



ARTICLE

Metapopulation regulation acts at multiple spatial scales: Insights from a century of seabird colony census data

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Abstract

Density-dependent feedback is recognized as important regulatory mechanisms of population size. Considering the spatial scales over which such feedback operates has advanced our theoretical understanding of metapopulation dynamics. Yet, metapopulation models are rarely fit to time-series data and tend to omit details of the natural history and behavior of long-lived, highly mobile species such as colonial mammals and birds. Seabird metapopulations consist of breeding colonies that are connected across large spatial scales, within a heterogeneous marine environment that is increasingly affected by anthropogenic disturbance. Currently, we know little about the strength and spatial scale of density-dependent regulation and connectivity between colonies. Thus, many important seabird conservation and management decisions rely on outdated assumptions of closed populations that lack density-dependent regulation. We investigated metapopulation dynamics and connectivity in an exemplar seabird species, the Northern gannet (*Morus bassanus*), using more than a century of census data of breeding colonies distributed across the Northeast Atlantic. We developed and fitted these data to a novel hierarchical Bayesian state-space model, to compare increasingly complex scenarios of metapopulation regulation through lagged, local, regional, and global density dependence, as well as different mechanisms for immigration. Models with conspecific attraction fit the data better than the equipartitioning of immigrants. Considering local and regional density dependence jointly improved model fit slightly, but importantly, future colony size projections based on different mechanistic regulatory scenarios varied widely: a model with local and regional dynamics estimated a lower metapopulation capacity (645,655 Apparently Occupied Site [AOS]) and consequently higher present saturation (63%) than a model with local density

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dependence (1,367,352 AOS, 34%). Our findings suggest that metapopulation regulation in the gannet is more complex than traditionally assumed, and highlight the importance of using models that consider colony connectivity and regional dynamics for conservation management applications guided by precautionary principles. Our study advances our understanding of metapopulation dynamics in long-lived colonial species and our approach provides a template for the development of metapopulation models for colonially living birds and mammals.

KEYWORDS

connectivity, conspecific attraction, dispersal, immigration, latent process, long-term population monitoring, marine conservation, metapopulation dynamics, Monte Carlo Markov Chain, *Morus bassanus*, Northern gannet, regulatory feedback

INTRODUCTION

The population dynamics of long-lived, far-ranging, colonially breeding species are a challenge for population ecology. The theoretical foundations of metapopulation theory and our understanding of the mechanisms and scales of metapopulation regulation stem from empirical insights into short-lived, short-ranging species, such as the Glanville fritillary butterfly (*Melitaea cinxia*) and the American pika (*Ochotona princeps*) (Clinchy et al., 2002; Hanski et al., 2017; Hanski & Gaggiotti, 2004; White & Smith, 2018). Colonial species such as seabirds and pinnipeds have very different characteristics: long life spans, delayed maturity, slow turnover, high mobility, and high levels of philopatry and breeding site fidelity leading to limited connectivity between colonies (Hamer et al., 2001; Lewison et al., 2012). Current metapopulation models do not sufficiently capture these challenging features of natural history, and, consequently, quantitative studies of seabird dynamics have not yet fully benefited from novel theoretical and inferential developments in metapopulation biology (Nur & Sydeman, 1999). Therefore, metapopulation dynamics are a research priority for seabirds, with a particular focus on “the form and importance of population structure” and “factors that regulate seabird populations” (Lewison et al., 2012).

Metapopulations are networks of discrete, spatially segregated subpopulations, connected through immigration of dispersing individuals (Hanski & Gaggiotti, 2004). Most seabirds breed in distinct terrestrial colonies dotted across large spatial expanses of marine habitat. Despite this obvious analogy to the spatial structure of metapopulations, seabird colonies have traditionally been understood and studied as discrete entities (Lewison et al., 2012; Wooller et al., 1992). Efforts to increase our understanding of seabird population dynamics over past decades, for example

through large-scale ringing and resighting efforts, modeling single seabird colonies as open systems and population genetics, have increased the evidence base for the importance of immigration in seabird metapopulation occupancy and dynamics (Bicknell et al., 2012; Coulson & Coulson, 2008; Dearborn et al., 2003; Fernández-Chacón et al., 2013; Inchausti & Weimerskirch, 2002; Spindelov et al., 1995). However, very few studies have quantified the link between network connectivity and whole-metapopulation dynamics using empirical data on population sizes and demography (but see Genovart et al., 2018; Inchausti & Weimerskirch, 2002). Despite these insights, based on a few intensively studied species, seabirds are still not generally regarded and modeled as metapopulations. The status quo of modeling closed populations in conservation management applications due to a “paucity of reliable connectivity estimates” (Miller et al., 2019) is particularly problematic, because ignoring interchange between colonies can fundamentally alter the predictions of population models (Matthiopoulos et al., 2005).

Modern metapopulation theory has advanced from the classic, simplifying assumptions of equal connectivity and identical subpopulations (Levins, 1969) to integrating variation in patch area, quality, and patch connectivity (Hanski, 2001; Hanski & Ovaskainen, 2003). These biologically realistic features require insights into how and why patches within a network are connected through dispersing individuals. Dispersal is generally one of the most poorly observed mechanisms of population regulation in general (Cappuccino, 1995), and this is even more evident for far-ranging, long-lived taxa such as seabirds (Coulson & Coulson, 2008). Seabird dispersal is an intriguing paradox (Milot et al., 2008). Outside the breeding season, many species migrate thousands of kilometers each year to and from distant wintering grounds (Fayet et al., 2017; Fort et al., 2012; González-Solís et al., 2007).

