and in a readable condition) and breeding at a visible location is estimated as $\hat{\psi} = 0.850\ (0.832, 0.868)$. This means that these guillemots become non-identifiable/non-resightable while still contributing to the Isle of May breeding population at a rate of about 15% per year.

The model is able to separate the contribution to the total breeding population of surviving adults $S_s(t)$ and immatures $R_s(t)$ that recruit to the Isle of May breeding colony, without counts of hatched chicks or immatures (Figure 5-10). Again, this is possible thanks to the species-specific IPM structures imbedded in the model. The crash in the puffin adult population after 2006 appears to be caused mainly by a reduction in adult survival, as R_P remains largely unaffected with an almost continuous growth (Figure 5-11); note that the new recruits in 2009 are offspring of the adult females of $d_P = 7$ years before, when the population was still in full growth. According to the model estimates, one would expect to see an increase in new recruits in the coming years, followed by a drastic reduction in 2015 onwards; the reduction could be even more severe if puffin chicks born in 2006-2007 have also suffered a reduction in e.g. their first-year survival (as we will see later, very high mortality is estimated in guillemot chicks in 2005-2008; Figure 5-8).

In guillemots, the population decline starting in 2004 results from the combined effect of a reduction in surviving adults and new recruits (Figure 5-10). As for puffins, the very low productivity in 2006-2007 should result in a lower number of guillemots recruiting a few years later (around 2012-2013). Note the irregularity in $R_G(t)$, largely driven by the large variations in first-year survival (Figure 5-8).

In the case of razorbill, the coincidence of the dips in both S_R and R_R for 1996, 2003 and 2008 is mediated by corresponding dips in adult survival that affect both adults and pre-breeders in the year before recruitment.

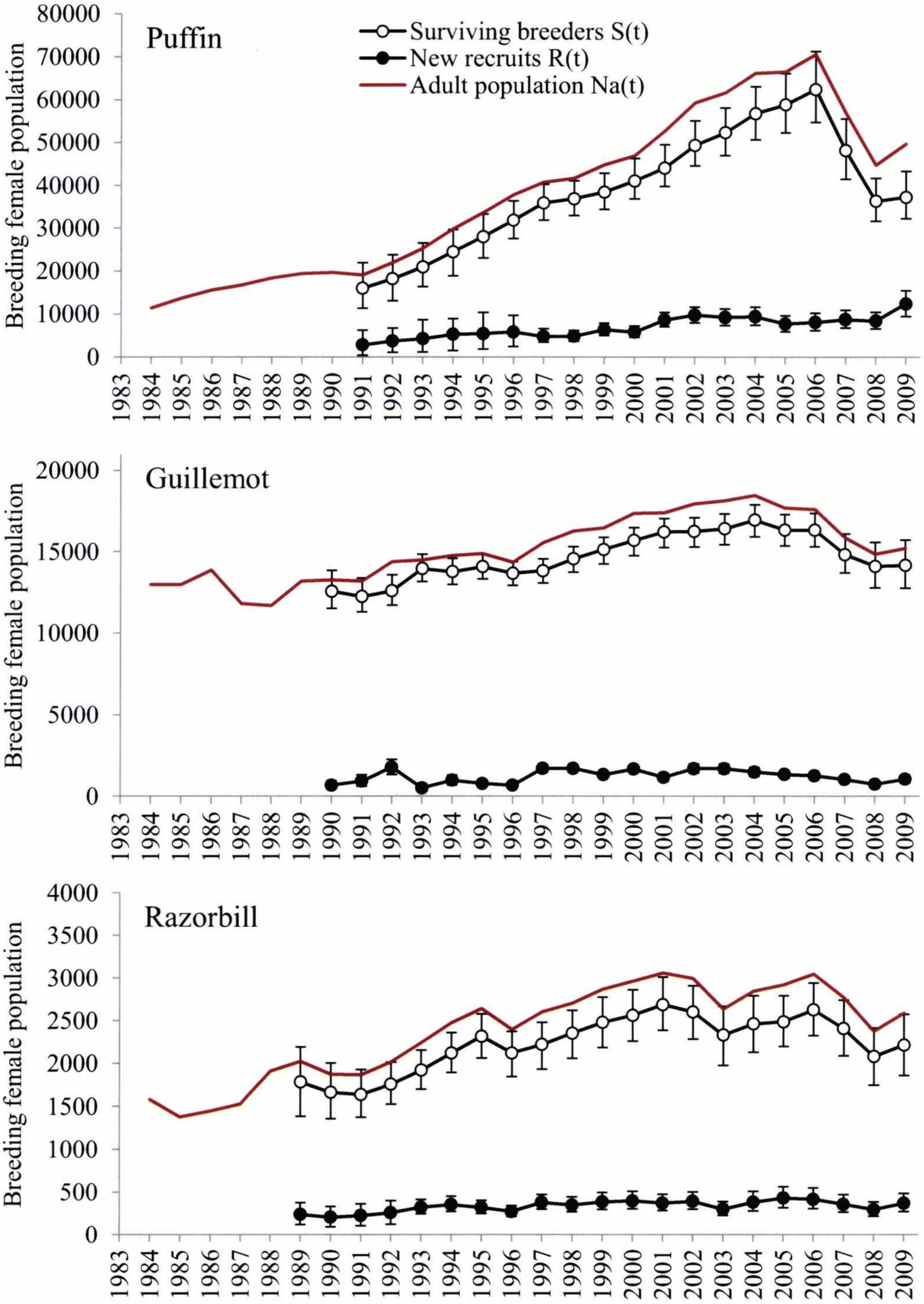


Figure 5-10 Estimates (median and 95% CI) of number of new recruits $R_s(t)$ and surviving breeders $S_s(t)$, for puffins, guillemots and razorbills. Note that these numbers represent a breakdown of the adult breeding population $N_{as}(t) = R_s(t) + S_s(t)$, which is shown with a red line (and in Figure 5-6). The estimates of $R_s(t)$ and $S_s(t)$ start at $t = d_s$ (first year after the population model initialization period). The scale has been modified compared to Figure 5-6 to maximise the detail in $R_s(t)$.

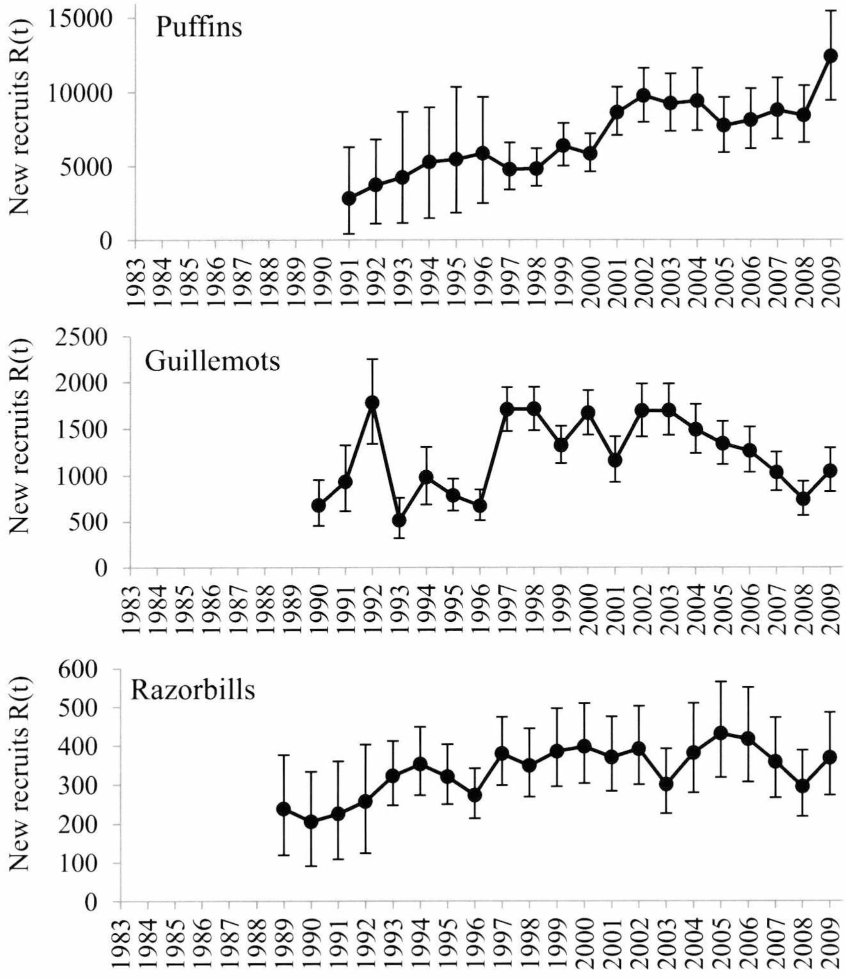


Figure 5-11 Number of immature puffins, guillemots and razorbills that recruit to the Isle of May breeding population in year t (fine detail of the $R_s(t)$ plots in Figure 5-10).

5.5.4 Comparison to non-synchrony and non-IPM models

In order to compare with the results from the msIPM, we run the single-species IPMs for the three auk species (without the synchrony structure, as described in sections 5.1-5.4) as well as analysing the different data sets (breeding success, adult MR, guillemot chick MRR) without the IPM structure, both with and without synchrony estimation (i.e. in single-species and multi-species frameworks). The case with no data integration and single-species (i.e. no synchrony) corresponds to a completely independent set of analyses which can be considered as the reference case. Table 5-3 details the different parameters included in these four sets of models.

Table 5-3 List of analyses run based on the same data sets from puffins, guillemots and razorbills, detailing whether they are integrated population models and/or multi-species (estimating synchrony in adult survival and productivity), as well as some of the estimated parameters. The symbols at the left are used when displaying model estimates in this section. The 'Independent' model (single-species non-IPM) effectively corresponds to analysing each data set independently for all species.

		IPM	Synchrony (multi-sp.)	$s_a(t)$	I_ϕ	$\rho(t)$	I_ρ	**N, S, R, s_1, F**
●	Multi-species IPM	✓	✓	✓	✓	✓	✓	✓
○	Single-species IPM	✓		✓		✓		✓
🟩	Single-parameter synchrony		✓	✓	✓	✓	✓	
◆	Independent (reference)			✓		✓		

We conduct all analyses with program JAGS v2.2.0 (Plummer 2003), setting priors for the parameters of the different models as outlined for the msIPM (section 5.5.2) when applicable (for models without synchrony estimation, we use flat priors $U(0,1)$ for adult survival and overall productivity). For all models, we obtain 1 million MCMC samples for each model parameter after a burn-in period of 1 million iterations (as all the models are simpler than the msIPM), except for the guillemot MRR(C)-only analysis (500000 MCMC iterations after discarding 200000 iterations). Convergence is assessed with the $\hat{R}$ Gelman–Rubin diagnostic calculated from two chains started from different values, which indicates that the burn-in of 1 million samples is sufficient. The comparison of the results is shown in several figures: adult survival $\hat{s}_a$ (Figure 5-12), overall productivity $\hat{\rho}$ (Figure 5-13), guillemot first-year survival $\hat{s}_1$ (Figure 5-14), indices of synchrony in adult survival and productivity (Figure 5-15) and abundance (Figure 5-17). The figures show species and models as appropriate for each parameter compared. The results are discussed in the next two sections.

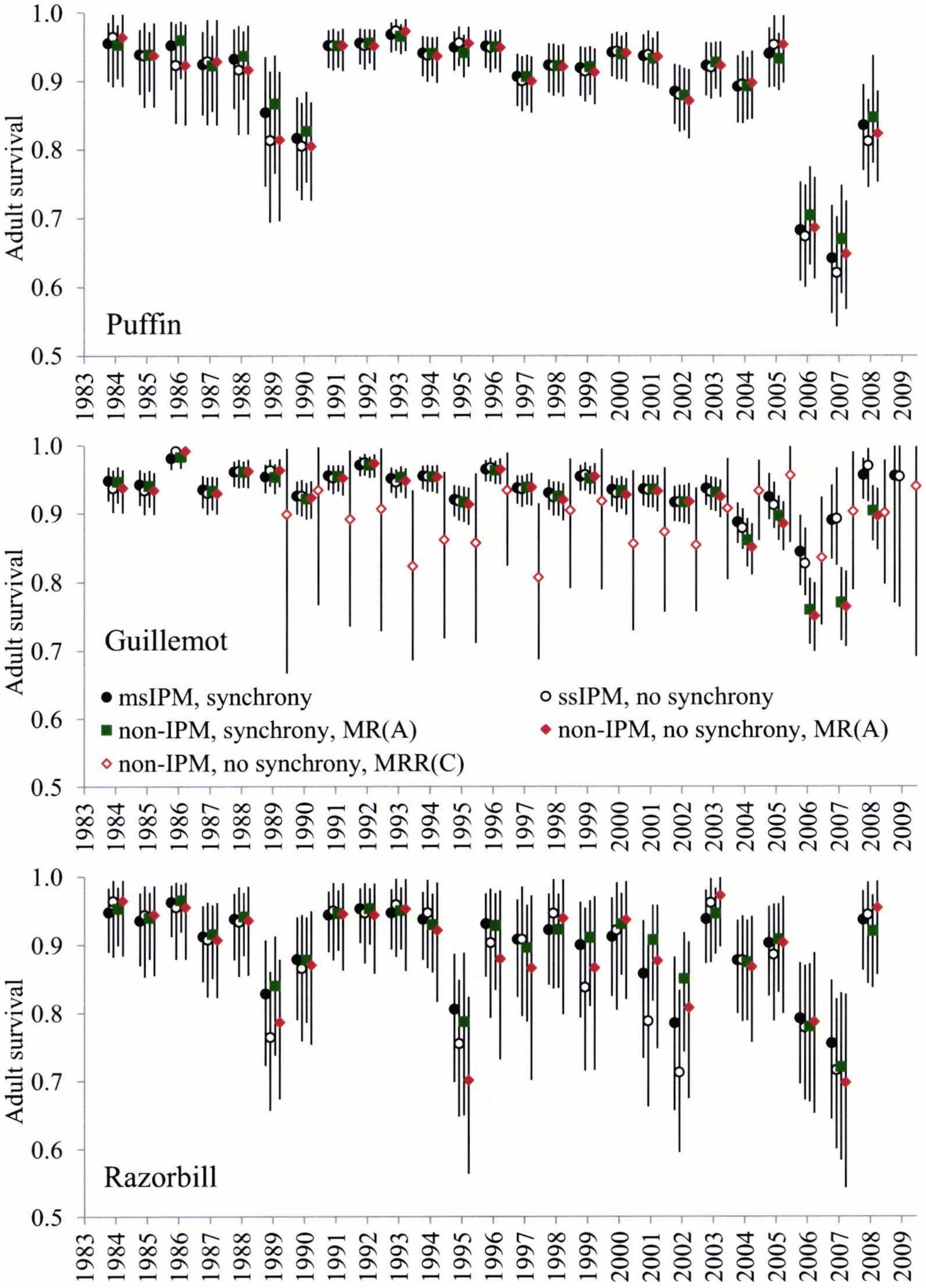


Figure 5-12 Comparison of adult survival for puffin, guillemot and razorbill estimated from models 'msIPM' (solid black circles), 'ssIPM' (open black circles), 'non-IPM+synchrony' (green squares) and 'non-IPM, no synchrony' (independent analysis; solid red diamonds for estimates from the adult MR data and for guillemots, also open red diamonds for estimates from the chick MRR data). Vertical bars indicate symmetric 95% credible intervals. Note the y-axis starting at 0.5.

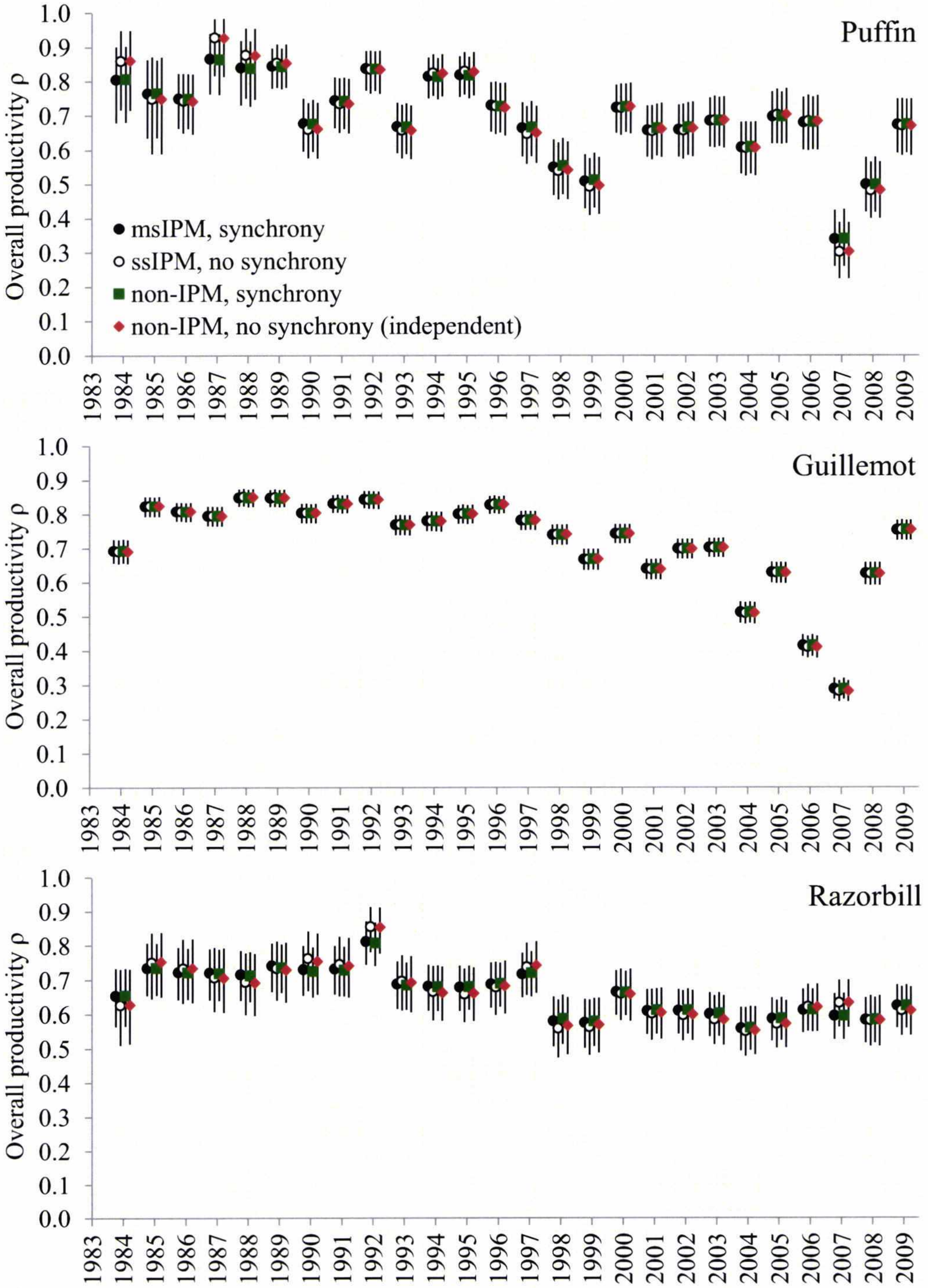


Figure 5-13 Comparison of overall productivity for puffin, guillemot and razorbill estimated from models 'msIPM' (solid black circles), 'ssIPM' (open black circles), 'non-IPM+synchrony' (green squares) and 'non-IPM, no synchrony' (independent analysis; red diamonds). Vertical bars indicate symmetric 95% credible intervals.

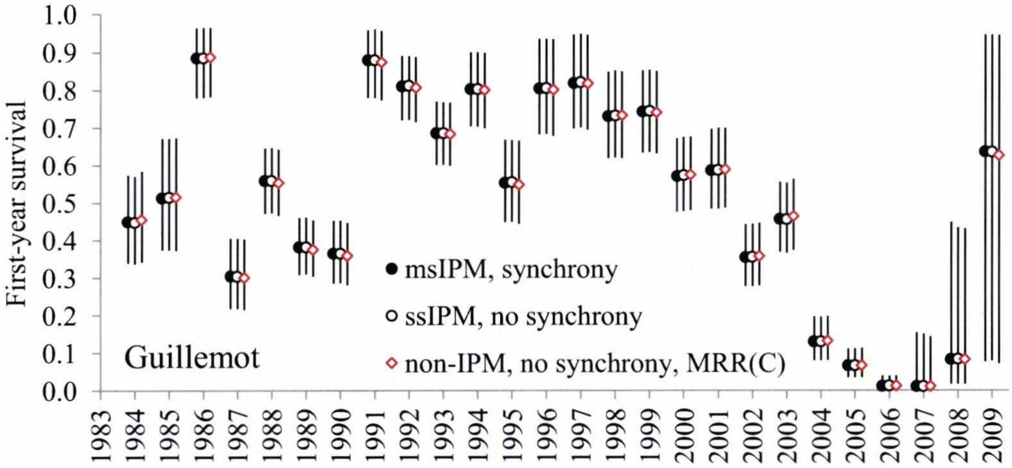


Figure 5-14 Comparison of guillemot first-year survival estimated from models 'msIPM' (solid black circles), 'ssIPM' (open black circles) and 'non-IPM, no-synchrony' (independent analysis of the MRR(C) data; open red diamonds). Vertical bars indicate symmetric 95% credible intervals.