During the rest of the year, they conform to a metapopulation structure and display a high degree of breeding and natal site fidelity (Hamer et al., 2001). These patterns are not absolute: some empirical and modeling studies have found emigration probabilities of more than 50% in particular age groups (Oro et al., 2004). A mechanism that is widely postulated to influence dispersal is the attraction toward conspecifics, that is, using the size of colonies as an index of the quality of feeding opportunities in the seas around the colonies (Ward & Zahavi, 1973). Extending and refining this concept, attraction to conspecifics may focus on a particular group such as recruits (Szostek et al., 2014) or may incorporate highly relevant information such as the breeding success of conspecifics (Danchin et al., 1998; Doligez et al., 2003). These mechanisms have rarely been implemented or compared in models of seabird metapopulations (but see Cam et al., 2004). Generally, the empirical evidence suggests that the density of conspecifics is relevant to the dispersal patterns of seabirds, and thus influences the connectivity between colonies in seabird metapopulations.

The density of conspecifics also plays a fundamental role in population regulation through density-dependent feedback. Population density can influence the fitness of individuals, consequently modulating the population growth rate (Hixon et al., 2002), and ultimately affecting the viability of populations. Research on the existence of density-dependent feedback for population regulation has supported their pervasiveness (Berryman et al., 2002; Brook & Bradshaw, 2006). Rather than investigating whether density dependence exists, the focus has shifted to its strength and generating mechanisms (Cappuccino, 1995; Hixon et al., 2002). In seabird populations, the scales and strength of density dependence are difficult to quantify, due to the large intergenerational lags and extensive spatial scales involved (Wooller et al., 1992). The availability of suitable terrestrial breeding habitats, particularly on rocky cliffs, stacks, and low-lying islands, poses obvious limits to colony expansion (Hatfield et al., 2012; Schumann et al., 2013). The marine productivity around breeding colonies also seems to play an important role: Ashmole (1963) and Storer (1952) both hypothesized that resource exploitation within the accessible radius around seabird colonies imposes limitations to colony size, which have since been demonstrated in a range of seabird species (Birt et al., 1987; Elliott et al., 2009; Jovani et al., 2016; Lewis et al., 2001). Yet, while it is now broadly accepted that density-dependent regulation plays an important role in seabird populations, influencing recruitment rate in particular (see above), it is not clear how strong this regulation is in open populations (Tavecchia et al., 2007, but see Genovart et al., 2018). In fact, the relative importance of density-dependent regulation in comparison to extrinsic

factors is so poorly understood (Lewison et al., 2012) that population models currently guiding seabird conservation and marine planning ignore density-dependent processes as part of a precautionary approach (Miller et al., 2019) or include it in a compensatory form that lacks empirical support (Horswill et al., 2017).

An important consideration of population regulation in long-lived species with relatively low population growth rates is the potential for delayed density-dependent effects (Hanski & Woiwod, 1991; Turchin, 1990), that is, time lags that are part of a particular life history (Sæther et al., 2005; Thompson & Ollason, 2001). In most seabird species, first-time breeders recruit into the breeding population with a delay (“delayed maturity”) of three to more than 10 years (Berman et al., 2009; Harris et al., 2016; Nelson, 2002; Nevoux et al., 2010; Oro & Pradel, 1999). These delays mean that the effect of intrinsic and external processes such as density dependence and climate may be observed on breeding population counts several years after they occur (Payo-Payo et al., 2016; Thompson & Ollason, 2001). Crucially, in many seabird species, dispersal and associated connectivity between colonies are predominantly influenced by first-time breeders (Greenwood & Harvey, 1982). Adult breeders are usually highly faithful to their breeding colony (although groups of species such as terns and gulls, e.g., Audouin’s gull, *Larus audouinii*, have much lower levels of breeding colony fidelity; Fernández-Chacón et al., 2013; Spendlow et al., 1995). This characteristic can additionally lead to stage-specific density dependence, where prebreeding and breeding birds are affected by different regulatory mechanisms (Ray & Hastings, 1996). For example, the number of conspecifics can have a negative effect on adult breeders in a colony, but a positive effect on prebreeders by attracting philopatric and immigrant birds to breeding colonies (Tenan et al., 2017). This complexity has yet to be implemented in metapopulation models of seabirds.

Density-dependent regulatory feedback can operate across different spatial scales (Cappuccino, 1995; Hixon et al., 2002). Early calls for attention to spatial scale remarked that “the nature of population growth can be greatly affected by processes operating on different spatial scales” (Ray & Hastings, 1996), and echo the principles of landscape ecology that were then developing as a discipline. Landscape ecology aims to understand spatial heterogeneity and the causes and consequences of spatial patterns at variable spatial scales (Turner, 2005). Landscapes are understood as hierarchical systems (Wu & Loucks, 1995). It is reasonable to assume that animal (meta)population dynamics mirror the spatial structure of the landscapes they live in (Turner, 2005), and thus to apply an integrative landscape perspective to large-scale spatial dynamics for animal populations, as has been

suggested for plants (Murphy & Lovett-Doust, 2004). Spatially realistic metapopulation theory incorporates such scale dependency by introducing spatial structure to metapopulation models, and distinguishing between a local scale of spatially homogeneous patch dynamics and a global scale of metapopulation regulation (Hanski, 2001; Hanski & Gilpin, 1991). Much early work focused on identifying the singular scale at which population regulation operated; that is, whether it was the result of local processes or the result of metapopulation dynamics (Murdoch, 1994). However, it has since become clear that the two processes are not mutually exclusive and the presence of local regulation does not preclude mechanisms operating at the metapopulation level (Cappuccino, 1995).

The spatial structure may not be limited to a local and a global scale. The spatial extent of many seabird metapopulations implies that colonies are located in various marine ecosystems with different physical oceanographic characteristics and productivity (Eveillard-Buchoux et al., 2017; Zotier et al., 1999). The comparative dynamics of seabird breeding colonies distributed in different biogeographic regions have attracted only limited analysis to date, despite the relevance of such spatial demographic variation for metapopulation dynamics and conservation management. For some seabird species, there is empirical evidence that the dynamics of colonies within regions of similar prey abundance are correlated (Frederiksen et al., 2005; Wolf et al., 2009). Yet, to our knowledge, there are no metapopulation studies that have detected and quantified density-dependent regulation across multiple spatial scales. Thus, combined with life history traits and behavior, it is valuable to extend current modeling approaches to incorporate more complex regulatory mechanisms that operate across multiple spatial scales, within a hierarchically structured metapopulation.

Northern gannets, *Morus bassanus* (gannets, hereafter), are highly suitable candidates for re-evaluating seabird populations as spatially structured metapopulations. Gannets occur in the northern Atlantic Ocean, although the western and eastern populations are considered segregated (Clark, 2017; Nelson, 2002). They are large, colonial breeding seabirds with colonies widely distributed across several distinct marine biogeographic regions. Gannets are highly mobile, traveling up to 540 km per day to forage during the breeding season (Hamer et al., 2000). They also migrate to wintering areas in the North Sea, the Mediterranean Sea, and off western Africa (Fort et al., 2012). Sparse evidence from tracking the exploratory movements of immature birds during the breeding season and records from ringing data suggests that colonies are connected over large distances through dispersing individuals (Barrett, 1988; Barrett et al., 2017; Pettex et al., 2014; Veron & Lawlor, 2009; Votier et al., 2011).

Like many seabird species, gannets have been extensively exploited by humans. At least in the United Kingdom, however, the species has been largely protected since the late 19th century, and the Northeast Atlantic population has grown consistently for much of the 20th and early 21st centuries (Murray et al., 2015). Despite a consistent increase in the Northeast Atlantic population through increasing colony sizes and the establishment of new colonies, there is evidence for density-dependent regulation in some of the larger colonies (Lewis et al., 2001). There are also empirical observations of variation in foraging characteristics and colony growth between colonies located in different biogeographic regions within the overall breeding range (Davies et al., 2013; Pettex et al., 2014). Since the early 20th century, gannet colony growth, establishment, and extinction have been monitored in detail across the entire breeding range (Barrett, 2008; Barrett et al., 2017; Barrett & Folkestad, 1996; Fisher & Vevers, 1943; Garðarsson, 1989, 2008, 2019; Gurney, 1913; Murray & Wanless, 1986, 1997; Newton et al., 2015; Olsen & Permin, 1974; Wanless et al., 2005). This exceptional long-term dataset of colony census data of more than a century has not previously been analyzed to its full temporal and spatial extent.

We investigated metapopulation regulation in the gannet, with a particular focus on the effects of generational time lags, nested spatial scales, and dispersal connections between colonies. We developed a novel hierarchical Bayesian state-space model and fit it to the century-long population census dataset of all gannet colonies across the entire spatial distribution of the Northeast Atlantic metapopulation. We investigated population regulation at different spatial and temporal scales by comparing five different and increasingly complex scenarios of metapopulation regulation through lagged, local, regional and global density dependence (for definitions see methods). We compared three connectivity scenarios: a scenario of closed populations as a null model, a scenario of equal connectivity between colonies and a scenario of positive density dependence at a global scale where immigrants preferentially dispersed into larger breeding colonies. With this comparison, we aimed to evaluate the prevailing assumption of colony closedness by obtaining population-level evidence of the influence of immigration, as suggested by the sparse individual-level ring resighting data. The distribution of colony sizes in gannets is strongly skewed to a few very large and many small colonies. Thus, the conspecific attraction might be a reasonable mechanism guiding dispersal patterns in gannets, and we explored whether a model with positive density dependence on the global scale could fit the population-level data better than a model of equipartitioning. We combined the comparison of

different connectivity scenarios with a comparison of different spatial scales in density dependence. We compared models where density dependence operated on a local scale and where colony growth was limited by the terrestrial carrying capacity with a scenario where density dependence operated on a local or regional scale, and where colony growth could also be limited by the regional carrying capacity, for example via regionally correlated marine resource availability. We hypothesized that the sparse evidence of variation in colony dynamics between biogeographic regions (Davies et al., 2013) could be indicative of a general pattern and that models with density dependence at these two spatial scales might fit the data better than a simpler model of local density dependence.