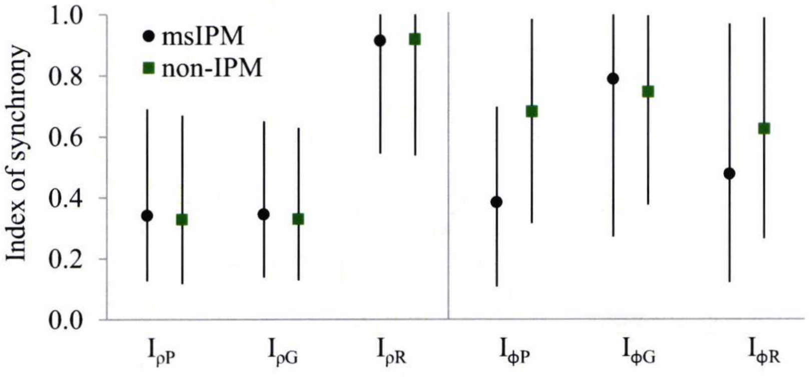


Figure 5-15 Comparison of the estimated indices of synchrony for overall productivity $(\hat{I}_{\rho s})$ and adult survival $(\hat{I}_{\phi s})$ for puffin ('P'), guillemot ('G') and razorbill ('R') obtained from models 'msIPM' (black circles) and 'non-IPM+synchrony' (green squares). Vertical bars indicate symmetric 95% credible intervals.

5.5.5 IPM: the effect of combining demographic data sets

We start by comparing the results of IPM and non-IPM analyses, that is, the effect of combining demographic data sets and population counts for a species on that species' estimates. For puffin adult survival (Figure 5-12) a slight effect is visible only in 2006-2008, with IPM-based models estimating lower survival than their respective non-IPM counterparts, although the CIs largely overlap. This effect may be caused by the need to accommodate the decreasing population in 2008-09. Guillemot adult survival displays a larger effect of demographic data integration: despite the generally small 95% CIs and coincidence in most of the series, the IPM-based estimates for 2006-2008 are notably higher than those from non-IPM analyses. This effect may be at least partially caused by the different values of $\boldsymbol{s_{aG}}$ estimated from the guillemots ringed as chicks (open diamonds in Figure 5-12), which may influence the IPM-based estimate in the period where the adult MR data set is the sparsest. The $\hat{s}_{aG}$ estimates from the MRR(C) data set are rather imprecise given that relatively few guillemot chicks survive until adulthood and thus such a data set contains less information about the survival of adults. For razorbills, $\hat{s}_{aR}$ is substantially lower when comparing the IPM models to their non-IPM counterparts in two particular years (2001 and 2002), possibly driven by the need to explain the population decline in 2002 and 2003 (although we note the generally larger degree of uncertainty in $\hat{s}_{aR}$). The generalised variance (Figure 5-16) indicates that overall the data integration increased precision in $\hat{s}_a$ only slightly; we note nevertheless that this is not a general result and greater increases in precision would be expected for other data sets if demographic data are fewer. The indices of synchrony in adult survival change slightly when using the IPM (Figure 5-15), with a small decrease for puffins and razorbills and increase for guillemots, possibly caused by the slight changes in guillemot adult survival at the end of the period that reduce the estimate of the common variance of the set.

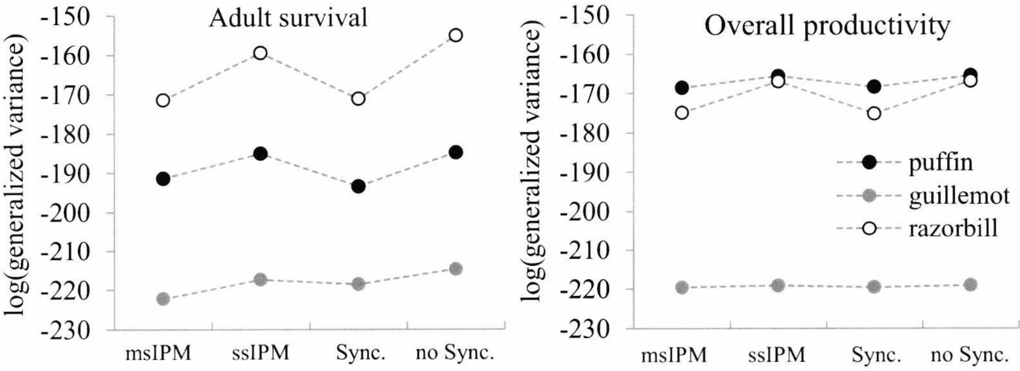


Figure 5-16 Logarithm of the generalised variance (determinant of the variance-covariance matrix) of adult survival and overall productivity estimates for puffins, guillemots and razorbills obtained from models 'msIPM', 'ssIPM', multi-species non-IPM ('Sync.') and single-species non-IPM ('no Sync.'). For both IPM guillemot models (ms and ss), only adult survival estimates for the first 25 years are used to allow comparison with non-IPM models and with the other 2 species.

No substantial effect of IPM integration can be found by simple inspection in the overall productivity estimates (Figure 5-13): the estimation of this demographic parameter is strongly driven by the data and is not influenced by other aspects of demography through data integration in an IPM. The generalised variance confirms the lack of a clear effect (Figure 5-16). Consequently, the indices of synchrony in productivity remain unaffected (Figure 5-15). Similarly, the estimates of first-year survival are not affected by having an IPM structure (Figure 5-14).

5.5.6 Multi-species: synchrony and shrinkage of the estimates

The estimation of synchrony in adult survival and productivity uses random effects, which are known to produce an effect of 'shrinkage towards the mean' (Schaub & Kery 2012). There is no apparent shrinkage of the guillemot adult survival estimates (Figure 5-12). This is not unexpected as it is the species that contributes most information (mark-resight data): 1.5 times more ringed guillemots than puffins, and over 5 times more than razorbills. The effect is visible in puffins (particularly in years 1986, 1989 and 2008), and is prevalent in razorbills, the species with least information (e.g. in 1989 and 1995, but visible in many others).

The guillemot breeding success data set contains over 5 times more monitored pairs than in the case of razorbills and puffins so, as in adult survival, guillemot productivity estimates do not show shrinkage (Figure 5-13). A slight shrinkage of the estimates exists for the other two species, particularly associated with the years that deviate most from the mean (e.g. 1984 and 1987 for puffins, and 1984 and 1992 for razorbills).

The generalised variance plots (Figure 5-16) indicate that, except for guillemot productivity, there is an overall increase in precision in the models with synchrony, irrespective of being IPM-based or not, for adult survival and, to a lesser extent, for productivity. As noted in the previous section, the estimation of guillemot first-year survival is not affected by effects acting in other demographic parameters, including those induced by the estimation of synchrony (Figure 5-14).

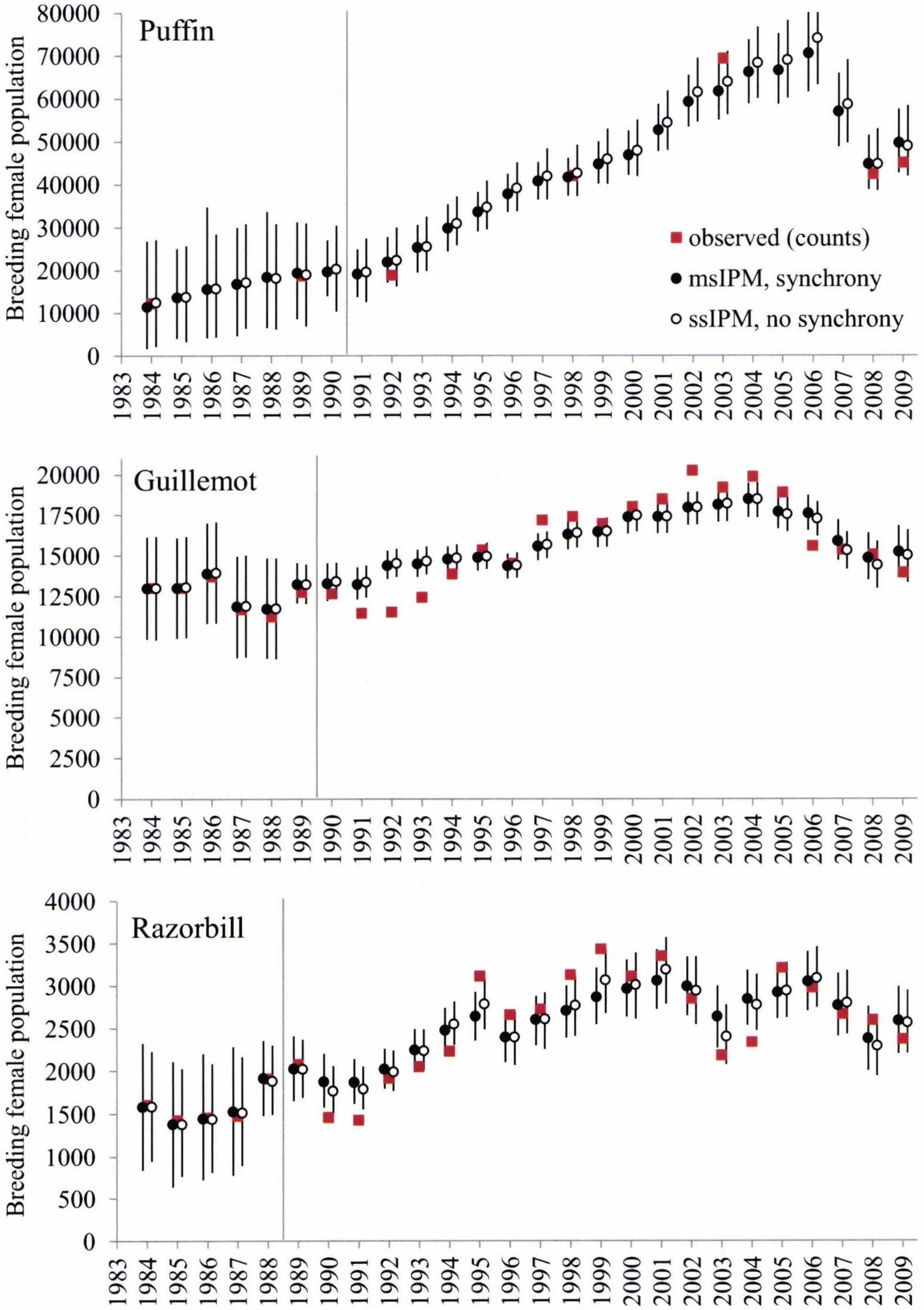


Figure 5-17 Comparison of female population abundance for puffin, guillemot and razorbill estimated from the multi-species IPM ('msIPM'; solid black circles) and single-species IPMs ('ssIPM'; open black circles). Vertical bars indicate symmetric 95% credible intervals. Note that the scale is different for each species. The vertical line marks the end of the initialization period for each species' model component.

Shrinkage in the estimation of demographic parameters does not appear to have a strong effect on the estimation of adult population abundance (Figure 5-17). As 'shrunk' estimates tend to affect the years with most extreme values (the ones further away from the species mean, mostly dictated by guillemots which display low variation in s_{aG} and ρ_G until 2004), the population trajectory estimated from the msIPM is slightly more 'averaged' than that from the ssIPMs. This effect is most visible in the case of razorbills (e.g. years 1995 and 2003).

5.6 Discussion

Combining information from demography and abundance in so-called integrated population modelling is a relatively recent but promising development in the area of statistical modelling of wildlife populations. In this chapter we describe how population models can be constructed independently for each of the three auk species that breed at the Isle of May (Atlantic puffin, common guillemot and razorbill) by combining the different demographic data sets available with island-wide population counts. We then move a step further by integrating data also across species in what is to our knowledge the first multi-species integrated population model, which allows the simultaneous estimation of synchrony in two demographic parameters, adult survival and productivity.

The period under study has seen dramatic changes in the population of auks at the Isle of May, as well as strong fluctuations in the underlying demographic parameters, whose relation to abundance is modelled explicitly through the IPM. In the mid-2000s, razorbills and guillemots had practically doubled their early 1980s population, while puffins had seen a 7-fold increase. Such increases were followed by a population crash in 2007 and 2008, especially notable in the case of puffins, with 2009 indicating a recovery for the three species. Interestingly, our estimates indicate that, for both adult survival and overall productivity, the part of the year-to-year variation that is common to all three auk species represents only a medium-to-low part of their overall fluctuations, as reflected by their respective indices of synchrony. The population decline at the end of the study period seems to coincide with high adult mortality in 2006 and

2007, particularly for puffins and razorbills, which is unusual for long-lived seabirds. Although also guillemot adult survival is estimated low for these years in the analysis of Chapter 2 (section 2.3.7), the inclusion of one more year of data and the combined analysis with MRR data from guillemots ringed as chicks shows a milder reduction in survival, although still unusual for a species that shows a rather constant adult survival overall. The low values of productivity synchrony in puffins and guillemots are related to their variable annual values that contrast with the rather constant (but slightly declining) razorbill productivity. It is notable that both puffins and guillemots had very poor breeding seasons around year 2007 (with probabilities of chicks fledging close to 0.3), while razorbill productivity was not affected; in any case, all three auk species share a long-term decline in productivity.

One of the advantages of data integration reported in the literature is that it can produce more precise estimators (Besbeas *et al.* 2002). We compare the results of the IPM-based models to the analyses of the same demographic data sets without the population counts (non-IPM models). We find only a slight increase in precision (particularly for razorbills, the species with least data), which indicates that the estimation of the demographic parameters is in our case dominated by their own rich data sets; this may not be the case for other data sets. Also, productivity estimates tend to remain rather unaffected by IPM modelling; a similar situation has been reported from simulation studies (Abadi *et al.* 2010a). The estimates of adult survival from the integrated model are nevertheless more precise than those obtained from the resightings and ring-recoveries of guillemots ringed as chicks. The second commonly-mentioned advantage of data integration is that, depending on data availability and model structure, it can sometimes permit the estimation of parameters which cannot be estimated from independent analyses of the different data sets involved (Besbeas *et al.* 2002). In the case of the Isle of May auk community, using an IPM (either single- or multi-species) allow the estimation of combined juvenile survival for razorbills and puffins, two species for which we do not have any source of direct information on the fate of individual juvenile birds. Finally, IPMs are also used to improve the estimation of abundance, compared to the naïve counts that include observation error.

We also compare the estimates from multi-species models (with random effects for the estimation of synchrony, either IPM or non-IPM) with those obtain from the corresponding single-species models (without the random effect structure). Interestingly, the inclusion of a common year random effect induces a slight effect of shrinkage towards the community mean in the estimation of adult survival (and to a lesser extent, in productivity), with associated increases in precision. As expected, the effect is stronger for razorbills, which is the species that contributes the least data.

Although the msIPM is obviously a complex model, the number of estimated parameters (641 non-derived parameters in total) does not appear so large when one takes into account that three species are modelled together (giving 121, 342 and 125 parameters for puffins, guillemots and razorbills, plus 53 shared parameters) and that, as is often the case in demographic models, some of the parameters are time-dependent for a period of 26 years. The amount of data used in the model is correspondingly very large (e.g. a total of 17303 '1's in the MR detection histories corresponding to resightings for the three species combined), as it is the combination of 8 data sets in total, and represents an important investment in field effort for data collection at the Isle of May over this period of time. We note that there is no inherent problem in extending the msIPM to include the other two focal species, kittiwakes and shags, although the Bayesian inference would take a considerable length of computing time and potentially memory issues given the resulting extremely large number of parameters.

There is currently no defined and tested framework for the assessment of goodness-of-fit (GOF) of integrated population models (Schaub & Abadi 2011). We assess the fit of the different components of the IPM to their respective data sets separately, which may actually be more informative about the origin of a potential lack of fit in the overall model. For the mark-resight data set collected from birds ringed as breeding adults, a study of model fit for each data set independently with the CJS model indicates some degree of trap-dependence in resight probabilities, and the model structure is subsequently modified to account for it (section 2.3.4). We calculate Bayesian p-values for the adult MR data sets (for the period 1984-2009) with the resulting adult survival synchrony model, which does not indicate lack of fit (puffin: 0.90, guillemot: 0.79, razorbill: 0.74; calculated with the Freeman-Tukey statistic as explained in section

2.3.8). The productivity model consists of independent binomial trials for each year, whose mean is estimated from a single data point per year; such a saturated model has perfect fit. The same is true of the guillemot probability of breeding in a particular year. The more complex age- and year-dependent structure of the guillemot chick MRR model is scrutinised in a frequentist framework in program MARK, estimating only a slight level of overdispersion ($\hat{c}$=1.185; details in section 6.1.4 in the next chapter). Finally, a visual inspection of the population estimates indicates that the estimates are in line with the population counts, so that at least a systematic lack of fit appears unlikely.

Integrated population models provide a way of separating the true population abundance and the observation error. Using counts with observation error instead of true population may dilute the relationship of abundance to other processes that may be the focus of a study (e.g. density-dependence, Freckleton *et al.* 2006). IPMs also allow the estimation of abundance in years when counts are not available. In our analysis for instance, we were able to estimate the year of the puffin abundance peak (2006) and the estimated maximum population (70540 breeding pairs), which is two years away from the closest puffin census, which took place in 2008. While population models can be populated with independent estimates for the different demographic parameters, their joint estimation within an IPM ensures that the demography of the population 'agrees' with an (imperfect) observation of the variation of population abundance in the form of censuses in at least some of the years.

Integrated population modelling makes explicit the relationship between changes in demographic rates and their impact on population fluctuations, and may bring insights into drastic population changes. Our extension of the IPM idea to encompass sympatric populations of several species allows at the same time the estimation of multi-species synchrony in a robust framework, and opens the door to further methodological developments such as multi-species density-dependence.

6 LIMITATIONS OF AN IPM TO COMPENSATE FOR REDUCED FIELD EFFORT IN A MONITORING PROGRAM

Long-term population monitoring is critical for many ecological studies and conservation, but often represents a significant investment in skilled staff time. This is particularly true for intensively monitored populations, in which several aspects of a species' demography may be studied alongside population abundance. It is therefore important to optimise the use of monitoring resources as monitoring programs increasingly come under pressure to reduce field effort given budgetary constraints. However, it is essential that this reduction does not negatively affect the ability of such programs to achieve their targets, which includes collecting enough data to detect relevant trends or ecological effects. In the particular case of seabirds, multi-decadal monitoring of breeding colonies exist in the UK (Mavor *et al.* 2008) and elsewhere, e.g. in the Pacific Ocean (Ainley, Sydeman & Norton 1995), Southern Ocean (Weimerskirch *et al.* 2003), Barents Sea (Sandvik *et al.* 2005), Western Atlantic (Montevecchi 2007), and Indian Ocean (Barbraud *et al.* 2011). This reflects the fact that seabirds have long been recognised as useful monitors of the status of their marine environment, as we have discussed in previous chapters.

With UK government funding for National Capability projects such as the Isle of May long-term-studies (IMLOTS) being reduced, organisations such as the Centre for Ecology & Hydrology are carrying out major reviews of their monitoring activities to see whether cost-savings can be made, with reductions in staff time being of particular interest. Ideally, savings should be made without compromising the quality of the data collected. Analyses of existing long-term data can be used to explore potential options for carrying out field projects (e.g. Sims *et al.* 2006; Chambert *et al.* 2012). The monitoring of the population of guillemots on the Isle of May involves annual assessments of (a) the total breeding population, (b) breeding success, (c) survival of breeding adults and (d) the survival of chicks after they leave the colony. The last is particularly important since the chick departs when only a quarter grown and is then fed for many weeks by the male parent while it completes its growth (Harris, Webb & Tasker 1991). However, estimating the survival of chicks is extremely time-consuming in terms of fieldwork. Not only must a sample of chicks be individually colour-marked each year, and this takes about 20 man-days, but the cliffs and sea-rocks must also be regularly searched for these birds as they return to the colony over many years. During the study reported on here, an average of 58 daily searches, each lasting 2-3 hours, were made to resight these colour-ringed birds each year. This is demanding work that must be made by an experienced observer familiar with the behaviour of guillemots and where in the colony these birds are likely to be seen. The question arises as to whether all this effort is required or whether input can be reduced while still producing the required results. Although the effectiveness of some of the aspects of the monitoring at the Isle of May has been studied (e.g. survey design to detect a trend in abundance, Sims et al. 2006), no such evaluation has been conducted to date for the MRR sampling methods. In this chapter we address an important aspect of study design, with the aim of optimising the use of resources to monitor the common guillemot at the island. As mentioned above, this work currently involves a major investment of time by (i) a team of ringers to maintain a marked population and (ii) a skilled observer to record ringed individuals returning to the colony.