MATERIALS AND METHODS

Data

Our dataset is a compilation of all available colony census data for the entire Northeast Atlantic distribution of the gannet, which currently extends from Brittany in northern France and Helgoland in northern Germany north to Iceland and Svalbard (Bjørnøya) and east to the Murman coast of Russia, with the bulk of colonies located in northwest Scotland. We collated 117 years of colony census data (1900–2016), either from the published literature or directly from researchers responsible for national, regional, or local monitoring programs. We defined a colony as two or more gannet pairs breeding in proximity (Evans et al., 2016), and we followed the conventions used during censuses and previous analyses for exact colony delineations. Fifteen gannet colonies existed before 1900, and 51 colonization events occurred between 1900 and 2016. Of these colonization events, 38 were, at least initially, successful and 13 colonization events were unsuccessful. In the latter cases, a single or a very small number of nests were occupied for a few years, but the “colony” was then abandoned and gannets were subsequently not recorded ashore (e.g., Petersen et al., 2021). We also categorized Rockall and Grimsey (the latter now extinct) where <50 pairs have been counted in some years as unsuccessful, because Atlantic storms and earthquakes, respectively, have repeatedly led to complete breeding failures (Einarsson, 1987; Murray, 2015). We excluded all 13 unsuccessful colonization events from the population model because of the very small colony size (in most cases only a single nest) and short duration of the individual time series (in most cases <10 years). We also excluded irregular nest-building or breeding attempts of

single birds or pairs in the Mediterranean, southern England and the Baltic (Fernandez & Bayle, 1994; Giagnoni et al., 2015; Lyngs, 2015; Palmer, 2001). Six colonies, (five successfully established colonies and one colony existing at the start of the time series) became extinct between 1900 and 2016 (Table 1).

Hence, the dataset consists of 53 different gannet colonies that have been counted at least every 10–15 years since 1900. Since the 1970s many colonies have been counted more frequently, in some cases annually. Improved coverage and more intensive monitoring also mean that the exact years of colonization and extinction are known. The number of censuses available for each colony ranged between three and 54 (Table 1). On average, counts were made in $44\% \pm 27\%$ (mean \pm SD) of the years each colony was extant between 1900 and 2016 (Appendix S1: Figure S1). Counting methods and count units have varied both among colonies and over time, for example, counts have been made from the air, land, and sea, at different times in the season and count units have included individuals, pairs, nest sites, and nests. No correction factors to convert counts to a standardized unit are available for gannets, but the most widely used unit and usual convention for more recent counts is the unit “Apparently Occupied Site” (AOS), defined as one or two Northern gannets present at a site irrespective of the presence of nest material (Mitchell et al., 2004; Murray et al., 2014; Nelson, 2002). A count in AOS is thus equivalent to the number of breeding pairs or the female fraction of breeders in a colony, but since “site” can easily be misunderstood in the context of seabird colonies, we use female breeders or gannet pairs in the text below.

Several studies have highlighted variations in population parameters of seabirds among different biogeographic regions, which are likely to be based on underlying differences in ecosystem productivity (Cook et al., 2011; Davies et al., 2013). We used the concept of regional seas and their extensions, proposed by the UK Joint Nature Conservation Committee (JNCC) to assign colonies in and around the UK to a biogeographic region. We assigned regional structuring for colonies in Norway following Barrett et al. (2006), and for Iceland, the Faroe Islands and colonies outside the regional seas extensions in Ireland and France, we used the global classification of marine ecoregions and pelagic provinces (Spalding et al., 2007) downloaded from <http://data.unep-wcmc.org/datasets/38> (Figure 1). For the seven colonies outside these recognized regions we assumed that Kharlov Kola, Bjørnøya, Helgoland, and Runde were all in discrete regions and that Les Etacs, Ortac, and Rouzic were in a shared region, based on their spatial distance and

TABLE 1 Overview of relevant data for each of the 66 northern gannet colonies and colonization attempts, organized by colonization year (or the year of first reference in the literature for colonies existing before 1900).