We start by analysing the full chick MRR data set (section 6.1). We have already seen from our previous analysis of the chick MRR data set (section 5.5.3) that first-year survival of common guillemots has been very low during the last years of the time period analysed. This was accompanied by unusually poor breeding success (section 3.1.5) and chicks fledging in poorer body condition compared to the long term average (*unpublished data*). Here we explore juvenile survival further by investigating the effect of two individual-level covariates on survival of the first year of life: the hatching date and body condition at the time of ringing (Harris, Frederiksen & Wanless 2007).

Then, in the context of optimising the use of monitoring resources at the Isle of May, we assess whether the dramatic variations in first-year survival and the ecological relationships with individual-level covariates could have been detected had field effort been reduced (section 6.2). We do so by following two different resource-saving strategies: (i) reducing the amount of time spent looking for ringed immatures; (ii) reducing the number of chicks ringed each year. We construct and analyse scenarios of increasingly reduced effort, using a random resampling of the mark-resight-recovery data already collected. For the case of reduced resighting effort, we also consider a non-random reduction, concentrating resighting effort to June and early July when most immature age-classes are visiting the colony (Halley, Harris & Wanless 1995). We derive recommendations regarding changes in field protocols by comparing the analyses of these scenarios.

Finally, we investigate a more extreme scenario of stopping altogether the ringing of guillemot chicks (section 6.3). This option saves the most resources but as a consequence we cannot count on immature resightings and ring-recoveries, that is, there is no direct source of information on immature survival. We therefore explore whether in that situation an integrated population model that incorporates data on adult survival and productivity together with population counts at the Isle of May, is able to recover guillemot first-year survival from the adult-related data sets only. This strategy of combining data sets that share demographic parameters has been shown to allow the estimation of demographic rates for which no direct data were available (Besbeas *et al.* 2002; Schaub *et al.* 2007; Tavecchia *et al.* 2009). Conversely, we explore whether the omission of data on juvenile survival degrades the estimation of adult survival and population abundance.

We consider finally a further hypothetical scenario, in which guillemot breeding success data were not collected at the Isle of May. We study the impact of including the guillemot chick MRR data in an IPM in its ability to estimate productivity from the rest of the data sets. Figure 6-1 summarises the different analyses carried out in this chapter.

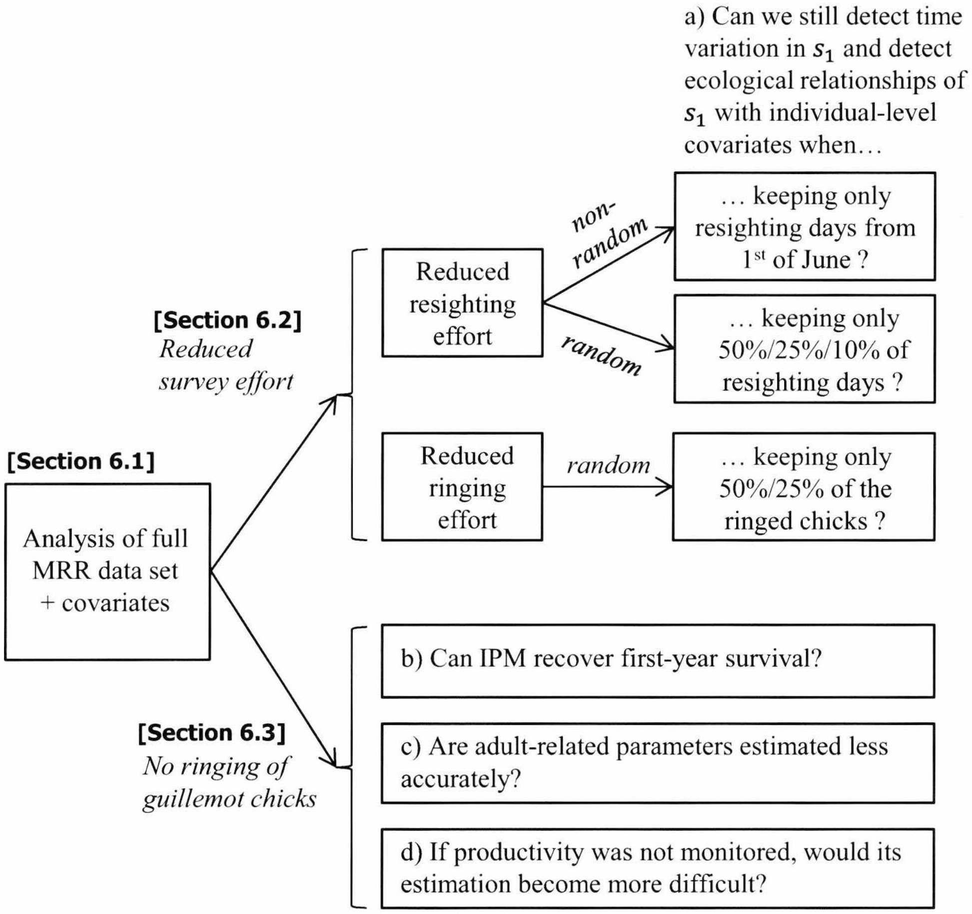


Figure 6-1 Diagram of the steps followed in the analyses carried out to investigate reducing fieldwork effort.

6.1 *Analysis of the full MRR data set*

The guillemot chick mark-resight-recovery data set is described in detail in section 5.4.2, although for this study we also include data from chicks marked in 1983, which is omitted from the multi-species IPM analysis so that the data sets for all species start in the same year. More details about the field methods are given in section 5.4.2 and in Harris, Frederiksen & Wanless (2007). In brief, a total of 6665 guillemot chicks were ringed at the Isle of May between 1983 and 2009 (annual totals ringed: between 96 and 325), with each chick given a unique colour ring on one leg and a numbered metal ring on the other. We recall that two areas were used in the study: 'area A' (a 400-m length of cliff) and 'area B' (a nearby skerry, of lesser visibility, where ringing only occurred until 1997). From 1984 to 2010, regular searches for ringed birds that had returned to the Isle of May produced 11152 individual resightings (excluding the initial capture) which translated into 4021 detections in the mark-resight history. The mark-resight-recovery data set also includes 242 ring recoveries from dead guillemots found on the Isle of May and elsewhere.

6.1.1 Individual-level covariates

At ringing guillemot chicks were weighed (±1g) using a spring balance and the length of the bent wing was measured (±1mm). We derive two individual-level covariates from these measures (see Harris, Halley & Wanless 1992 for details):

(i) Relative hatch date (RHD): calculated as the chick hatch date (HD = ringing date – estimated age at ringing) minus the annual mean hatch date of all chicks ringed that year. Age at ringing (AR) is estimated for chick i from its wing length W_i as:

$$AR_i(\text{days}) = 0.373\ W_i(\text{mm}) - 5.8.$$

Therefore for chick i: $RHD_i = (J_i - \bar{J}) - 0.373(W_i - \bar{W})$,

where J_i is the ringing date in June and the bars represent the average over the chicks in the same cohort.

(ii) Body condition index (BCI), the raw residual (observed mass – expected mass):

$$BCI_i = M_i - (\beta_0 + \beta_1 W_i^{-1}),$$

where chick mass is modelled as a linear function of W_i^{-1}, with the regression conducted separately for each year.

RHD is significantly correlated with age at ringing ($\rho = -0.761$, $p < 0.001$) but there is no statistical evidence of correlation with BCI.

6.1.2 MRR model

We analyse the guillemot chick mark-resight-recovery data set in the frequentist framework with program MARK (White & Burnham 1999), using the 'combined live-dead encounter' model (Burnham 1993) which handles live resightings and dead-recoveries simultaneously. MARK uses the Seber parameterization (Seber 1970) instead of the original one in Burnham (1993): the estimated parameters are thus true survival s, fidelity F, resight probability p and recovery probability r; the inclusion of rings recovered outside the Isle of May enables to estimate s and F.

Following the approach used in a previous analysis of juvenile survival at the Isle of May for a shorter time period (Harris, Frederiksen & Wanless 2007), we restrict the analysis to the first 9 years of life for each cohort; after that age most guillemots have started breeding. Resightings and recoveries for individuals older than 8 years are thus discarded and the corresponding 'adult' survival, resight and recovery probabilities consequently forced to zero in MARK when analysing the data set.

We use as a reference (i.e. without covariates) the model structure defined in section 5.4.2, adapted to the fact that the 'adult' class is not modelled. The model structure is as follows

(i) Year-dependent first-year survival $s_1(t)$, but constant survival separately for older age classes (s_2, s_3, s_4 and s_{5-9});

(ii) Year-dependent resight probabilities, separately for 3 age classes: $p_2(t), p_3(t)$ and $p_{4-8}(t)$. Note $p_1 = 0$ as young guillemots do not return to their natal colony in the first year of life. All resight probabilities were estimated independently for ringing areas A and B;

(iii) Constant fidelity for each of the classes '5' and '6' (F_5, F_6), and $F_{1-4} = 1$;

(iv) The probability of 'retaining a readable ring and continuing to breed at visible location' ('ring retention' for short, denoted ψ) is defined for '7-9' years of life;

(v) Ring reporting probability $r(t)$: linear trend with time on the logit scale, common to all ages;

(vi) All parameters related to adult individuals (over 8 years old) are set to zero in the analysis.

This model structure is also similar to that used by Harris, Frederiksen & Wanless (2007) for data collected up to 2002, but has a time trend in recovery probability that gives added flexibility. For an analysis of the full time period, our reference model shows an improvement of 120 QAICc units compared to their model structure.

The reference model is then used to test for relationships of first-year survival with the individual-level covariates, relative hatch date (RHD) and the body condition index (BCI). We carry out model selection based on the $QAIC_c$, comparing the reference model (no covariates, only cohort) to models with additive (including quadratic) and interaction relationships between cohort and the two covariates, considered independently. The covariates are introduced in first-year survival as a regression in the logistic scale.

6.1.3 Results for the reference model

The juvenile-related results from the reference model are very similar to those obtained from the msIPM in section 5.5.3, where data from adult guillemots is also included. We only repeat here the highlights (see Figure 6-2) and do not show detailed results for the sake of brevity. First-year survival displays a large amount of year-to-year survival, declining to extremely low levels in the last five years of the study. Resight probabilities (areas A and B) show the same patterns described in section 5.5.3, where a possible interpretation is given based on a long-term behavioural change in immature guillemots. A significant decline is estimated in ring-recovery probability, with an estimated slope (and 95% confidence intervals) of -0.603 (-0.764, -0.442), similar to the msIPM result. The estimates of fidelity are 0.835 (0.769, 0.884) for age

5, 0.756 (0.693, 0.809) for age 6. 'Ring retention' $\hat{\psi}$ is 0.778 (0.717, 0.828), for older guillemots (ages 7-9).

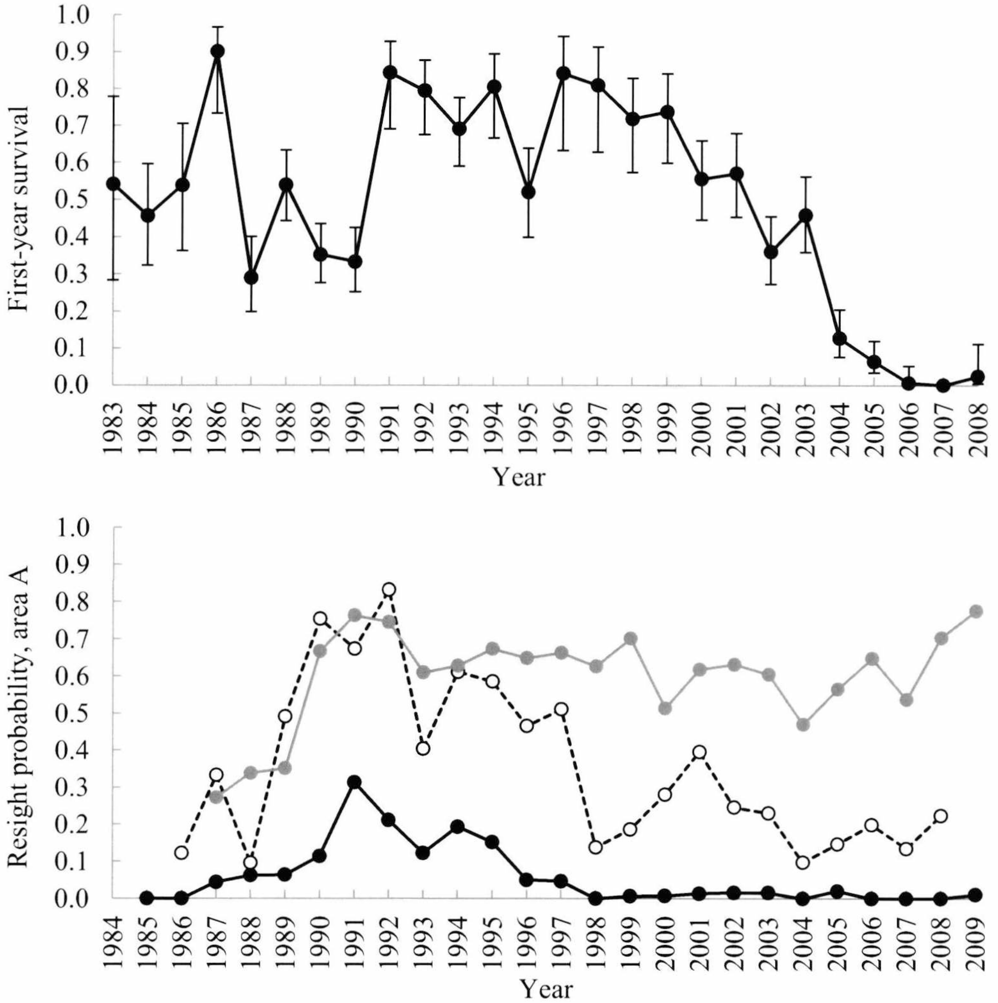


Figure 6-2 Top panel: estimated first-year survival (median and 95% CI) for cohorts ringed 1983-2008. The point estimate for 2007 is zero and the variance cannot be estimated. The 2009 estimate (not shown) is very imprecise. Bottom panel: estimated resighting probabilities (median; CI not shown for clarity) of immatures aged 2 (black line), 3 (dashed line) and 4-8 (grey line) years, ringed in area A. Several years that are estimated as 0 for 2 year old resight probability represent boundary estimates. The 2009 estimate for age 3 is also boundary estimate (1), probably due to the smaller amount of resightings at the end of the period.

6.1.4 *Individual-level covariates for first-year survival*

Using the median-$\hat{c}$ procedure in MARK, we estimate a slight overdispersion in the reference model (estimated $\hat{c}$=1.1850, SE: 0.0107). The top ranking model does not have a full interaction structure but an additive one (Table 6-1).

Table 6-1 Model selection for individual covariates (with $\hat{c}$=1.1850). The reference model with year-dependent first-year survival is denoted $s_1(t)$ in the table (highlighted in bold), where t represents cohort. '+' signs represent additive effect of the individual covariate while '*' signs represent full interaction terms between cohort and the covariate. 'RHD'=Relative Hatch Date, 'BCI'=Body Condition Index. Covariates are introduced through a logit-link function.

Model	QAICc	ΔQAICc	Weight	Parameters	-2log(L)
s1(t+RHD)	18263.58	0	0.56	161	21254.9
s1(t+RHD+RHD^2)	18265.25	1.67	0.24	162	21254.4
s1(t)	**18267.31**	**3.73**	**0.09**	**160**	**21261.8**
s1(t+BCI)	18267.81	4.24	0.07	161	21259.9
s1(t+BCI+BCI^2)	18269.14	5.57	0.03	162	21259.0
s1(t*RHD)	18281.37	17.79	0.00	187	21212.3
s1(t*BCI)	18300.22	36.65	0.00	187	21234.6

Models with full interaction, particularly with RHD, decrease the deviance but are penalised by the extra number of parameters. There is no evidence that body condition (BCI) affects first-year survival, with both additive and interaction models ranking low, and 95% confidence intervals of the estimated slopes always including zero. However, relative hatch date does appear to explain individual variations in first-year survival. The estimated slope of the relationship with RHD in the top ranking model is negative and its 95% CI does not include zero: -0.029 (-0.053, -0.005). Thus, early hatched chicks have higher chances of survival compared to late chicks. Figure 6-3 shows some example plots of the actual relationship for selected years of high and low average first-year survival.

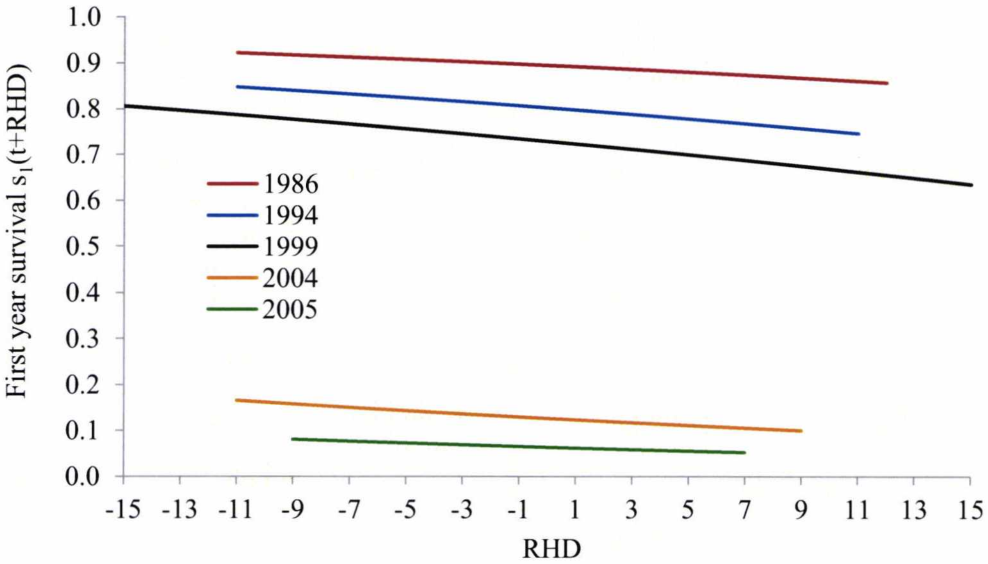


Figure 6-3 Examples of the relationship between first-year survival and relative hatch date (RHD) in the top ranking 'cohort + RHD' additive model, for a) some years of very low average survival; b) some years of high average survival. For each curve, only the range of RHD values that appear in ringed chicks in that particular year is plotted.

Although penalised by the larger number of parameters, estimates from the model with the full interaction 't*RHD' would be selected over the 't+RHD' model in a likelihood ratio test ($\chi^2_{26,0.05}$=38.89). It is interesting to look at the estimated slope and intercept for this RHD interaction model (Figure 6-4). In many years, the estimated slope of the RHD covariate is close to zero and has 95% confidence intervals that include it, so there is no clear evidence of a year-specific relationship with relative hatch date. However, in some other years the estimated slope is far from zero and confidence intervals do not include it (or only marginally).

Figure 6-5 shows the estimated relationship of first-year survival with RHD for some selected years. During the years of lower first-year survival, e.g. from 2004 to 2008, both intercept and slope are negative. The effect of hatching early is pronounced, except in 2006 and 2007 when survival is practically zero irrespective of hatch date. In 2005 for example, with average chick survival of 0.044, only the very early chicks have a chance of over 20% of surviving their first winter according to this model. The intercept is positive in the years when survival is highest, and the resulting relationship indicates in most cases that survival is high except for the very latest hatching chicks.

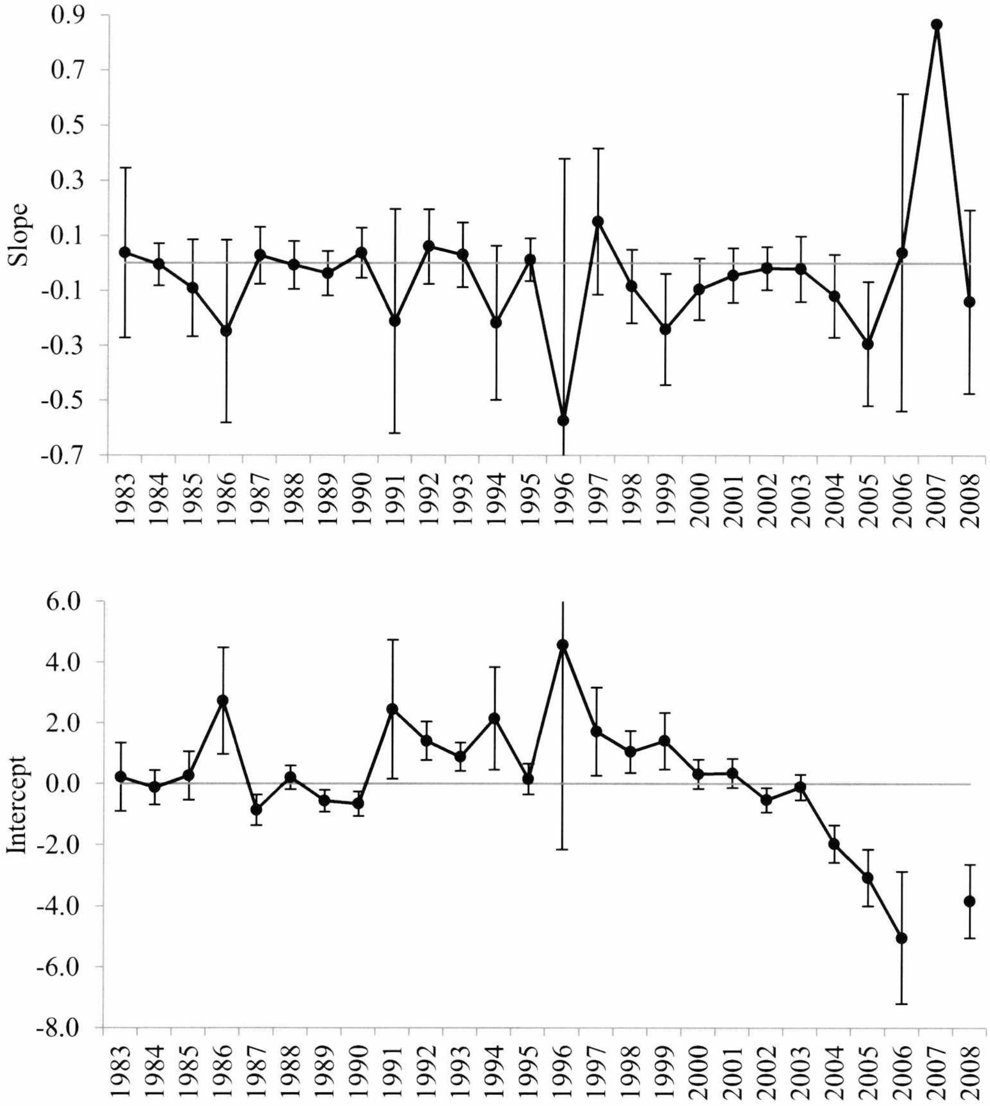


Figure 6-4 Year-specific estimates of slope and intercept of the relationship between first-year survival and relative hatch date (RHD) for the period 1983-2008, with 95% confidence limits. In all cases when the estimated slope is positive, its value is close to zero and its 95% CI includes zero so we cannot exclude the possibility of no real relationship.

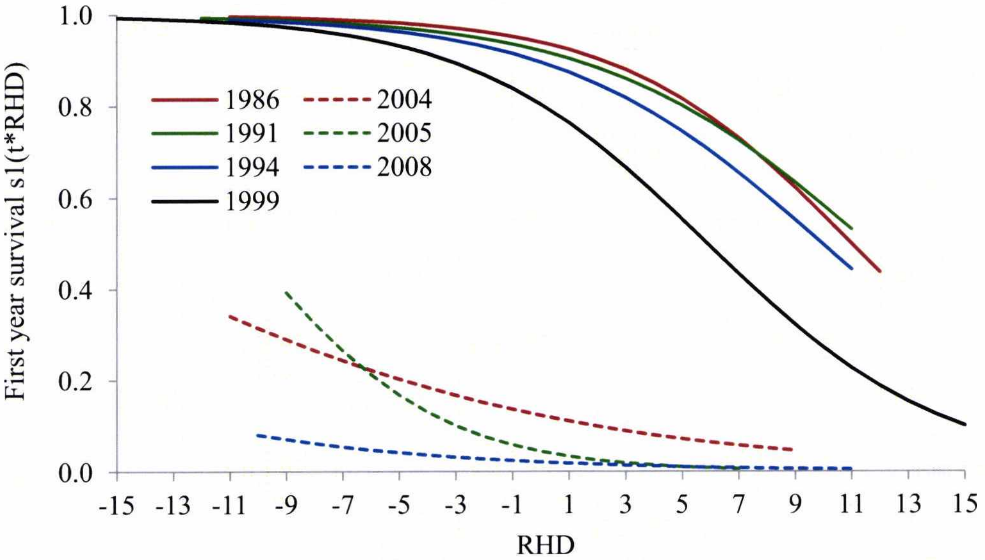


Figure 6-5 Examples of the relationship between first-year survival and relative hatch date (RHD) in the 'cohort x RHD' full interaction model, for a) some years of very low average survival; b) some years of high average survival. For each curve, only the range of RHD values that appear in ringed chicks in that particular year is plotted.

6.2 Reduced survey effort

6.2.1 Optimising monitoring resources

The relevance of study design in ecological studies is widely recognised, as well as the fact that in practice it is an often disregarded aspect (Yoccoz, Nichols & Boulinier 2001). Survey design rules have been developed for different wildlife monitoring frameworks (e.g. distance sampling, Buckland *et al.* 2001; site occupancy, Mackenzie & Royle 2005). In the context of the study of marked individuals, design considerations may include accounting for a range of issues (e.g. band loss and temporal emigration; see e.g. Williams, Nichols & Conroy 2002, pp. 490-492; or Lindberg 2012) that can cause bias and/or affect precision of the estimates. In this section we concentrate on one particular aspect: the amount of survey effort required to meet the objectives of a monitoring program, specifically the implications of varying ringing and resighting effort. Sample size rules have been developed for the estimation of abundance in closed population CMR (Otis *et al.* 1978) as well as for survival in open population band recovery models (Youngs & Robson 1975; Wilson, Nichols & Hines 1989). Burnham *et al.* (1987) provide considerations of the power of hypothesis tests (control-experiment) in the context of survival experiments using CMR methodology, in setups with marks that identify either group (treatment or control) or individual within group. However, general sample-size recommendations are typically based on rather simplistic model structures. For more complex and targeted structures, two radically different general approaches have been suggested for sample size determination: (i) computer-intensive Monte Carlo simulations, where many data sets are generated and analysed, and (ii) a method based on a single data set of expected values (Burnham *et al.* 1987) that is valid under large sample approximations. Of these two approaches, the use of simulations appears to be more widespread. For example, Converse *et al.* (2009) used simulations to compare two variations of robust design survey (Kendall *et al.* 2009), looking at the optimal allocation of survey effort; and Chambert *et al.* (2012) used simulations in a Cormack-Jolly-Seber model to explore optimal scheduling of surveys to maximize resight probability and minimize individual detection heterogeneity. A recent example of the method based on expected values is Devineau, Choquet & Lebreton (2006).

6.2.2 *Reducing resighting effort*

To investigate the effect of reducing resighting effort on the ecological inferences that could be made from the data, we use the 27 years (1984-2010) of resighting data to construct plausible scenarios of changes in field protocols. Searches for ringed birds were made regularly from mid-April to mid-July and the number of days per year when searches were made varied from 8 to 109 (mean: 58 days). Based on this information we create four new mark-resight-recovery data sets to investigate outcomes if survey effort had been less over the study period:

(i) Resightings restricted to those made from 1st of June onwards (data set 'DJune'), when most immature age-classes are visiting the colony (Halley, Harris & Wanless 1995);

(ii) Resightings drawn from 50% ('D50%'), 25% ('D25%') and 10% ('D10%') of the calendar days each season selected at random.

Of the original 11152 raw resight records collected during these years, the reduced data sets have 6095, 5585, 2809 and 1054 records respectively, corresponding to an approximate reduction of field effort of 50%, 50%, 75% and 90%. Because birds are often resighted more than once in a season, the actual number of resightings in the MR detection history reduce from 4021 to 2796, 2695, 1669 and 811 respectively. These corresponded to effective reductions in resight information of 30%, 33%, 58% and 80% respectively. As expected, for any given reduction in resighting, field effort translates into a smaller reduction of resight information in the history to be analysed, since each detection in the history corresponds to the overall effort of resighting a bird over the whole season. As the ring recovery data come from members of the public and are independent of field effort at the Isle of May, these are left unchanged in all analyses.

The four reduced data sets are then analysed using the reference model (where first-year survival is fully time dependent) and also with the model with relative hatch date as additive covariate ('t+RHD'), which is the top ranking model of the full data set analysis (Table 6-1). We compare first-year survival estimates with the ones obtained from the analysis of the full data set. To verify whether we could still detect the effect of an individual covariate when field effort is reduced, we compare the most parsimonious model with individual covariate with the reference model.

6.2.3 Reducing ringing effort

A similar approach is used to explore two further simulated scenarios, representing in this case a reduction in ringing effort while maintaining the resighting effort and the ring recoveries at the real level. In these reduced data sets we retain 50% or 25% of the ringed chicks, randomly chosen (data sets 'Ring50%' and 'Ring25%' respectively). The corresponding number of resightings in the MR detection history is reduced from 4021 to 1961 and 1000 respectively (51% and 75% data reduction). The number of recoveries associated with the reduced number of guillemot chicks declines from 242 to 122 and 72 respectively (50% and 70% data reduction). The reduced-ringing effort data sets are also analysed with both the reference model and the model with additive RHD effect, as described in the previous section.

6.2.4 *Impact of reduced survey effort*

We start by reporting the comparative results for the reference models with no covariates in first-year survival. The estimates of $s_1(t)$ appear robust to the decrease in resighting field effort, and the consequent reduction in the amount of resighting data (Figure 6-6). The general pattern is reflected even in the D10% data set where a model with constant first-year survival has much poorer fit (91 QAICc units) than having year-variation, probably driven by the extreme variation in first-year survival.

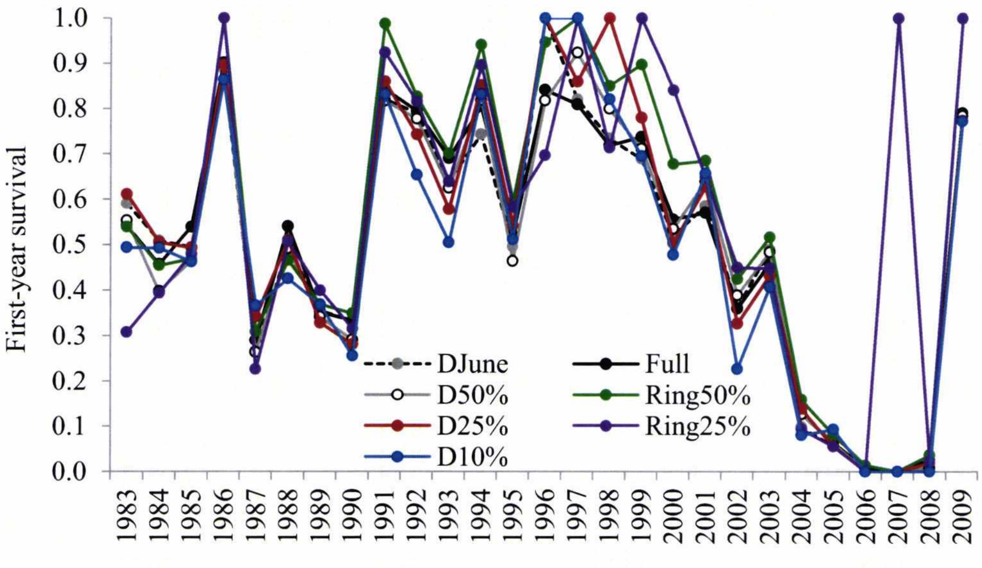


Figure 6-6 First-year survival probability estimated from the different data sets with increasingly sparse resightings. 'Full': complete data set; 'DJune': only resightings June onwards; 'D50%/25%/10%': keeping only the resightings of 50%/25%/10% of the calendar dates; 'Ring50%/25%': using only 50%/25% of the ringed chicks.

Despite the relative robustness of the estimate of $s_1(t)$, the associated uncertainty increases with data sparseness, as can be seen in the increasingly wide confidence intervals and SDs, as well as the larger number of boundary estimates (Figure 6-7). As an overall measure of precision, we calculated the generalised variance (the determinant of the estimated variance-covariance matrix) for the regression coefficients corresponding to the estimates of $s_1(t)$ of each data set (excluding years with parameters estimated at the boundary). Its value increases steadily from $5 \cdot 10^{-25}$ to $6 \cdot 10^{-16}$ as the data sets became sparser (Figure 6-8).

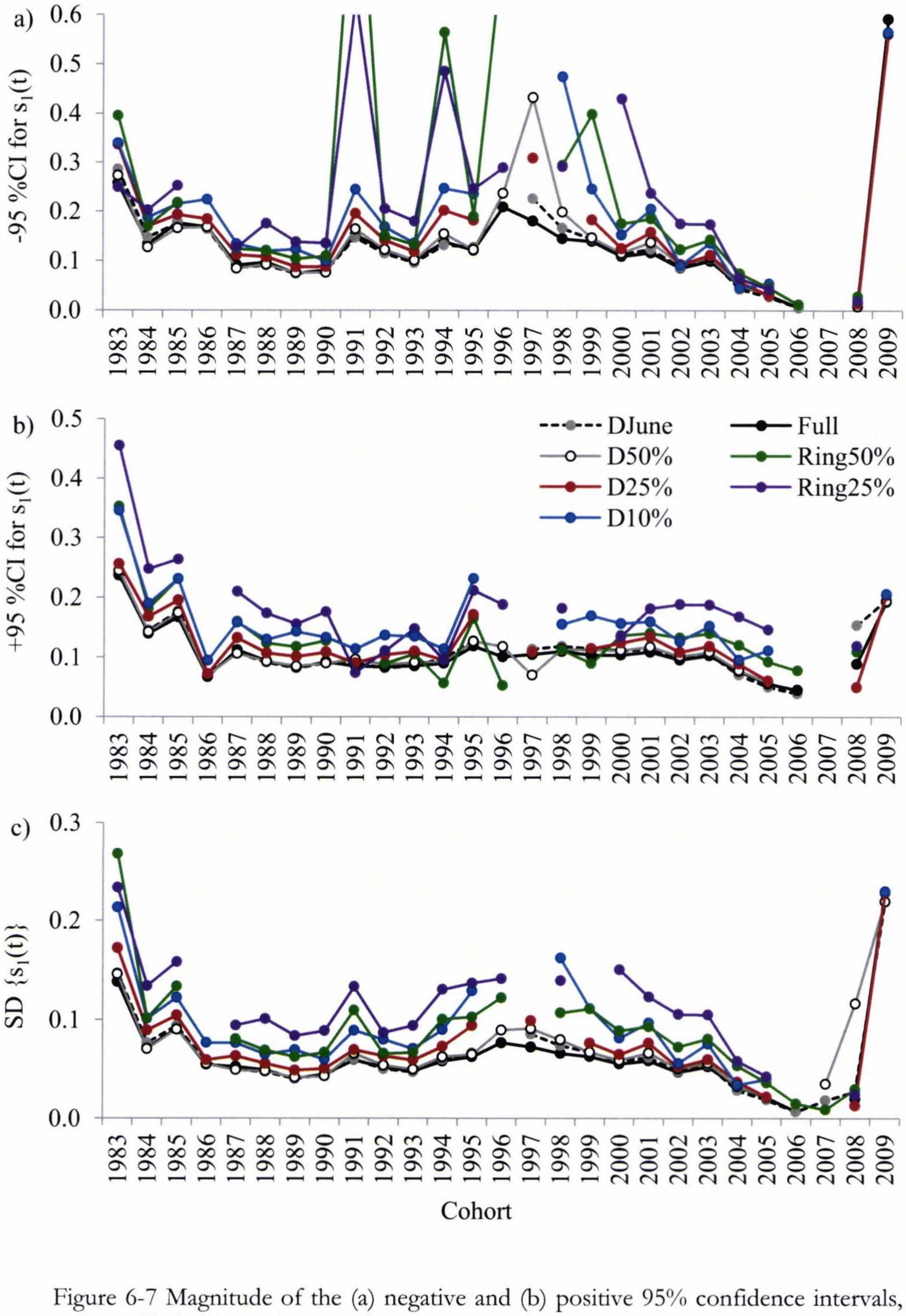


Figure 6-7 Magnitude of the (a) negative and (b) positive 95% confidence intervals, and (c) SD for the estimates of first-year survival. Values of zero or one (representing cases where the model could not calculate them) are not displayed. 'Full': complete data set; 'DJune': only resightings June onwards; 'D50%/25%/10%': keeping only the resightings of 50%/25%/10% of the calendar dates; 'Ring50%/25%': using only 50%/25% of the ringed chicks.

Reductions in the number of ringed chicks have a much greater effect; even a 50% decrease in ringing effort brings more boundary estimates in the estimation of first-year survival (Figure 6-6) as well as a noticeable decrease in precision (Figure 6-7, Figure 6-8).

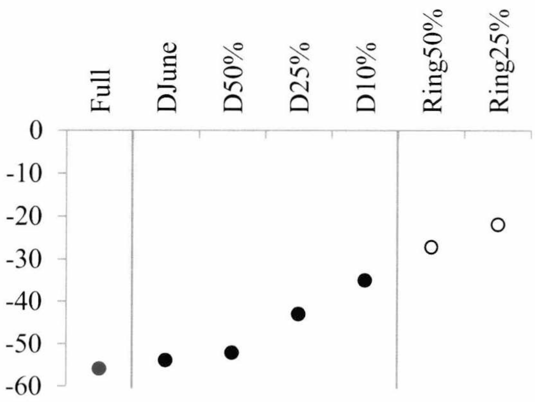


Figure 6-8 Logarithm of generalised variance (determinant of the Variance-Covariance matrix) for the regression coefficients of $s_1(t)$, computed for data sets Full, DJune, D50%, D25%, D10%, Ring50% and Ring25%. Parameters estimated at the boundaries are eliminated from the computation.

The estimates of survival for the 2nd, 3rd, 4th and 5-9th years of life have an increasing uncertainty and bias as the amount of resighting or ringing effort decreases (Figure 6-9). Reducing resighting effort appeared to bias these estimates negatively but the effect is less clear for the scenarios of reduced ringing effort.

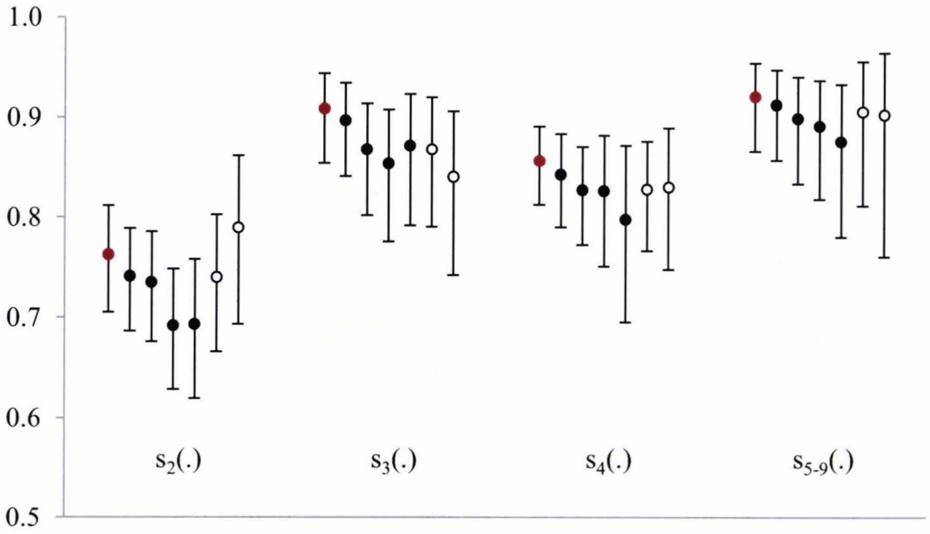


Figure 6-9 Survival probabilities for the 2nd, 3rd, 4th and 5-9th years of life, estimated from the different data sets with increasingly sparse resightings or with fewer ringed chicks. For each parameter, from left to right: 'Full': complete data set (red dots); 'DJune': only resightings June onwards; 'D50%/25%/10%': keeping only the resightings of 50%/25%/10% of the calendar dates; 'Ring50%/25%': using only 50%/25% of the ringed chicks (white dots).