Colony	Country	Biogeographic region	N	E	Colonization year	Extinction year	No. counts
Mykines ^h (My)	Faroes	Faroer Plateau	62.09	-7.58	800		10
Lundy ^h (Ln)	UK	Celtic Seas	51.18	-4.67	1274	1905	4
Bass Rock (BsR)	UK	Northern North Sea	56.08	-2.64	1447		16
Ailsa Craig (AC)	UK	Minches and Western Scotland	55.25	-5.12	1526		54
Sula Sgeir ^h (SISg)	UK	Scottish Continental Shelf	59.09	-6.16	1549		10
St Kilda ^h (SK)	UK	Scottish Continental Shelf	57.82	-8.58	1600		12
Brandur ^h (Br)	Iceland	South and West Iceland	63.39	-20.37	1687		13
Geldungur ^h (Gl)	Iceland	South and West Iceland	63.34	-20.40	1687		12
Hellisey ^h (Hll)	Iceland	South and West Iceland	63.36	-20.37	1687		12
Sulnasker ^h (Sl)	Iceland	South and West Iceland	63.33	-20.40	1687		12
Little Skellig (LS)	Ireland	Celtic Seas	51.78	-10.51	1700		16
Sule Stack ^h (SlSt)	UK	Scottish Continental Shelf	59.02	-4.51	1710		12
Eldey ^h (El)	Iceland	South and West Iceland	63.74	-22.96	1752		13
Grimsey*	Iceland	North and East Iceland	66.55	-18.00	1819	1946	6
Grassholm (Gr)	UK	Celtic Seas	51.73	-5.48	1820		28
Bull Rock (BIR)	Ireland	Celtic Seas	51.51	-10.30	1856		14
Noss (Ns)	UK	Scottish Continental Shelf	60.14	-1.00	1914		20
Copinsay *	UK	Scottish Continental Shelf	58.90	-2.68	1915	1916	2
Hermaness (Hr)	UK	Scottish Continental Shelf	60.82	-0.91	1917		24
Isle of May*	UK	Northern North Sea	56.19	-2.56	1922	1923	2
Bempton Cliff (BC)	UK	Northern North Sea	54.15	-0.17	1924		41
Great Saltee (GS)	Ireland	Celtic Seas	52.11	-6.62	1929		52
Rouzic (Rz)	France	Western Channel	48.78	-3.44	1938		52
Scar Rocks (SR)	UK	Irish Sea	54.66	-4.70	1939		31
Ortac (Or)	UK	Western Channel	49.62	-2.29	1940		17
Skrudur (Skrd)	Iceland	North and East Iceland	64.90	-13.62	1943		11
Les Etacs (LE)	UK	Celtic Seas	49.70	-2.24	1945		20
Raudinupur (Rd)	Iceland	North and East Iceland	66.51	-16.54	1945		13
Holy Isle*	UK	Minches and Western Scotland	55.53	-5.07	1946	1952	3
Runde (Rn)	Norway	Norwegian Sea	62.40	5.66	1946		41
Kerling*	Iceland	North and East Iceland	65.94	-19.68	1949		1
Skoruvikurbjarg (Skrv)	Iceland	North and East Iceland	66.39	-14.84	1955		9
Skittenskarvholmen (Skt)	Norway	Norwegian Sea	67.67	12.72	1960	1978	8
Syltefjord (Sy)	Norway	Barents Sea	70.52	30.30	1961		27
Mafadrangur*	Iceland	South and West Iceland	63.39	-19.14	1962		1
Skarvklakken ^h (Skrvkl)	Norway	Norwegian Sea	69.13	15.65	1967	2003	24
Flannan Isles (FII)	UK	Scottish Continental Shelf	58.29	-7.59	1969		12
Hovsflesa (Hv)	Norway	Norwegian Sea	68.32	14.00	1975	2002	14
Fair Isle (FrI)	UK	Scottish Continental Shelf	59.55	-1.64	1975		42
Clare Island (CI)	Ireland	Celtic Seas	53.80	-9.99	1978		11

(Continues)

TABLE 1 (Continued)

Colony	Country	Biogeographic region	N	E	Colonization year	Extinction year	No. counts
Shiant Islands*	UK	Minches and Western Scotland	57.90	-6.36	1979	1987	3
Foula (Fl)	UK	Scottish Continental Shelf	60.13	-2.10	1980		13
Storstappen, Gjesvaer (SG)	Norway	Barents Sea	71.12	25.30	1987		15
Troup Head (TH)	UK	Northern North Sea	57.69	-2.30	1987		17
Ireland's Eye (IE)	Ireland	Irish Sea	53.41	-6.06	1989		18
Helgoland (Hlg)	Germany	Southern North Sea	54.19	7.87	1991		26
Rockall*	UK	Rockall Trough and Bank	57.60	-13.68	1992		5
Kharlov Island (KKP)	Russia	Kharlov Kola Peninsula	68.81	37.34	1995		18
Fyllingen (Fy)	Norway	Norwegian Sea	68.54	14.25	1997	2008	7
St Ulvøyholmen (SU)	Norway	Norwegian Sea	68.45	14.52	1997		13
Utfloeyсан*	Norway	Norwegian Sea	68.57	14.24	1998	2002	2
Kvitvaer (Kvt)	Norway	Barents Sea	70.17	18.62	2001		10
Kvalnesflesa (Kvl)	Norway	Norwegian Sea	68.31	13.95	2002	2015	11
St Margarets Island*	UK	Celtic Seas	51.64	-4.71	2003	2005	3
Sule Skerry (SlSk)	UK	Scottish Continental Shelf	59.08	-4.41	2003		8
Westray (Ws)	UK	Scottish Continental Shelf	59.33	-3.07	2003		11
Lambay (Lm)	Ireland	Irish Sea	53.49	-6.02	2007		5
Barra Head (BH)	UK	Scottish Continental Shelf	56.78	-7.64	2007		5
Buholmene (Bh)	Norway	Norwegian Sea	67.67	12.75	2008		6
Kvitholmen*	Norway	Norwegian Sea	69.13	15.65	2008	2010	2
L. Foroy (LF)	Norway	Norwegian Sea	69.26	15.97	2010	2015	5
Oddskjaeren (Od)	Norway	Norwegian Sea	68.29	14.25	2010		5
Bjørnøya (Bj)	Norway	Bjørnøya	74.44	19.04	2011		6
St Forøya (SF)	Norway	Norwegian Sea	69.26	15.98	2012		3
Langikambur*	Iceland	South and West Iceland	66.43	-22.51	2016		1

Note: Colonies marked with ^h were harvested at any point throughout the time series of counts, including published evidence of egg collection in a single year (e.g., Skarvklakken). Entries marked with * are unsuccessful colonization events (see *Materials and methods* for definition) and were omitted from the modeling dataset. Latitude and longitude are expressed in decimal degrees. No. counts includes the first count of 0 for colonies that went extinct.

proximity, respectively. Thus, the metapopulation was spatially structured into 15 different biogeographic regions (Table 1).