One obvious and direct consequence of reducing resighting effort is that the probability of resighting a marked individual is reduced as less time is spent searching for birds This effect is apparent in all age classes (Figure 6-10 and Figure 6-11 for chicks ringed in areas A and B respectively). In contrast, when ringing effort is reduced we would expect resight probabilities to be unaffected as long as resighting effort remains at the same level. The estimates from data sets 'Ring50%' and 'Ring25%' support this expectation (Figure 6-12). A reduction in precision of the resight probability estimates is nevertheless likely to follow the lower number of ringed birds.

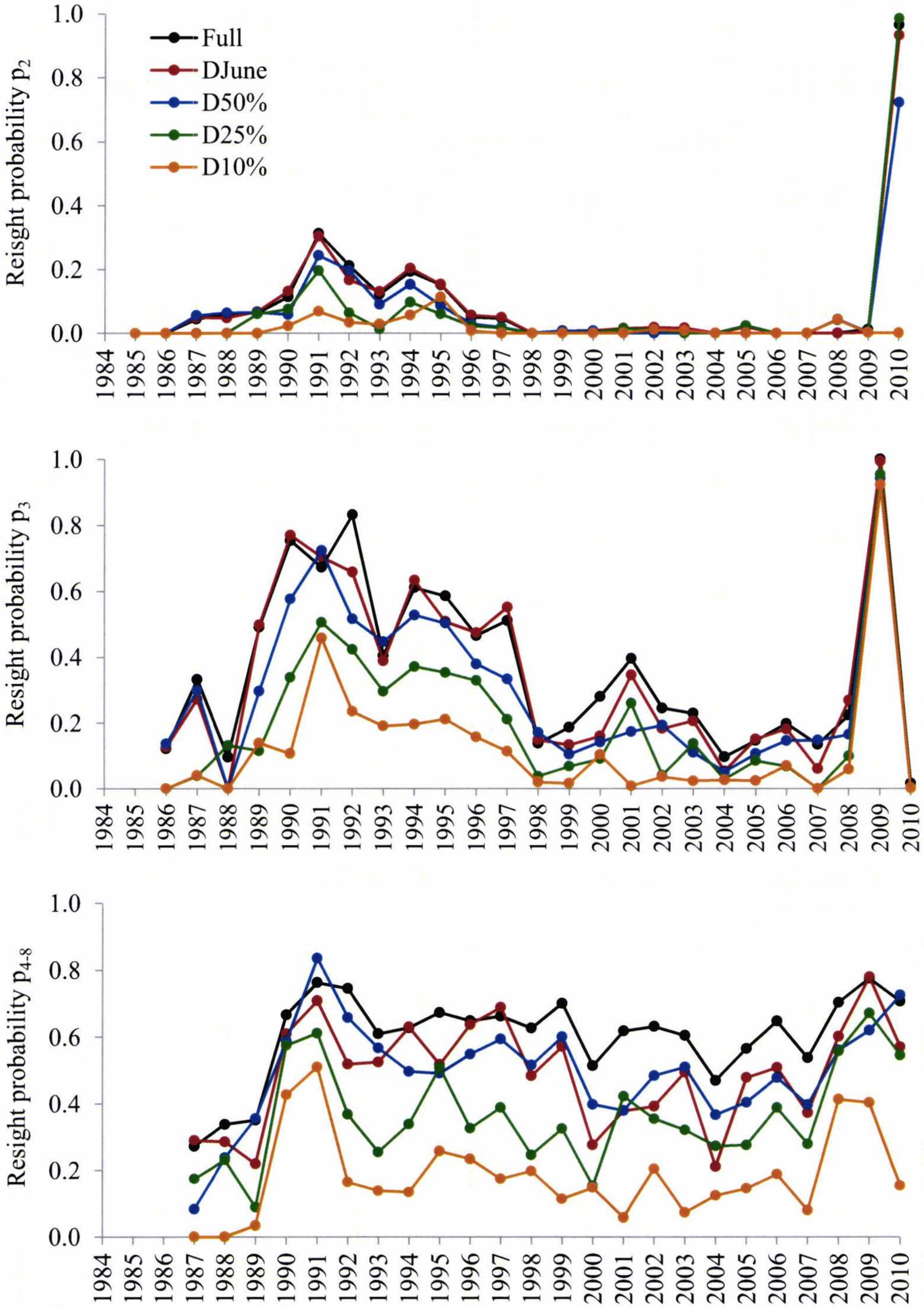


Figure 6-10 Resight probability for guillemots ringed in area A for different levels of resighting effort reduction. Confidence intervals are not shown for the sake of clarity.

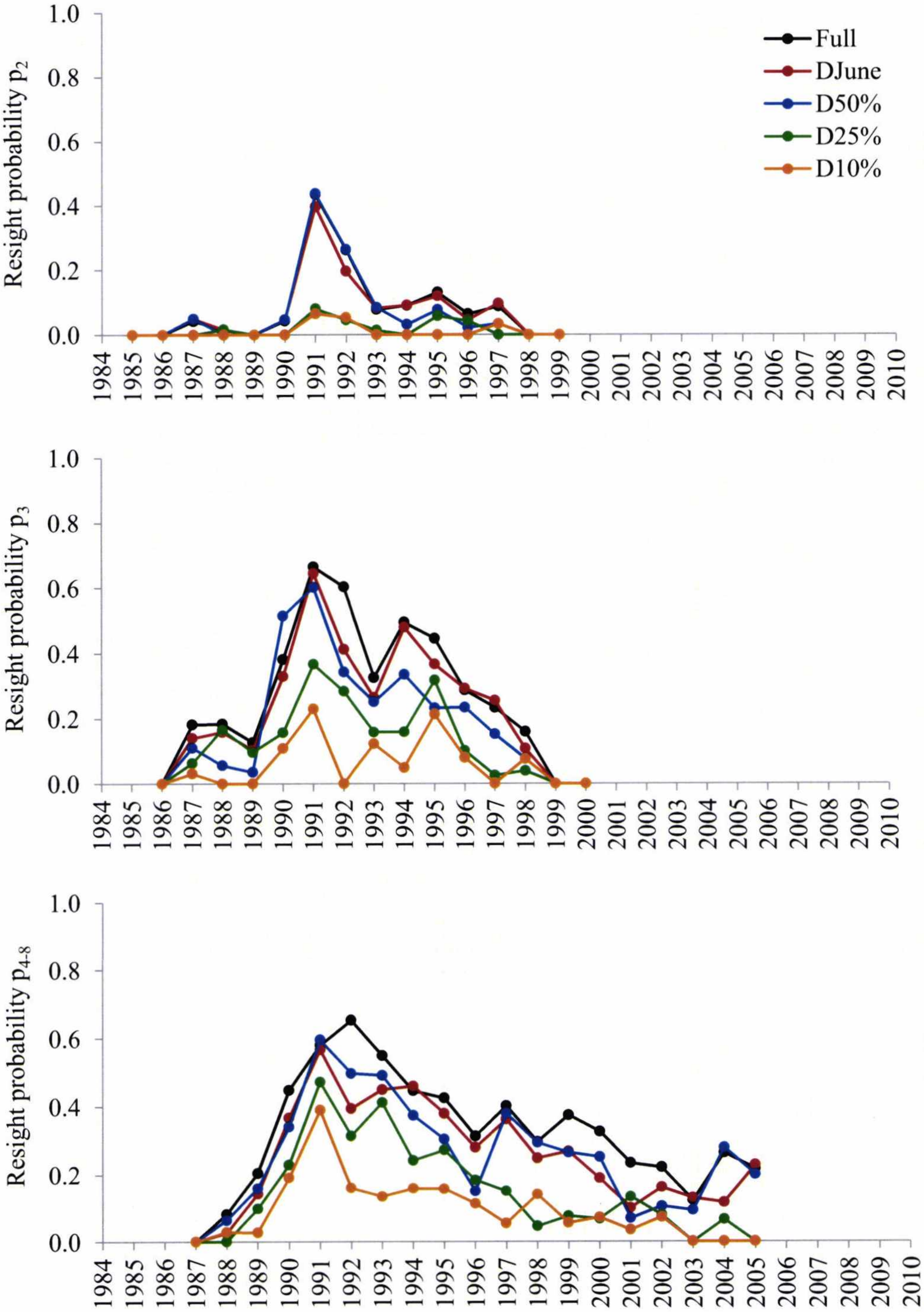


Figure 6-11 Resight probability for guillemots ringed in area B for different levels of resighting effort reduction. Confidence intervals are not shown for the sake of clarity.

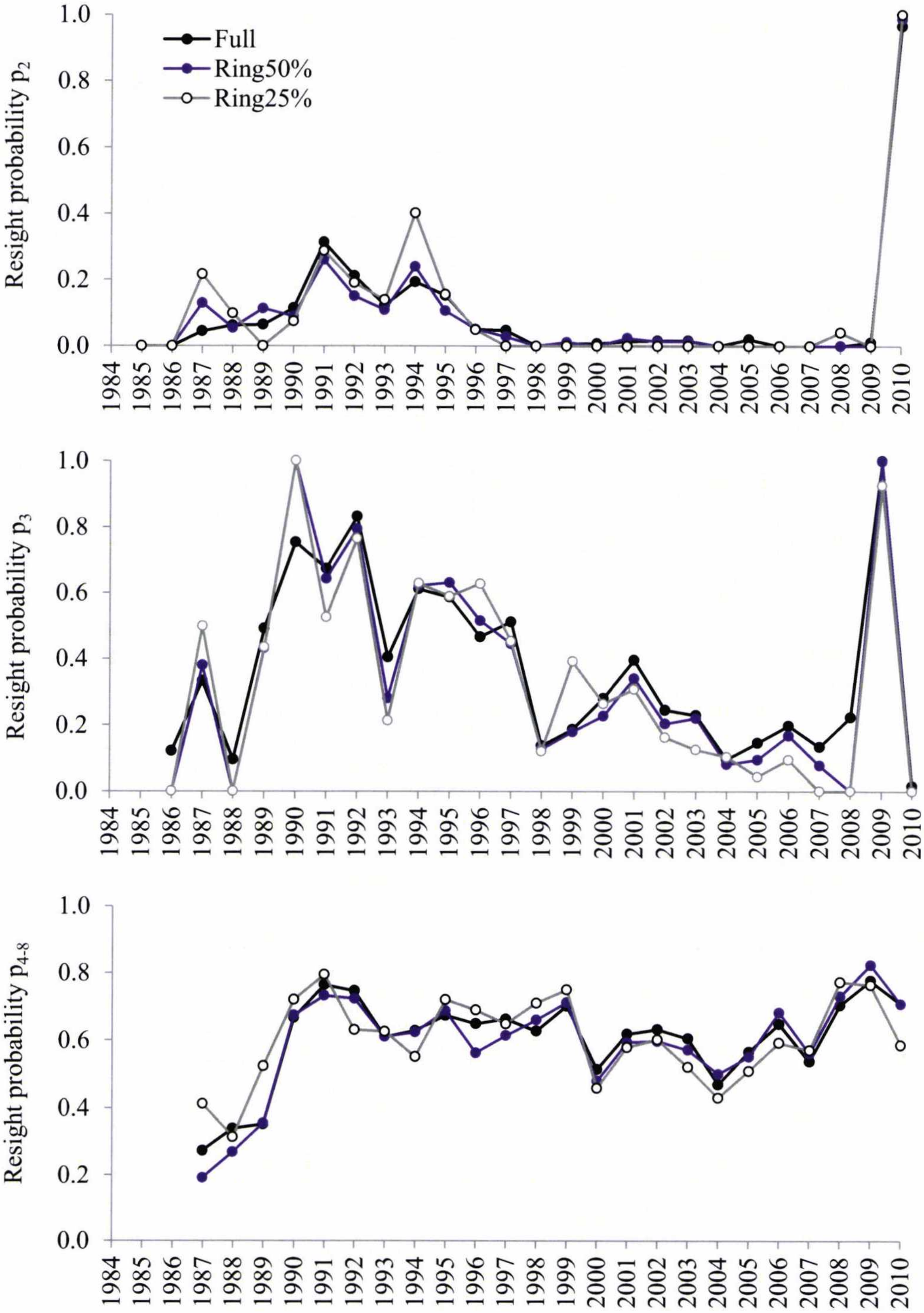


Figure 6-12 Resight probability for guillemots ringed in area A as the amount of ringing effort is reduced. Confidence intervals are not shown for the sake of clarity. Note that, unlike in the case of resighting effort reduction, resight probability stays at similar levels.

The uncertainty in the estimates of fidelity F and 'ring retention' ψ (Figure 6-13) increases both as resight data become sparser and as ringing effort is reduced, particularly for the 'D10%' and 'R25%' data sets.

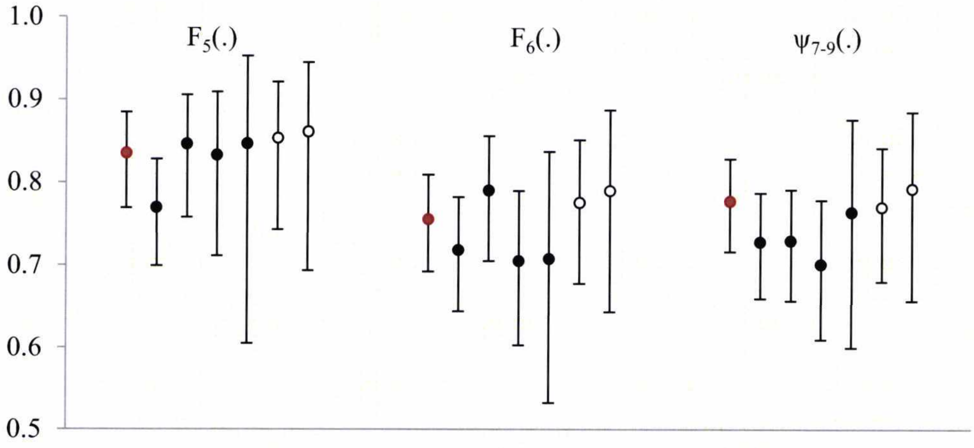


Figure 6-13 Estimated fidelity F (age 5 and 6) and 'ring retention' ψ (age 7-9). For each parameter, from left to right: 'Full': complete data set; 'DJune': only resightings June onwards; 'D50%/25%/10%': keeping only the resightings of 50%/25%/10% of the calendar dates; 'Ring50%/25%': using only 50%/25% of the ringed chicks.

The estimates of recovery probability should be relatively unaffected by a reduction in resighting effort, but be less precise when fewer chicks are ringed. In accord with this, the precision of the estimated slopes and intercepts of the regression of recovery probability (Figure 6-14) change little as less time is spent resighting immatures, although there is some indication of a slight negative bias being introduced in the estimation of the intercept. The estimates for reduced ringing effort scenarios show not only increasing confidence intervals but also positive bias, both in intercept and slope, which translates into a less precise and flatter variation over time (Figure 6-15).

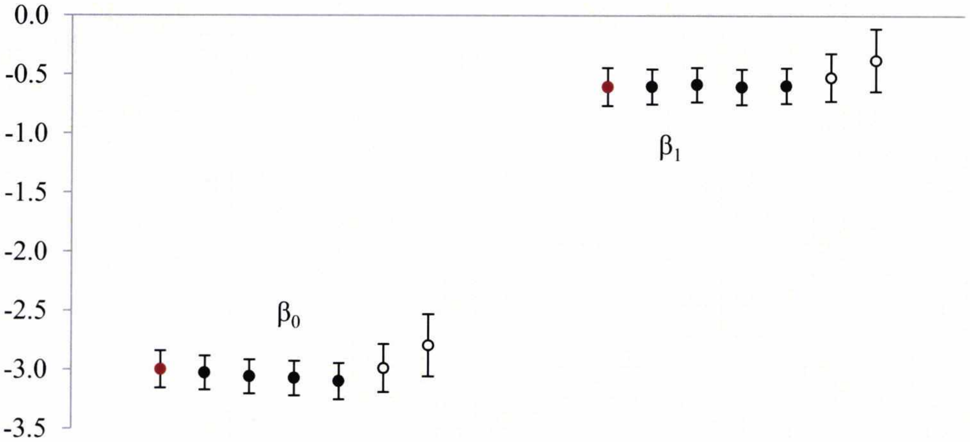


Figure 6-14 Estimated intercept (β_0) and slope (β_1) of the logistic regression of recovery probability with time. For each parameter, from left to right: 'Full': complete data set; 'DJune': only resightings June onwards; 'D50%/25%/10%': keeping only the resightings of 50%/25%/10% of the calendar dates; 'Ring50%/25%': using only 50%/25% of the ringed chicks.

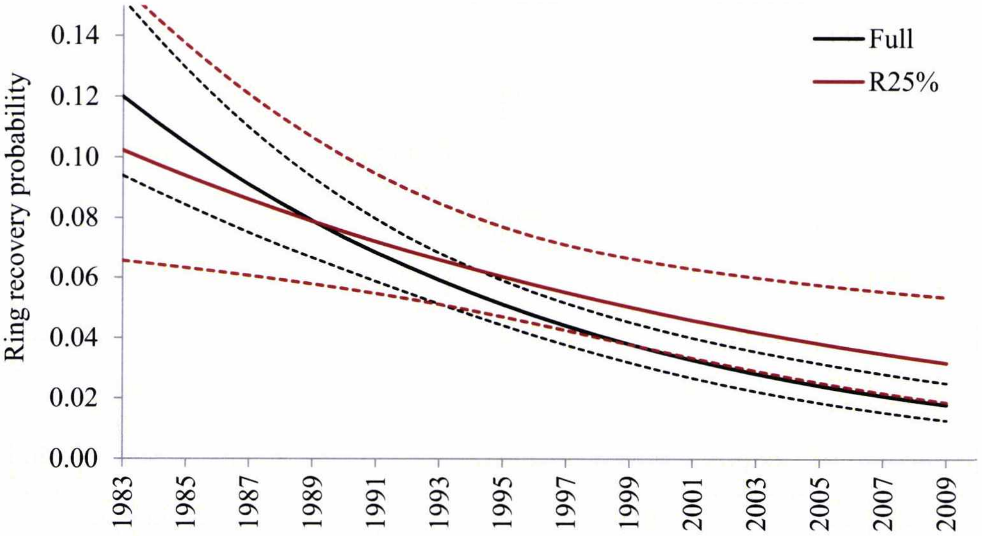


Figure 6-15 Estimated ring recovery probabilities for models 'Full' (black line) and 'R25%' (red line). Dotted lines represent the limits of the 95% confidence intervals.

For the models with RHD as individual covariate for first-year survival, the inference is relatively robust to some reduction in effort (Figure 6-16). Compared to the analysis of the full data set, the estimate of the additive regression coefficient (β_{RHD}) is very similar when 50% of the days are removed, and only slightly different when the reduction of resighting effort is 75%. When resight data are retained for only 10% of days, the uncertainty increases to the point that the effect of RHD is no longer statistically significant (α=0.05). The decrease in QAICc when including RHD as an additive covariate in first-year survival goes from 3.73 in the full data set, to 4.13, 3.42 and 4.03 respectively for the data sets DJune, D50% and D25%. For the D10% data set, QAICc increases by 0.95 units when the covariate is introduced, which is consistent with the fact that the estimated 95% confidence interval of its corresponding regression coefficient includes zero. Thus if resighting effort had been reduced by 90% we would not have been able to detect a statistically significant effect of RHD on first-year survival.

When the reduction is in ringing effort, the decrease in QAICc is 0.86 and 1.20 units for data sets Ring50% and Ring25% respectively; the difference is small and the 95% CI of the RHD regression coefficient includes zero in its right tail: we might have not been able to detect a significant effect of RHD had the ringing effort been halved.

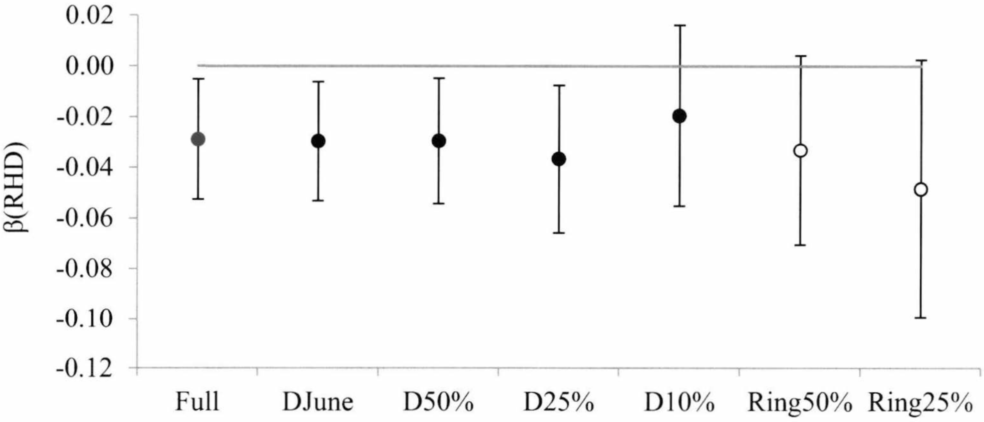


Figure 6-16 Estimated regression coefficient for RHD, with 95% CI. 'Full': complete data set; 'DJune': only resightings June onwards; 'D50%/25%/10%': keeping only the resightings of 50%/25%/10% of the calendar dates; 'Ring50%/25%': using only 50%/25% of the ringed chicks.