State-space model

To quantify the timing, scale, and interactions between different aspects of density dependence and connectivity, we developed a state-space model for the coupled dynamics of the entire metapopulation of 53 colonies in the 15 regions (Figure 2). State-space models are mechanistic time-series models that distinguish between the biological processes that influence the ecological dynamics and

the observation process that is used to collect partial and imperfect observations of the underlying biology (Auger-Méthé et al., 2021; Newman et al., 2014).

Observation model

We modeled the colony census data, that is, the female fraction of the observed population size C in colony n and year t using a normal distribution centered at the true underlying colony size P in colony n and year t with a coefficient of variation of 0.05, representing a time-invariant observation error of 10% above and below the actual sizes:

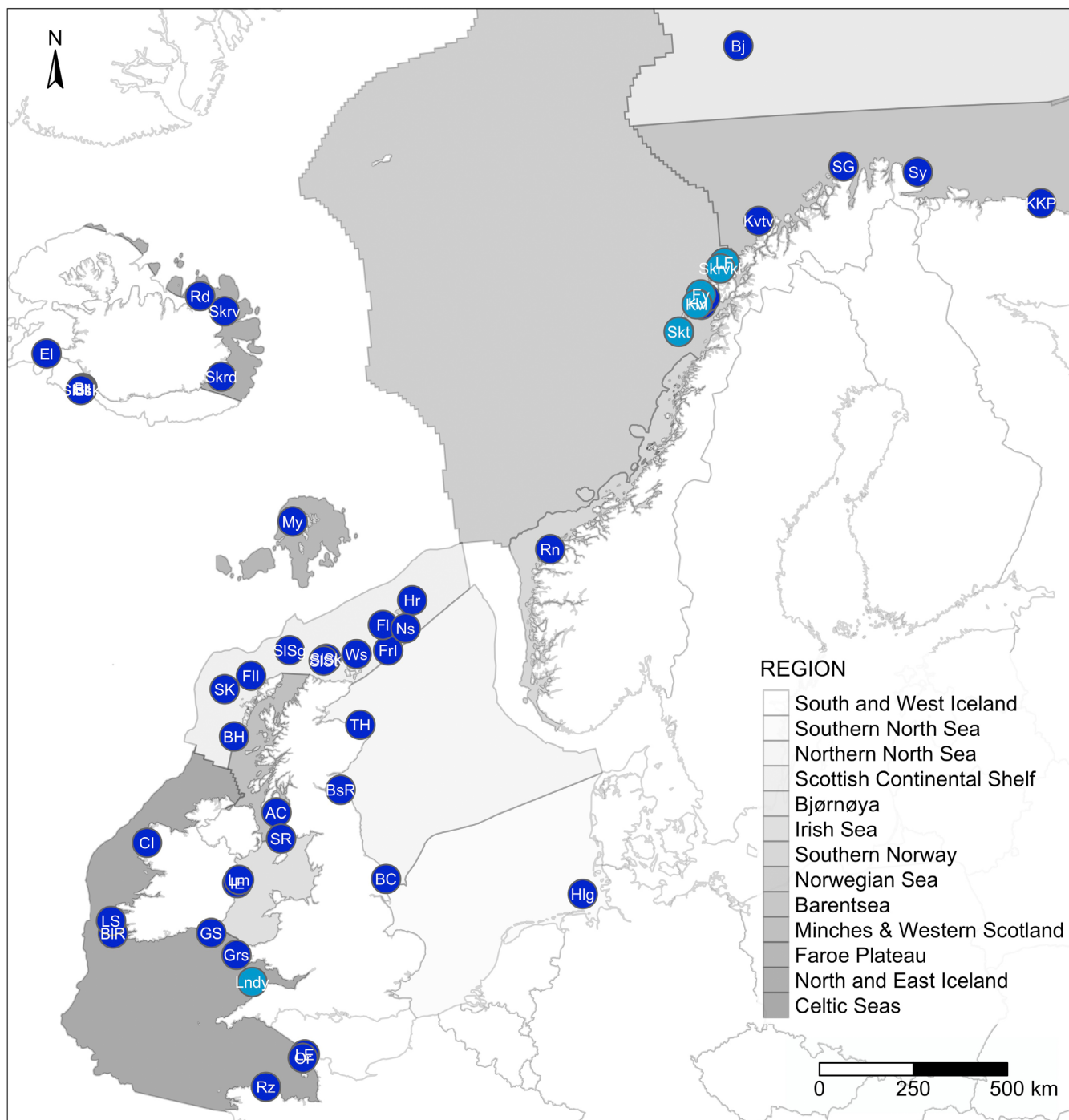


FIGURE 1 Map of all gannet colonies in the Northeast Atlantic metapopulation up until 2016. Colonies in light blue became extinct during the time series 1900–2016 (Table 1). Colony abbreviations are explained in Table 1. Note that the colonies KKP and LE, Or and RZ were assigned to two new separate regions, based on their spatial segregation from the other colonies.

$$C_{n,t} \sim \text{Normal} \left(P_{n,t}, \frac{1}{0.05(P_{n,t})^2} \right). \quad (1)$$

The fit of state-space models can be improved by estimating population census data based on replicate

observations or individual standard errors associated with each observation (Knappe et al., 2011, 2013). It was not possible to incorporate this recommendation into our model because the earlier part of the census data time series did not contain estimates of the observation error.