6.3 *Stopping fieldwork on immature guillemots*

6.3.1 *Integrated population models*

To explore the consequences of stopping ringing guillemot chicks and thus being unable to estimate immature survival directly, we develop several variations of the guillemot integrated population model in section 5.4, which uses the breeding adult mark-resight data set together with annual counts of the number of breeding pairs and data on annual breeding success. In this scenario no information is collected for individual chicks, so we cannot study the effect of individual covariates on first-year survival. Rather we compare the estimates of annual first-year survival probabilities obtained from the IPM that included the guillemot chick MRR data set (model 'IPM1', with a structure for the MRR part equivalent to our initial reference model in MARK) with those inferred using an IPM without the chick MRR data set (model 'IPM2'). We note that whenever the MRR data set is omitted from the population model, we estimate apparent survival (denoted with letter 'ϕ') instead of true survival 's'.

We further investigate the potential gain in estimating adult-related parameters (survival, productivity and population abundance) by incorporating direct information on juvenile and immature survival into an IPM, as the integration of independent data sets may bring higher estimate precision than their independent analysis (Besbeas, Lebreton & Morgan 2003). Thus, we compare adult-related estimates from IPM models with and without the guillemot chick MRR data set, that is, models 'IPM1' and 'IPM3' respectively, where the latter has constant combined juvenile survival $\phi_{1+}(.)$.

Finally, in a hypothetical scenario where no direct data on breeding success of guillemots were collected at the Isle of May, we explore whether our ability to recover information on productivity $\rho(t)$ using an IPM improves when the guillemot chick MRR data set is incorporated. For this we compare the estimates of productivity obtained when breeding success data are available (IPM1) as a reference, to models in which such data are not incorporated, and either include (IPM4) or omit (IPM5) chick MRR data. In these cases, productivity becomes a hidden parameter and its estimation rests upon its effect on population abundance, as described by the Leslie matrix.

In total, five IPM models are fitted to various components of the data set (summarized in Table 6-2). All of them include population counts and adult mark-resight data sets. Productivity is estimated as time-dependent $\rho(t)$ in all cases, including when no direct productivity data are modelled (IPM4 & IPM5). The comparisons carried out are summarised in Figure 6-17.

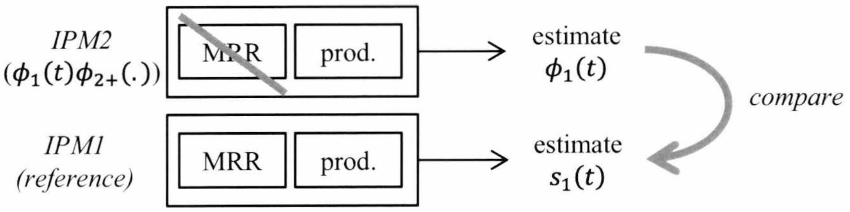
Table 6-2 Integrated population models fitted for investigating the effect of not ringing guillemot chicks. Different data sets are included (✓) or excluded (×) from the models. 'MRR(C)': chick mark-resight-recovery data; 'prod(A)': adult productivity data. The last column shows the hidden parameters for which there is no direct information; these are estimated from the rest of the data sets through the population model. $\phi_1(t)$: time-dependent first-year survival; $\phi_{2+}(.)$: constant immature survival (age ≥ 2); $\phi_{1+}(.)$: constant immature survival (all ages), equal to $\phi_1 \cdot \phi_{2+}$.

Model	MRR(C)	prod(A)	Hidden parameters
IPM1 (reference)	✓	✓	--
IPM2	×	✓	$\phi_1(t), \phi_{2+}(.)$
IPM3	×	✓	$\phi_{1+}(.)$
IPM4	✓	×	$\rho(t), \phi_{1+}(.)$
IPM5	×	×	$\rho(t), \phi_{1+}(.)$

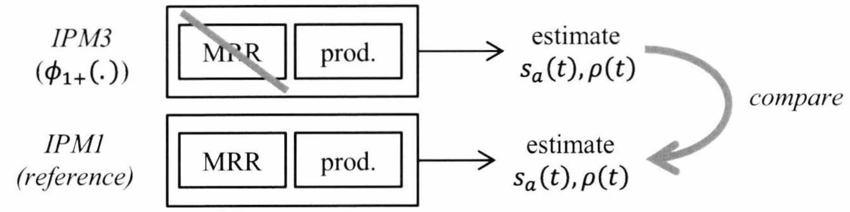
The full chick MRR data set is used, including resightings and recoveries for birds older than 8 years. The structure of its related likelihood component (modelled using a multi-state likelihood approach, see section 5.4.2) is based on the reference model used above in MARK, except that adult parameters are not forced to zero and adult survival $s_a(t)$ (defined for breeders, i.e. age ≥ 5) is a common parameter with the adult MR likelihood component.

We briefly recall here that in the population model, the quantity monitored is the female guillemot adult breeding population, and that we assume an age at first breeding of 6 years, negligible adult emigration and a balanced sex ratio at birth. The model includes 'retention of colour rings and recruitment to a visible location' ψ for the older age class (details in section 5.4).

A) Can IPM recover first-year survival?



B) Are adult-related parameters estimated less accurately?



C) If productivity was not monitored, would its estimation become more difficult?

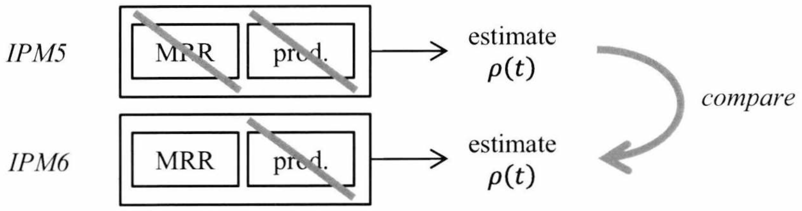


Figure 6-17 IPM comparisons carried out to evaluate the impact of not ringing guillemot chicks.

For models that include chick MRR data (IPM1 & IPM4), we use $s_1(t)$ and age-dependent true survival for 2^{nd} to 5^{th} year of life. In models without chick MRR data, fidelity is confounded so we actually estimate apparent survival ϕ instead of true survival s. Model IPM2 has $\phi_1(t)$ but a combined immature survival and fidelity for the remaining age classes

$$\phi_{2+}(.) = s_2 s_3 s_4 s_5 F_5 F_6.$$

The structure is simplified further in models IPM3 and IPM5, with an overall combined juvenile survival

$$\phi_{1+}(.) = s_1 s_2 s_3 s_4 s_5 F_5 F_6.$$

In models without breeding success data (IPM4 and IPM5), productivity $\rho(t)$ is estimated from the rest of the data sets through the population model.

As in section 5.4, the fitting of the IPMs is carried out in a Bayesian framework with program JAGS v2.2.0 (Plummer 2003). In all Bayesian analyses, 400000 MCMC iterations are discarded as burn-in to ensure convergence of the chains, with a further 400000 iterations kept for analysis. Uninformative priors are used for all parameters, reflecting a lack of prior knowledge.

6.3.2 *Impact of not ringing chicks*

When we attempt the estimation of fully time-dependent first-year survival $\phi_1(t)$ with an integrated population model without data on juveniles (IPM2), the model is not able to recover this demographic parameter properly (Figure 6-18): credible intervals are very wide and the point estimates are not close to the ones estimated when chick MRR data are included in the model (IPM1). This inability does not affect the estimation of other parameters, which are largely driven by their respective data sets (see Figure 6-19 for an example with productivity). Also, the estimation of $\phi_1(t)$ cannot be attempted for the last 6 years of the period, as the corresponding immatures will not have recruited into the breeding population and thus there is no information in the adult-related data sets that can inform this parameter.

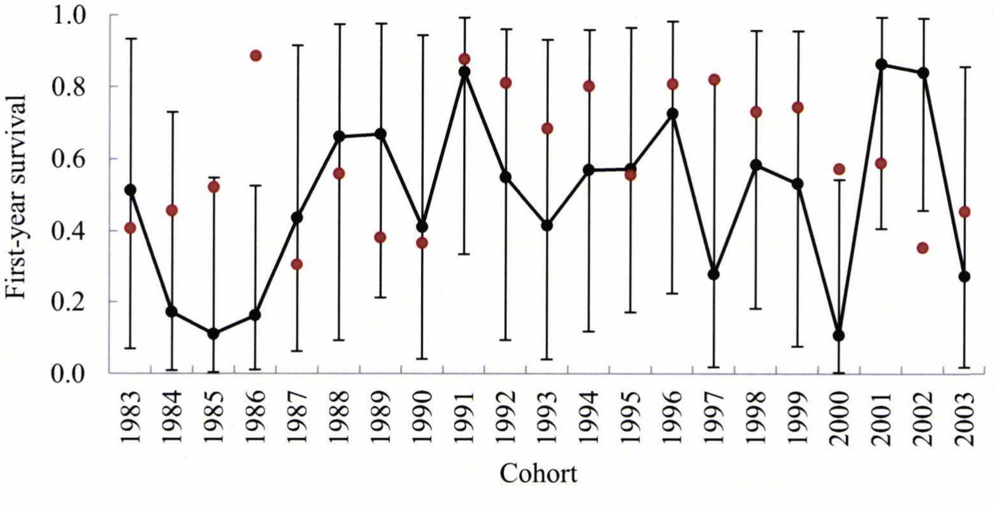


Figure 6-18 Comparison of the estimates of first-year survival obtained with model IPM2 without chick MRR data (black dots and line, with 95% CI) and the reference model with chick MRR data (IPM1; red dots).

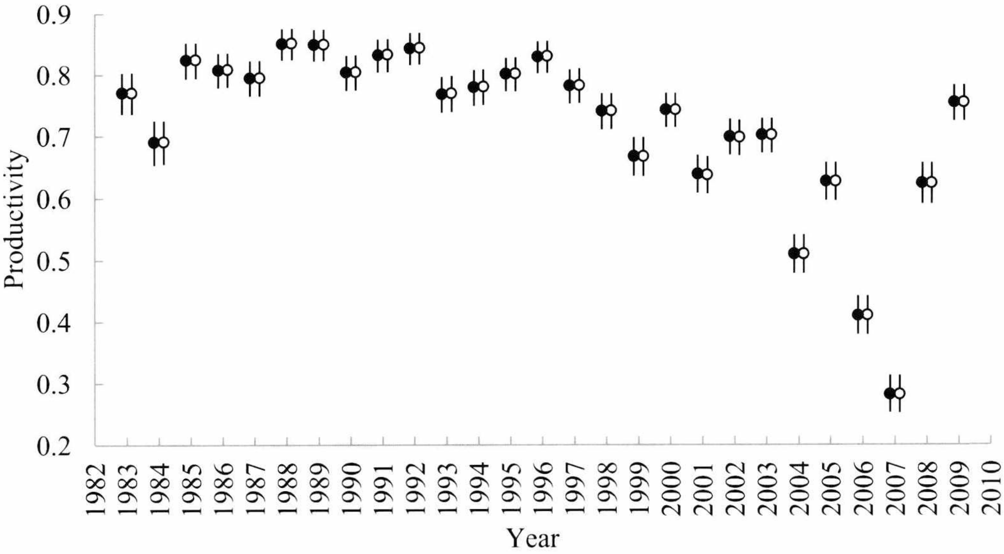


Figure 6-19 Comparison of the estimates of productivity (and 95% CI) obtained with models IPM1 (with chick MRR data) and IPM2 (without chick MRR data; with $\phi_1(t)$).

We then explore what impact removing chick MRR data set from an integrated population model that does not attempt to estimate time-dependent first-year survival (IPM3) had on the estimation of other parameters. Figure 6-20 shows that in the case of adult survival the effect is rather small for most of the years (but note the last five years), indicating that the estimation of $s_a(t)$ is strongly driven by the adult MR data set. Again, the estimates of productivity appear not to be affected by the lack of immature data (Figure 6-21).

A scatterplot of the SD of the estimates for the different years from both models (Figure 6-22) confirms the visual impression that removing the MRR data set from the integrated population model does not affect the estimation of productivity. A slight decrease in precision in adult survival estimates appears to follow the removal of the MRR data set, except for the years of larger differences in the point estimate (2006 and 2007). Overall, the log of generalised variance increased from -225.9 to -224.4.

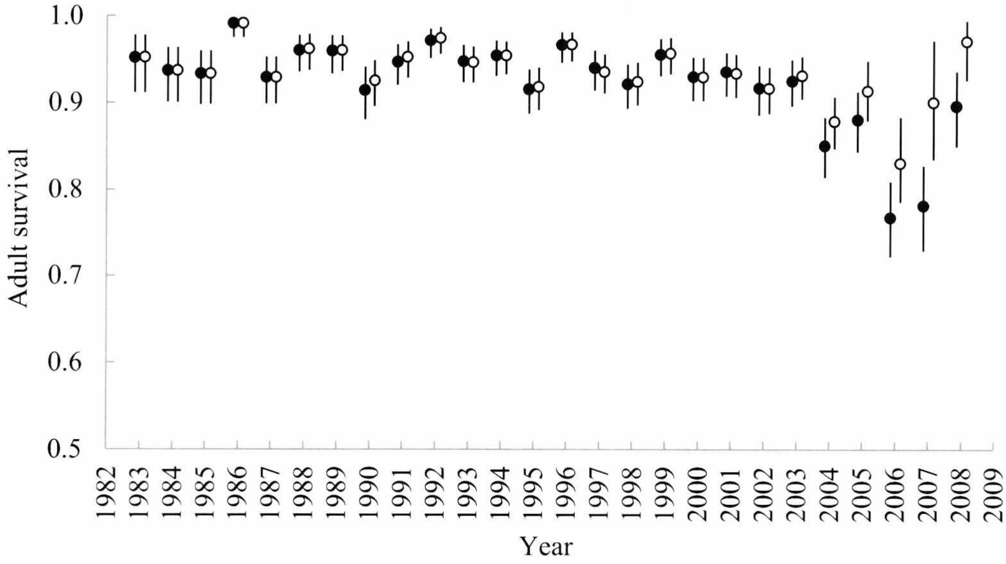


Figure 6-20 Comparison of the estimates of adult survival (with 95% CI) obtained with models IPM1 (with chick MRR data; white circles) and IPM3 (no chick MRR data and constant combined juvenile survival $\phi_{1+}(.)$; black dots).

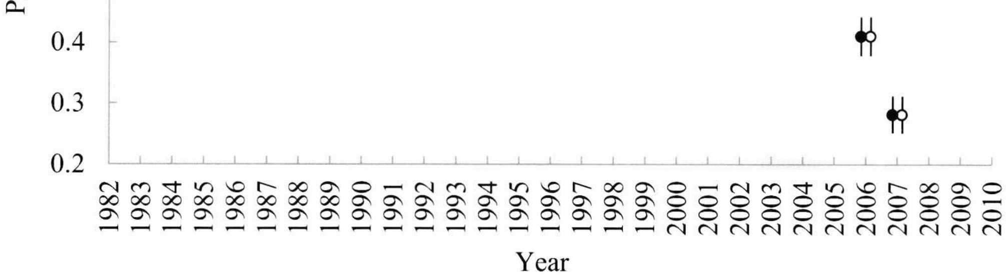


Figure 6-21 Comparison of the estimates of productivity (with 95% CI) obtained with models IPM1 (with chick MRR data) and IPM3 (without chick MRR data; with constant combined juvenile survival $\phi_{1+}(.)$).

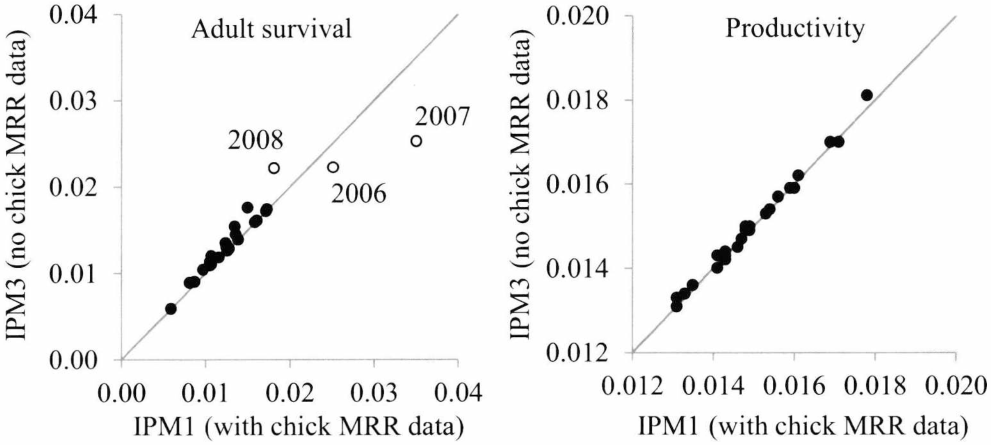


Figure 6-22 Scatterplot of the SD of the estimates of adult survival (left) and productivity (right) for the different years, for models IPM1 vs. IPM3. The grey line shows the 1:1 case. White circles: adult survival estimates for years 2006, 2007 and 2008.

Finally, we attempt the estimation of productivity when no direct data on breeding success is incorporated into the integrated model (Figure 6-23). When such estimation is carried out without chick MRR data (IPM5; assuming a constant combined juvenile survival), the estimates are completely unreasonable i.e. no significant correlation with accurate estimates from model IPM1 (r=0.14, p-value=0.54). If direct information on juvenile survival is added into the model (IPM4), the integrated population model is able to estimate productivity with some success (correlation with estimates from IPM1: 0.75, p-value=0.0001). These estimates are nevertheless very imprecise, with 95% CI spanning in all years over 50% of the probability values.

So far we have looked at the consequences of including or omitting the chick MRR data set on demographic parameters. Considering now the effect of the different data sets and structures on the estimation of population abundance (Figure 6-24), it is clear that the models described above in which it is not possible to estimate a fully time-dependent hidden parameter (first-year survival $\phi_1(t)$ in IPM2 and productivity $\rho(t)$ in IPM5) are associated with overfitting in the estimation of the female breeding population. The model structure has too much flexibility and the values of the hidden parameters are estimated so that the population estimation can match the observed counts closely; the estimated variance of the observation error is consequently small ($\hat{\sigma}_N =$ 606 and 533 respectively). It is interesting to note that model IPM4, despite a very imprecise estimation of productivity, follows the population estimates of IPM1 closely; the imprecision is reflected in the observation error, which is slightly larger for the former ($\hat{\sigma}_N = 1636$) than for the latter ($\hat{\sigma}_N = 1480$). This effect, linked to the estimation of fully time-dependent hidden parameters, has been observed in a previous IPM study (Tavecchia *et al.* 2009).

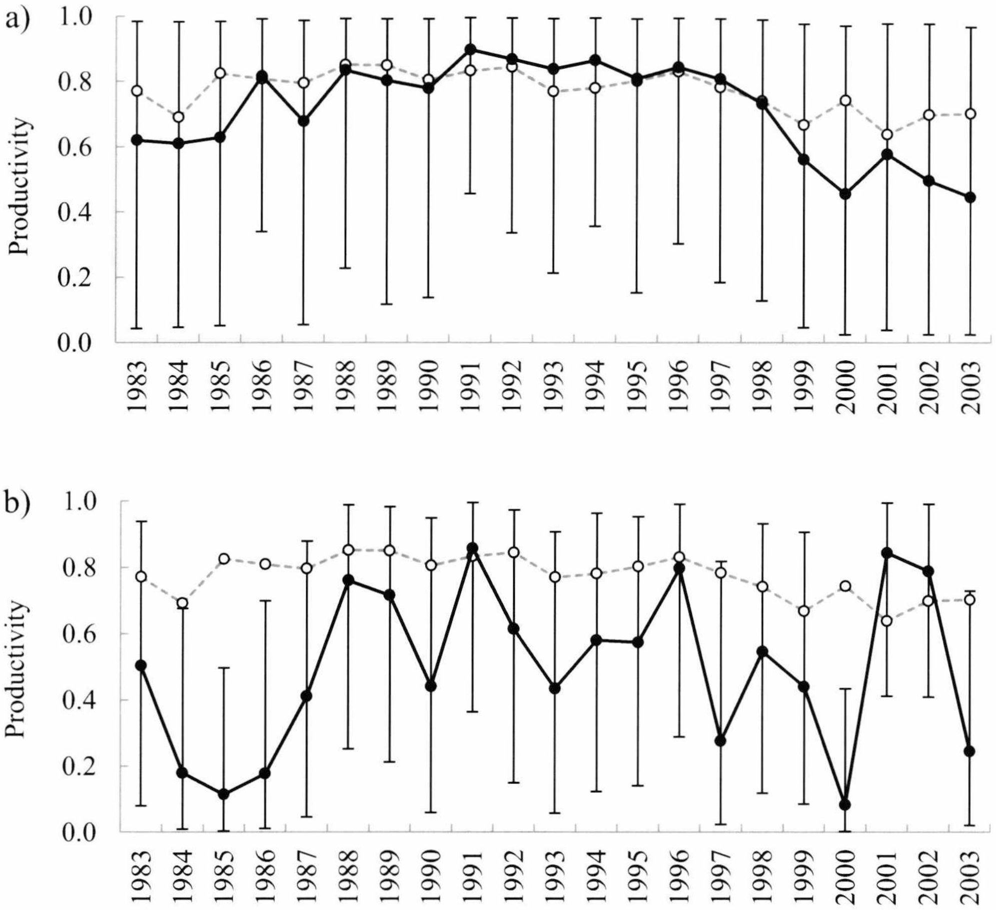


Figure 6-23 In black, estimates of productivity (with 95% CI) obtained from integrated population models with no breeding success data, including (IPM4, panel a) or omitting (IPM5, panel b) chick MRR data. The accurate estimates from a model with breeding success data (IPM1) are shown (white circles) for reference.

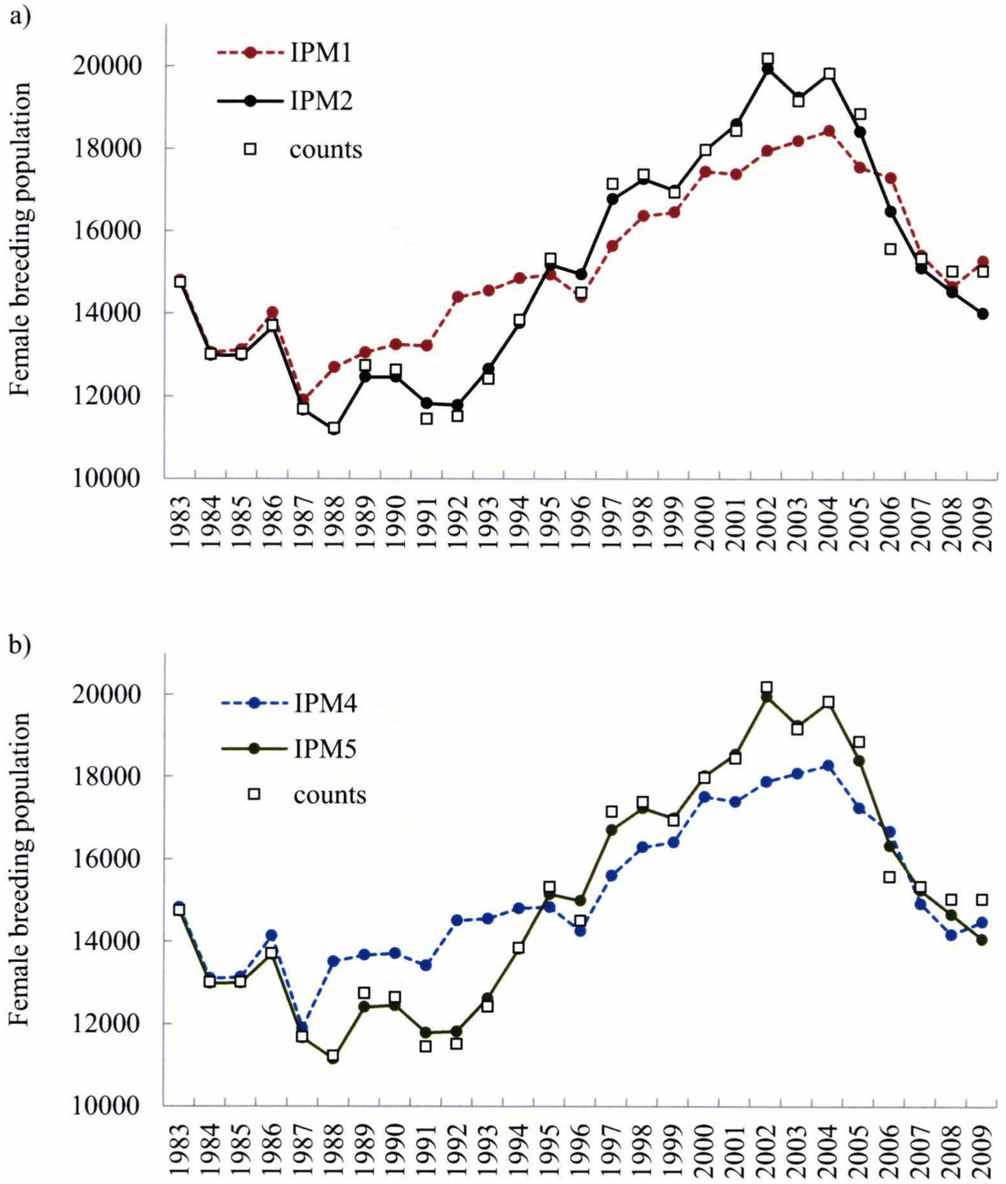


Figure 6-24 Estimated guillemot female breeding population according to different integrated population models. Panel a) compares the outcome of models IPM1 (with chick MRR data; red dashed line) and IPM2 (no chick MRR data and $\phi_1(t)$ estimated from the rest of the data sets; solid black line). Panel b) compares two models with no breeding success data, in which productivity has to be estimated from the rest of the data sets: IPM4 (with chick MRR data; blue dashed line) and IPM5 (no chick MRR data; green solid line). In both panels, the white squares represent the value of the annual island counts (observed population).

6.4 Discussion

In this chapter we study common guillemot juvenile survival for chicks ringed at the Isle of May between 1983 and 2009, a period that includes years of extremely low survival. We evaluate the effectiveness of the current level of field effort invested in both ringing chicks and resighting immatures, by constructing plausible scenarios of changes in field protocols. This method helps us identifying potential field effort reductions that would still allow us to make ecological inferences, in this case to estimate the relationship of first-year survival with an individual-level covariate. We also assess the impact that stopping ringing chicks would have on our ability to study the demographic rates of the Isle of May guillemot population, including the estimation of year-specific probabilities of survival over their first winter. We explore several scenarios using an integrated population model, which combines the various data sets collected from breeding adult guillemots.

6.4.1 Guillemot juvenile survival

Our study extends a previous analysis with individual covariates conducted up to year 2001 (Harris, Frederiksen & Wanless 2007). The extended period includes a series of consecutive years of extremely low first-year survival, notably 2004-2008. At the individual level, the relative hatch date is an important factor affecting first-year survival, with chicks hatching early in the season having higher chances of surviving than later ones (also observed in shags; Daunt *et al.* 1999). In contrast, the body condition index, a measure of actual weight relative to the weight expected for a given chick wing size, is non-significant. This result agrees with previous studies at the Isle of May (Harris, Frederiksen & Wanless 2007) and in other regions (e.g. Hedgren 1981) and is probably due to fledged chicks being fed for several weeks at sea during which time they quadruple their weight, thus chick weight in the colony may not be strongly associated with condition when the chick becomes independent (Harris, Webb & Tasker 1991). Weight at time of fledging (which usually coincides with chicks becoming independent) has a positive influence on first-year survival in some seabird species, e.g. Manx shearwater *Puffinus puffinus* (Perrins, Harris & Britton 1973), but such an effect has not been demonstrated in razorbills (Lloyd 1979), which have a breeding strategy similar to that of guillemots. It is nevertheless interesting that ΔQAICc of the model with BCI is much smaller when the complete time period is analysed (4.24 in our study compared to 8.43 in Harris, Frederiksen & Wanless 2007), suggesting that body condition at fledging may have some effect on survival over the first winter, in years of extremely poor overall first-year survival.

In contrast to the results in Harris, Frederiksen & Wanless (2007), in our analysis the top ranking model has an additive effect of RHD and cohort, instead of a full interaction. Again this may be a consequence of the extended period consisting mainly of years of very low average first-year survival, for which an additive effect of RHD is a good approximation (except for 2005, s_1 is either practically linear with RHD or very close to zero for all values of RHD). In any case, the interaction model brings evidence that the effect of hatching at an early date becomes critical in some years of low chick survival like 2004 and 2005, when only very early hatching chicks have a survival probability over 0.20. This effect is less relevant in years of high average survival, when s_1 is very high for most chicks, dropping only to mid-low values for chicks hatching in the last quarter of the dates.

6.4.2 Reducing field effort

The estimates of first-year survival are robust with respect to decreasing the current level of resighting field effort, with the quality of the estimation starting to fail at a 90% effort reduction. This shows that in our particular case a substantial part of the current resighting effort may go into redundant resightings. However, a second more general factor may also contribute to this robustness in that, for each marked bird, a resighting in a particular year is not directly relevant to the estimation of first-year survival if the animal is seen in later years. The critical piece of information, i.e. that the individual survived its first winter, is still contained in the history even if the bird is missed in some of the years. This is less true when estimating survival for older age classes, for which a) there is less information as fewer immatures survive to that age, and b) a resighting in later years is less likely to be followed by other resightings in following years and thus becomes more valuable as a source of information. This suggests that inference for early year parameters would require less resighting effort.

Removing ringed chicks from the data set has a more direct impact on the number of resightings and therefore the estimates of first-year survival are less robust to a decrease in ringing effort. Noticeable reductions in precision are associated with 50% reductions in the number of chicks ringed. We conclude that, for the common guillemot population at the Isle of May, the current amount of ringing is adequate but the resighting effort could be significantly reduced while still maintaining the capacity of monitoring first-year survival and detecting the effect of hatch date on this demographic parameter.

A further design aspect that we have not considered here is whether concentrating the resight effort of immatures in a particular period of the breeding season would optimise the use of field resources. Chambert *et al.* (2012) used simulations based on estimated values to show that, for adult kittiwakes at a colony in Norway, it was more efficient to spend resighting effort early in the breeding season when resight probability was highest, based on the behaviour ecology of the species that creates patterns of variation of resight probability along the season. It would be potentially useful to consider such type of study for the guillemots at the Isle of May, although we note that one would also need to take into account the timing requirements of other monitoring activities happening at the Isle of May during the same period.

To our knowledge, our study represents the first use of artificially simplifying existing real data sets to explore the effect of field effort in capture-mark-recapture studies. As mentioned in the introduction of this chapter, Monte Carlo simulations matched to estimated parameters have been used to explore design issues in the context of capture-mark-recapture studies. While we acknowledge the rigour and utility of that computer-intensive approach, an advantage of our method is that it is fairly simple and less time-consuming. Also the reduction of the data sets is carried out at the level of daily individual resighting occasions rather than directly from the capture histories, which represent summaries. Monte Carlo simulations would typically consist in generating data using the parameter values estimated by the model. This would not be enough to mimic our scenarios, and the generation of individual resightings on a day-by-day basis would have to be implemented. However, some degree of replication could be nevertheless obtained by randomly sampling the historic data set repeatedly.

Post-study evaluation is no substitute for study design carried out before starting a monitoring program, but it can help streamline an existing program when data have already been collected for several years, as it allows us to explore specific relationships (e.g. the effect of early hatching) that could otherwise not have been predicted (and therefore simulated) before the monitoring commenced.

6.4.3 Integrated population models

In section 6.3 we analyse the impact of stopping completely the substantial investment in field effort needed to collect mark-resight-recovery data by marking guillemot chicks. This is especially relevant when breeding success is low and few immatures are available for resighting unless a considerable effort is put into marking large numbers of chicks. To do this, we simulate the case where all ringing of guillemot chicks would stop and we would not have data directly informative about immature survival. We experiment with artificial, but biologically plausible, scenarios using integrated population models, exploring their capabilities and limits to deal with the mentioned lack of data.

Our IPM model had limited capacity to recover year-specific first-year survival although the joint modelling of the adult-related data sets allowed the estimation of a constant probability that combined survival from chick until recruiting age. This is of relatively limited value if the primary interest of a monitoring program lies in first-year survival. It is also clear that we cannot carry out ecological inference regarding individual-level covariates without marked chicks, as no direct information on the fate of individual juveniles is available. An IPM could potentially be considered for investigating cohort-level covariates, a case not addressed in this study. Also, site fidelity cannot be studied if ring-recovery data are not included, as fidelity becomes confounded with mortality.

When the primary interest is in monitoring adult-related demographic parameters like survival and productivity, or abundance of the breeding population, an IPM appears quite robust to the absence of the chick MRR data set. Productivity estimates were practically identical in both models (with and without such data) with no detectable loss in precision. Omitting the MRR data set reduced slightly the precision of the adult survival estimates, with very similar estimated values except for the last 3 years (possibly due to the increasing sparseness of the adult MR data set). Finally, the IPM framework allowed the exploration of a further hypothetical change in the monitoring scheme: in an artificial scenario of breeding success not being monitored, the inclusion of the chick MRR data set was essential in order to obtain productivity estimates, albeit imprecise ones.

As a summary, we would like to highlight that the decision to stop fieldwork on guillemot chicks ultimately depends on the specific objectives of monitoring this species; and in particular, the importance given to estimating year-dependent first-year survival and to carrying out ecological inference regarding this demographic parameter.

Integrated population models can be very useful tools in ecological (McCrea *et al.* 2010) and conservation (Schaub *et al.* 2007) studies as they can bring improved precision and the possibility to estimate hidden parameters for which no direct data are available. Furthermore, they allow the evaluation of alternative monitoring scenarios for intensively monitored populations where individual-level data are collected on different aspects of demography and abundance. As we have shown, this can be done by artificially removing data sets from the analysis, exploring the impact in our ability to study and monitor a population. Such exploration can be important in monitoring programs for planning or revising the collection of field data related to particular aspects of demography, like survival or productivity, especially when such individual-based data are difficult or expensive to gather. This type of IPM-based exploration is still uncommon. A notable exception is that of Tavecchia *et al.* (2009) that attempt the estimation of various demographic parameters and the prediction of abundance for one year, after artificially removing the corresponding individual-based data sets. They specifically test the estimation of productivity, which they obtain with better precision than in our case, although their model includes counts not only of adults but also of immatures, bringing a more direct source of information on productivity.

Our analysis of guillemot juvenile survival highlights the existence of some dramatic changes in recent years that are of conservation importance. However, research programmes are coming under increasing pressure to make the collection of field data more streamlined and cost effective. Therefore it is important to consider whether any part of fieldwork can potentially be scaled down or even stopped, without losing the ability of the monitoring program to track important demographic changes and identify key individual covariates that indicate which birds are more likely to recruit subsequently into the population. We provide an example of how this exploration can be carried out in the context of mark-recapture-recovery studies, using an existing data set to construct artificial scenarios of reduced field effort, and exploring the benefits of data integration through integrated population models.

7 DISCUSSION AND FURTHER WORK

Synchrony and asynchrony are important concepts in ecology, both theoretical (e.g. Moran effect in spatial synchrony, Hudson & Cattadori 1999) and applied (e.g. effect on extinction risk, Heino *et al.* 1997). They are also relevant in understanding community structure (Mutshinda, O'Hara & Woiwod 2011) and its response to environmental changes, providing clues to guide further investigation (McCarthy 2011). Analytical techniques to test for effects or examine the importance of environmental covariates are therefore of great interest. In this thesis we have applied a novel multi-species synchrony framework to study the degree of common year-to-year variation in adult survival as well as in overall productivity, in a community of seabirds breeding together at the Isle of May. We have done so independently for each demographic parameter, and then within the context of a multi-species integrated population model, in which the changes in abundance and demographic parameters are estimated simultaneously, for a time span of over two decades that include important changes in the Isle of May marine environment.

7.1 Modelling synchrony and abundance in a community

The multi-species synchrony modelling framework is very adaptable and we have demonstrated its use in demographic parameters as different as adult survival and the amount of clutch size underdispersion. We have also discussed several model extensions as well as its possible application in conceptually very different contexts, from the single-species multi-population case proposed by Grosbois *et al.* (2009) to its use in the site-occupancy framework (MacKenzie *et al.* 2006); in the context of the study of seabird populations in the Northeast Atlantic, a logical extension would be to develop a multi-species multi-colony model (section 4.2.5) to study synchrony in the same species assemblage across the region.

We have also explored the properties of the framework and explained its interpretation: for each species in a set, we quantify the proportion of the total year-to-year variation in a parameter of interest that is shared with all the other species in a set. The method therefore looks at an aspect of synchrony that is different from the more traditional pairwise comparison of species; it is also more comprehensive: each species' synchrony index is related to all species in the set under study. We see this framework as another tool in the ecological statistics toolbox, which we hope ecologists will find useful to deal with some questions.

Using simulations, we show that the estimation of synchrony improves as more years are added to the data set, with short studies (< 10 years) having the risk of producing biased and imprecise estimators of synchrony, particularly if the set under study consists only of two or three species. The need for long time series highlights the relevance of long-term intensive monitoring programs when aspects of synchrony are of interest. Simulations can also be used to assess the level of synchrony that may be estimated by chance from species with completely independent year-to-year variations. The values obtained provide a benchmark to which the estimates of synchrony from a real data set can be compared. We demonstrate this method with the Isle of May productivity analysis, in which we obtain synchrony estimates well above the expected spurious level for all the species considered. This finding not only gives us more confidence in the results we present from the empirical studies but is also highly relevant in supporting the continuation of long-term ecological studies and the effort invested on the different species.

A central aim of this project was to extend the concept of the single species integrated model (ssIPM) to the multi-species scale (msIPM). This approach was developed using a large combined data set of three auk species of the Isle of May seabird community and integrating several data sets per species within a single multi-species integrated population model. Such an analysis allows the estimation of demographic parameters, related synchrony indices and population abundance in a robust way. A key assumption in integrated population modelling is that of the independence between census and demographic data sets, whose likelihoods are multiplied to form the joint likelihood of the IPM model (Besbeas, Borysiewicz & Morgan 2009). Often this assumption will not be strictly met in the case of the Isle of May seabird data where some of the data sets are obtained from the same colony areas and therefore include information from different life history aspects of the same individuals, which are also counted in the census. For example, adult survival and productivity of guillemots are monitored in the same study plots. In practice, population counts can be considered independent of the other data sets because the total number of individuals counted in the whole island is much larger than the sample of monitored birds. The impact of the lack of independence of data sets in integrated population modelling has yet to be thoroughly studied but it is reasonable to expect that it will strongly depend on the nature of the dependent data sets and the degree of overlap in the number of individuals that are shared between them. Simulations are the obvious framework for studying this issue, although the number of possible combinations is large and obtaining general results may be challenging. Besbeas, Borysiewicz & Morgan (2009) found bias when ring-recovery data were integrated with strongly dependent counts in a simulation study. Other papers report no significant effect of the lack of independence, based on either empirical data (Cave, King & Freeman 2010) or simulations (Abadi *et al.* 2010a); this may be caused by one of the data sets contributing most of the information for the parameter under study so that the degree of dependence with other data sets may not have a big impact in practice. Non-independence in IPM remains an active area of statistical research. Extending the IPM framework to encompass several species may create a new form of dependence between data sets, in this case across species.

We did not carry out model selection formally on the integrated population models, but did it locally when needed for particular data sets (e.g. the guillemot chick MRR, section 5.4.2). During model exploration, attempts were made to fit the puffin, razorbill and guillemot data sets to more flexible IPM structures (e.g. fully time-dependent juvenile survival when no data were available to provide information directly about that parameter; section 6.3.2) but the resulting inaccurate demographic estimates indicated that such parameters were not identifiable; this was further confirmed by the true population estimates often displaying a clear overfit to the census values, as the model structure was too flexible for the amount of data available. We note that methods to assess formally parameter redundancy for IPMs have only been developed very recently (Cole & McCrea 2012); such methods could be applied in Chapter 6 when studying the impact of stopping the ringing of guillemot chicks. We also assessed goodness-of-fit for the different data sets independently. Clear methods and guidelines for checking the overall fit of IPMs are still lacking (Schaub & Abadi 2011), but the verification for each separate data set may provide more informative detail about the origin of a potential lack of fit in the overall integrated model.