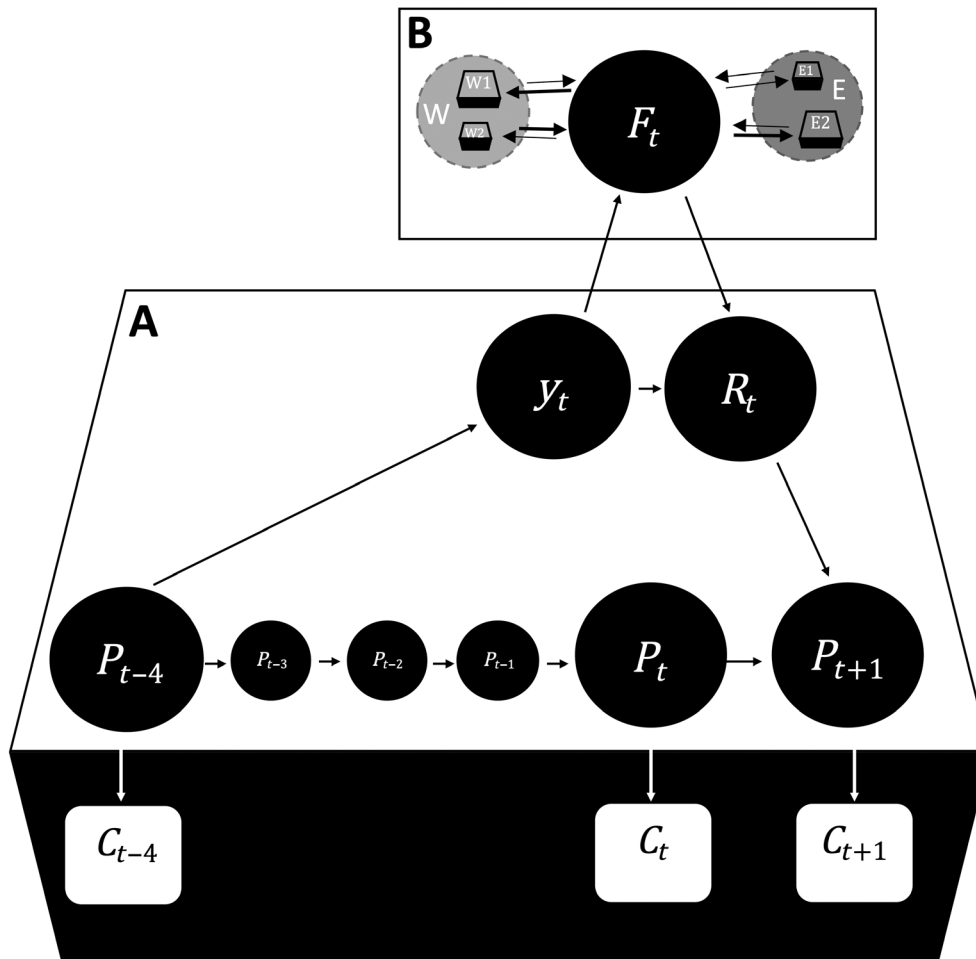


FIGURE 2 Schematic of the gannet metapopulation model. (A) The process model at the local level (i.e., within a single colony, white box) and the observation model (black box). (B) Illustration of processes at the regional level (dashed circles) and global level (black circle). The two exemplary colonies in the region on the right are dominated by regional density dependence (same sized arrows sending individuals to the pool of floaters), but the bottom colony is bigger and receives more immigrants. The colonies in the region on the left are locally regulated (arrows of varying size, and the top colony is bigger, thus receiving more immigrants from the global pool. C = colony census data in AOS, P = colony size (number of pairs, modeled as the number of breeding females in the colony), y = immature gannets (subject to immature survival and fecundity rate), R = available recruits, subject to recruitment rate, F = floaters (immature birds, globally available for immigration), t = time in years.

Process model

Single-colony dynamics

To facilitate biological interpretation, we present our model in terms of three state variables: $P_{n,t}$, the size of colony n in year t , $R_{n,t}$, the number of recruits into colony n in year t , and $Y_{n,t}$, the number of young birds reaching recruitment age in each colony n in year t (Figure 2). We initially modeled colony growth as a Poisson process:

$$P_{n,t+1} \sim \text{Poisson}(\lambda_{n,t}), \tag{2}$$

where $\lambda_{n,t}$ is the expected colony size in each colony n in year t . Using this form, we compared all model

scenarios described below with an extended version of the model using a Poisson–Gamma (i.e., Negative Binomial) growth process with the same rate parameter $\lambda_{n,t}$ and a scale parameter $s_{n,t}$ (Greene, 2008), to accommodate overdispersion in the data:

$$P_{n,t+1} \sim \text{Poisson}(\lambda_{n,t}s_{n,t}) \text{ where } s_{n,t} \sim \text{Gamma}(\theta, \theta). \tag{3}$$

Models with a negative binomial growth term fitted the data much better than models with a simple Poisson growth term (Appendix S3: Table S3), hence we focused our model comparison below on models that included this form of overdispersion.