Having several species in the same IPM allows another interesting development, which does not rely on a structure of synchrony: one or more demographic parameters could be regressed on the adult population abundance, in order to estimate whether they exhibit density-dependence (Begon, Townsend & Harper 2006, p.134). In IPM the novelty is in letting each parameter depend not only on its own species' abundance, but also on that of other sympatric species that may be competing for shared resources (e.g. food or nesting sites). Multi-species synchrony as defined in this thesis may reflect the fact that species respond similarly or differently to variations in some aspect of their common environment; in contrast, this 'density-dependence msIPM' is multi-species because it takes inter-specific competition into account as a structural relationship. The fact that the model is an IPM is important as it allows the estimation of relationships with estimated true populations instead of counts, which are imperfect observations, and the Bayesian framework is ideal for inference in this case. We describe here as an illustration how this idea could be applied to productivity in the Isle of May seabird community. The overall model structure would be as defined for the razorbill, puffin and guillemot ssIPMs in sections 5.2, 5.3 and 5.4 respectively (i.e. with no random effects in productivity for estimating synchrony). We then introduce in the logistic regression of the parameter of interest the numbers of adults $\boldsymbol{N_a}$ of all the species in the set, which are themselves parameters within the IPM. For productivity ρ we could have, for each species s and year t,

$$\text{logit}(\rho_s(t)) = \beta_{0s} + \sum_{i=1}^{S} \beta_{is}\widetilde{N}_i(t) + \varepsilon_s(t),$$

where β_{0s} are species-specific intercepts (baseline productivity), β_{is} represents the effect of abundance of species i on the productivity of species s, and $\varepsilon_s(t)$ are independent, identically distributed normal error terms (with $\varepsilon_s(t) \sim N(0, \sigma_s^2)$, and variances to be estimated). $\widetilde{N}_i(t)$ are the adult true population abundances, standardised for each species. The regression coefficients β_{is} would estimate either intra-specific ($i = s$) or inter-specific ($i \neq s$) density-dependence. This fully parameterised model can account for all possible combinations of effects, including species being affected only by intra-specific competition or by the combined abundance of some or all species (with the relevant β_{is} in each case being estimated close to zero). Although in a preliminary analysis of the Isle of May data set we found no strong evidence for such density-dependence in productivity, applying the approach to other species assemblages where density dependence may be operating would be highly informative. Also, the density-dependence structure described above (linear on the logit scale) is rather simple and it may be worth exploring alternative more complex structures (e.g. population thresholds; Besbeas & Morgan 2012b) as well as dependence acting with time delay (Begon, Townsend & Harper 2006, p.424). Density-dependence has been included in single-species IPMs (Besbeas, Borysiewicz & Morgan 2009; Péron, Nicolai & Koons 2012) but to our knowledge a multi-species density-dependence IPM would be a novel development.

By their nature, IPMs tend to contain many model parameters, and that number obviously increases when several species are modelled simultaneously, as we have seen in our multi-species IPM. This is not necessarily a problem in terms of parameter identifiability, as the greater number of parameters is accompanied by a larger amount of data. However, there is an obvious impact, at least in the Bayesian framework, in terms of computing time, and to a lesser extent also in computer memory requirements. The continued increase in computer processing power will partially compensate for this. Alternatively, it will be worth considering that, when a data set contributes the most information regarding a particular set of parameters, it can be analysed independently and one can then incorporate the parameter estimates using a multivariate normal approximation in the IPM (Besbeas, Lebreton & Morgan 2003), therefore reducing model complexity and the required amount of processing time.

7.2 The Isle of May seabird community

In our analysis of the Isle of May seabird community, we found medium-high synchrony in adult survival among the three auk species. However, synchrony in overall productivity for the set of five species was much more variable although there was a clear a common signal indicating a significant decline in productivity between 1986 and 2009. For the two species for which we have more detailed data, the environmental contribution to overall productivity synchrony is driven principally by effects operating at the chick stage rather than during incubation. The results for the full Isle of May data set suggest that the seabird species show complex and varied responses to the shared environmental conditions, with no single climatic or oceanographic covariate considered emerging as a clear overall explanatory variable controlling all aspects of these species' demography. The contrasting results in terms of synchrony in adult survival and productivity are most probably related to the fact that the factors affecting them operate at different times of the year and in different geographical locations. Thus adult mortality occurs mainly during the winter when the species disperse into the North Sea, and in some cases the Atlantic, while productivity is likely to reflect conditions during the spring and summer in the vicinity of the colony. Both the environmental covariates considered here (wNAO and SST) are often selected with time lags suggesting that their effects on survival and productivity are operating indirectly through some aspect of the food chain. In the context of the Isle of May seabird community, climate-mediated effects on the sandeel population, an important prey species for all the seabird species included in our data set, is a likely candidate. The presence of a commercial sandeel fishery appeared significant only for kittiwake productivity (as noted in previous studies, with a shorter time series; Frederiksen *et al.* 2008b), the species that is assumed to be most sensitive to changes in prey abundance. Nevertheless, in both adult survival and productivity, a large part of the common and species-specific variances is not explained by our set of covariates, which indicates that there is scope for further investigation about the aspects of these species' environment that contribute to synchronising and desynchronising these demographic parameters. The most promising avenue is to consider more direct measures of prey availability such as estimates of prey biomass or, specifically for productivity, the quality and composition of the diet fed to the chicks.

Exploring covariates that may be able to explain part of the year-to-year variations (and therefore synchrony and asynchrony) in some demographic parameters of interest is a first step. The next stage would be to relate the synchrony indices and the degree to which synchrony and asynchrony are explained by environmental covariates (the C_δ and C_s coefficients) to different characteristics of the species considered. Puffins, guillemots, razorbills, kittiwakes and shags all share life history characteristics typical of seabirds such as high adult survival, deferred maturity and small clutch sizes, and rely on a common food source to feed their chicks when breeding at the Isle of May. However, some other traits are shared only among some of the species, in a complex overall combination (Table 1-1), and it is possible that these similarities and differences create the varied spectrum of responses to environmental variation. New research into the ecology of these species may bring insight into more subtle differences (e.g. different use of the water column by guillemots and razorbills when foraging; Thaxter *et al.* 2010). How to relate synchrony parameters to aspects of the species' ecology is not a trivial question and the development and testing of sound methods to do this could be an area of future work.

Perhaps the clearest example is the potential for a relationship between synchrony in adult survival and the overlap of wintering areas, given that most adult mortality happens during the winter months. Reynolds *et al.* (2011) adopted a similar approach for a single-species multi-population case study with guillemots, based on pairwise comparisons. Extending the approach to the set of species considered in our study is hindered because we still know relatively little about their distribution outside the breeding season when many of the species, e.g. kittiwake and puffin, disperse widely. Ring-recoveries can be used to infer the likely levels of overlap in winter distributions (Figure 7-1). However, such data have many sources of bias for example they indicate where birds have died not where they have survived, recoveries are more likely after periods of onshore wind and on coastlines with sandy beaches frequently visited by humans. Winter surveys at sea can provide less biased information (Fauchald *et al.*

2011) but in this case the origin and status of the individuals recorded is unknown and such surveys are costly to carry out at the scale needed to reflect wintering distributions of most Atlantic species. With the increasing use of geolocation loggers, small devices attached to leg rings that record the geographical position of the animal (Harris *et al.* 2009; Bogdanova *et al.* 2011), more direct information can be obtained and a clearer picture is starting to emerge, which is in some cases changing the traditional views. More individuals will be fitted with such devices at the Isle of May in the coming years, which will hopefully shed light on where the species spend winter, and help relate winter distribution to environmental covariates in these areas.

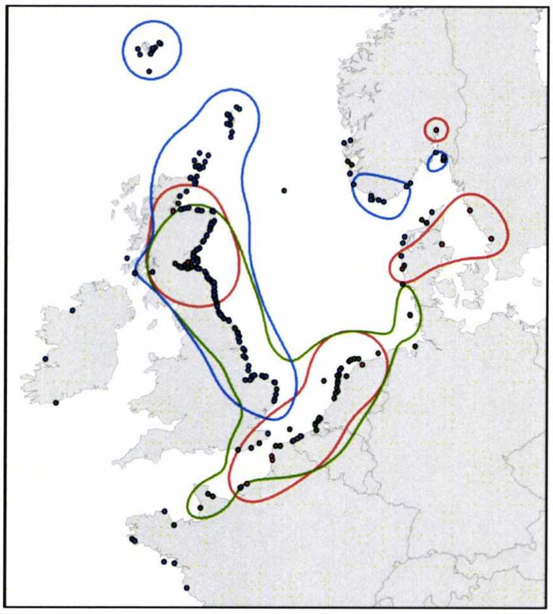


Figure 7-1 Location of ring-recoveries and derived kernel density contours (75%) for puffins (blue), guillemots (green) and razorbills (red) ringed at the Isle of May and recovered as adults during the non-breeding season (September to April) within the period 1980-2009. Data processed in ArcGIS9.3.

The population of seabirds breeding around the British Isles is of international relevance and the species considered in this thesis are still very abundant (the guillemot is the most common seabird in the area with over 1.5 million individuals; Mavor *et al.* 2008). A comparison of counts conducted in Britain and Ireland in the 1970s, late 1980s and late 1990s/early 2000s shows that the populations of the three auks increased over this period, but that of shags and kittiwakes decreased markedly, particularly since the 1985-88 census (Mitchell *et al.* 2006). In the North Sea, conditions were favourable for seabirds during the 1970s, but the 1980s saw reductions in numbers and/or productivity of some species (Harris 1994). The counts at the Isle of May indicate that since the mid-2000s the breeding population of puffins, guillemots and razorbills have declined, as reflected in our population models. Sea-surface temperature has been increasing in the North Sea since the 1980s, which triggered an abrupt ecosystem shift in the early 1990s (Beaugrand *et al.* 2008), a rapid change in plankton community composition resulting in poorer sandeel recruitment (van Deurs *et al.* 2009). Sandeel body length-at-age has also declined markedly during the last 30 years in the Wee Bankie/Firth of Forth population (Wanless *et al.* 2004). These large-scale changes have impacted seabirds at the Isle of May, with a series of years of very low breeding success for some species (Centre for Ecology & Hydrology 2010) and a general declining trend, as indicated also by the common signal in our analysis of productivity. The overall response of a species to changes in climate is likely to be complex, and it is difficult in general to predict which populations of which species will be 'winners' or 'losers' under changing environmental conditions (Hamer 2010). Nevertheless, given that current climatic scenarios all predict further increases in sea surface temperature in the North Sea (Frederiksen *et al.* 2006), a negative impact of future climate change could be anticipated in the sandeel-dependent seabird community at the Isle of May, with coming decades likely to witness large-scale changes in the breeding and wintering distributions of these species.

Long-term monitoring schemes are essential ecosystem sentinels and provide the necessary time-frame for an improved understanding of the relationships between demography, population and environment at a multi-decadal scale. IMLOTS (Centre for Ecology & Hydrology 2010), the seabird monitoring programme established in 1973 at the Isle of May, is an excellent example of the value of such schemes. Over several decades, it has provided what probably constitutes the most comprehensive colony-based data set on seabird ecology in Europe, with many studies (including this thesis) conducted on ecological aspects but also on statistical developments, and results even influencing policy (Frederiksen *et al.* 2008b). The increased availability of new monitoring devices such as geolocation loggers, coupled with statistical modelling developments will likely provide exciting new opportunities to improve further our understanding of the seabird communities in general and the Isle of May in particular.

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APPENDIX: PRIOR SENSITIVITY FOR THE VARIANCE OF RANDOM EFFECTS

We carry out a prior sensitivity study for the variances of the random effects in the multi-species adult survival synchrony model. We use the model $\{\phi(\beta + \delta + \varepsilon)p(t + a)\}$ without covariates, where all the year-to-year variation in adult survival has to be absorbed by the random effects, and the I_s can be interpreted as the overall synchrony. See details of the model in section 2.3.6.

In our synchrony analyses, we specified uniform priors on the standard deviations ('priors 1'). We test alternative priors directly for the variances, in the form of inverse gamma distributions. As WinBUGS specifies a normal distribution through its precision instead of variance, in practice we have to specify a gamma distribution for the precision $\tau = \sigma_x^{-2}$. We try two different values of the gamma distribution parameters. In total, the following sets of priors are explored

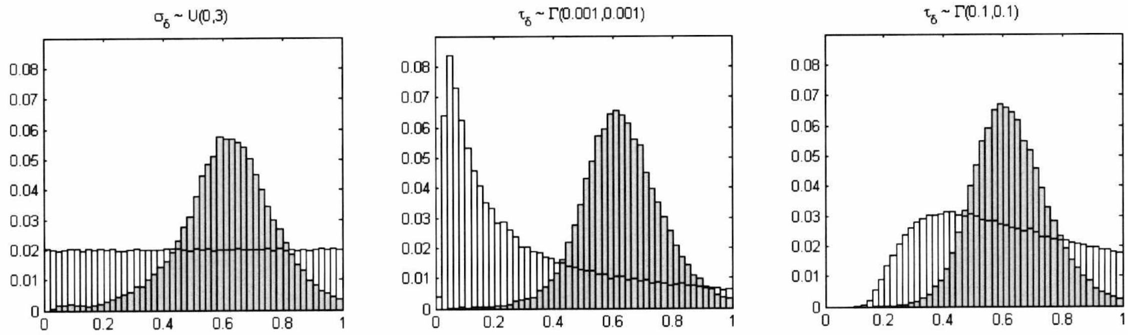
(i) Priors 1: $\sigma \sim \mathrm{U}(0,3)$

(ii) Priors 2: $\tau = \sigma^{-2} \sim \Gamma(0.001,0.001)$

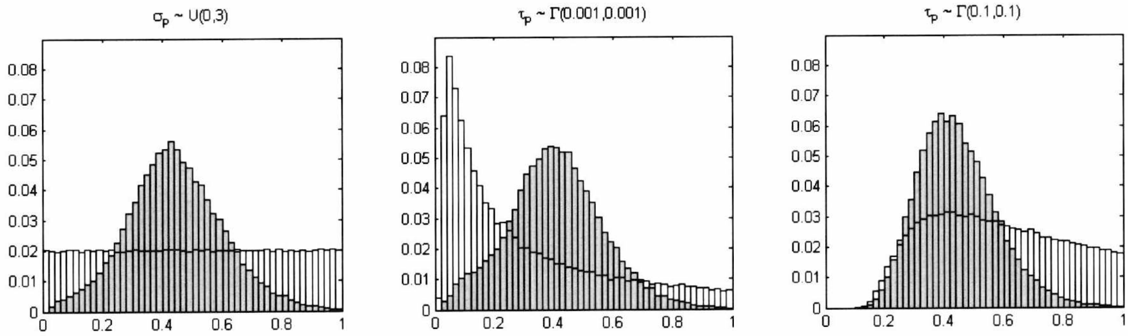
(iii) Priors 3: $\tau = \sigma^{-2} \sim \Gamma(0.1,0.1)$

The following figures compares the prior (light grey) and marginal posterior (dark grey) when using the different sets of priors, for the standard deviations of the common and species-specific terms, for puffins, guillemots and razorbills.

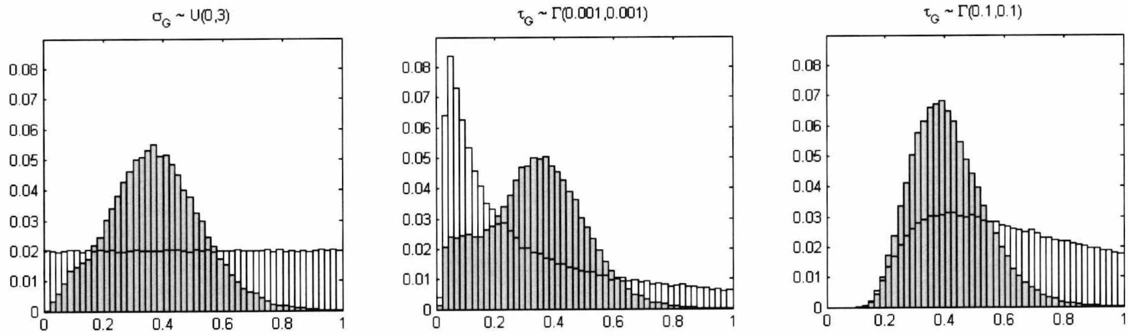
Standard deviation of the common random terms $\boldsymbol{\delta}$:



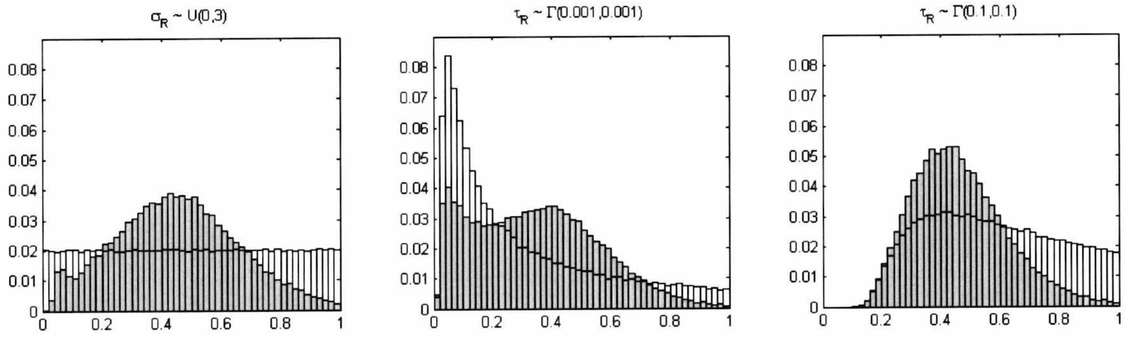
Standard deviation of the puffin-specific random terms $\boldsymbol{\varepsilon_P}$:



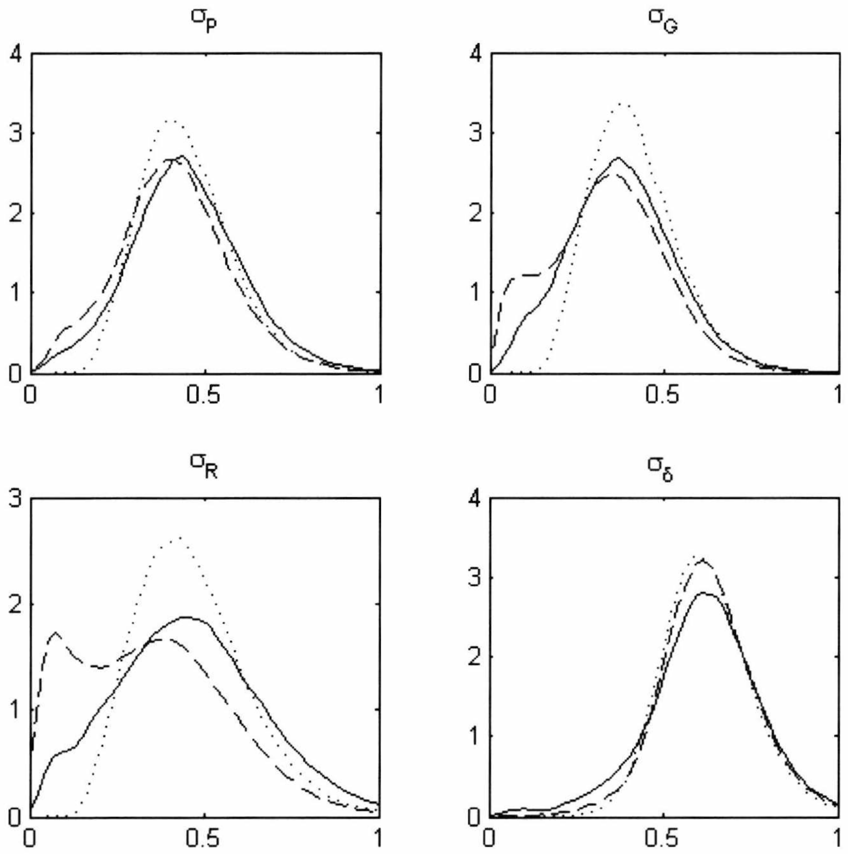
Standard deviation of the guillemot-specific random terms $\boldsymbol{\varepsilon_G}$:



Standard deviation of the razorbill specific random terms $\boldsymbol{\varepsilon_R}$:



For a better appreciation of the effect of changing the prior, the following figure shows kernel density estimates (calculated in Matlab) for the marginal posterior distributions of the standard deviations of the common terms (σ_δ) and species-specific terms ($\sigma_P, \sigma_G, \sigma_R$ for puffins, guillemots and razorbills respectively). The results of using priors 1, 2 and 3 are represented by solid, dashed and dotted lines respectively.



For puffins and guillemots (the species with very rich data sets) and the common random effects δ, specifying more informative gamma priors does not have a strong effect. On the other hand, for razorbills (with less ringed birds and resightings), the use of inverse gamma priors appears to have a noticeable effect. We therefore opted for using uniform priors on the standard deviation of the random terms.