The count unit of the observations was AOS (equivalent to breeding pairs). By retaining the count unit AOS, we

effectively modeled the states P , R and Y as the female part of the population, and accordingly applied necessary corrections (e.g., by halving the fecundity parameter, see below).

We modeled the expected colony size $\lambda_{n,t}$ in terms of mean adult survival (s_a) of established adults and the expected number of new recruits R (see below):

$$\lambda_{n,t} = s_a P_{n,t} + R_{n,t}. \quad (4)$$

In the single-colony model (model 1), the expected number of recruits $R_{n,t}$, that is the immature birds that enter the pool of breeders in the respective year, is simply the proportion of recruiting young birds $Y_{n,t}$:

$$R_{n,t} = r_{n,t} Y_{n,t}, \quad (5)$$

where $r_{n,t}$ is the recruitment rate (derived as a function of density; Figure 2, see below). Gannets start breeding, on average, at age five (Nelson, 2002). We therefore modeled the number of young birds $Y_{n,t}$ as the surviving female chicks born 4 years ago, at the prevailing fecundity rate $b_{n,t-4}$:

$$Y_{n,t} = s_i b_{n,t-4} P_{n,t-4}, \quad (6)$$

where s_i is the compound probability of immature survival over this 4-year period and $b_{n,t-4}$ is equivalent to the proportion of female gannets with successfully fledged chicks 4 years ago.

While adult survival in seabirds is generally high and varies little, breeding success is highly sensitive to environmental variation (Chastel et al., 1993; Jenouvrier et al., 2005). We implemented annual breeding success as a stochastic process:

$$b_{n,t} = \text{logit}^{-1}(\varepsilon_{n,t}), \quad \varepsilon_{n,t} \sim N(a_0, \sigma_\varepsilon), \quad (7)$$

using a fixed baseline fecundity value a_0 and a standard deviation σ_ε . Both of these values were set from independent sources (for values, see parameterization below).

Density-dependent processes

Density dependence is a complex process that may be shaped by a number of contributing factors, for example the availability of breeding sites, the quality of these and the availability and accessibility of food. Some of these obviously act on the local scale (e.g., the availability of terrestrial breeding space within a colony) but others, such as marine food resources, may extend over larger areas. The delineation of marine ecoregions (Spalding et al., 2007) for example, is based on the similarities of the biodiversity

composition and abundance of species within larger regions of space. The dynamics of colonies within one region might thus also be regulated on the regional scale. We were interested in comparing a scenario regulated solely by local density dependence with a scenario where either local or regional dynamics influenced colony dynamics. We therefore built our metapopulation model in a nested way to incorporate one or two density-dependent terms acting at these two different spatial scales.

Generally, density-dependent regulation acted on the recruitment probability. In the simpler scenario, the probability of recruitment $r_{n,t}$ was dampened by local density dependence:

$$r_{n,t} = \text{logit}^{-1}(\alpha - \nu_n P_{n,t}), \quad (8)$$

whose strength was regulated by the colony-specific parameter ν_n , for example through colony-specific availability in breeding space (local carrying capacity). The parameter α was a constant, here set to 100, to ensure that recruitment is practically 1 when $\nu_n P_{n,t}$ is zero, that is, when no density-dependent effects applied.

For the more complex model scenario where we considered density dependence on the local or regional scale (models 4 and 5), we extended Equation (8) to:

$$r_{n,t} = \text{logit}^{-1}(\alpha - \max(\eta_{k_n}, \nu_n) P_{n,t}) \quad (9)$$

Here, the parameter η_{k_n} represented regional density dependence, a dampening effect on recruitment that applies to each colony n in each region k in the same way. Regional carrying capacity could be defined as the maximum number of individuals (i.e., the sum of all colony sizes within one region) depleting a common resource pool. This definition would be appropriate for species with overlapping foraging ranges and freely moving prey across the entire regional space. Alternatively, we define regional carrying capacity as a characteristic of the region-specific marine resource richness that sets a common limit to colony size within that region. Under this definition, all colonies in a region experience a similar density of resources by virtue of geographical proximity but do not compete for spatially predictable prey fields. This implementation is appropriate for central place foragers who cannot choose foraging locations indiscriminately, but where marine space use is constrained to an area around their colony by the need to attend to their fully dependent chick. Gannets in particular forage in nonoverlapping colony-specific home ranges during the breeding season (Wakefield et al., 2013) on prey occurring predictably at the mesoscale (Pettex et al., 2010; Scales et al., 2014; Wakefield et al., 2015), hence gannets from different colonies do not

directly compete for marine resources in the same unit of space. Due to these constraints in space use, the number of individuals that can be sustained by the resources around each colony is limited, and under the parsimonious assumption of regional similarity of marine resource distribution, the upper limit (regional carrying capacity) is common to all colonies within one region.

The model estimated both parameters η_{k_n} and ν_n for each time step and, by selecting the larger of both, chose the parameter that served as the limiting factor for recruitment. The absolute values of η_{k_n} and ν_n were estimated in relation to the baseline of the constant α , but we were mainly interested in the relative importance of the two regulatory mechanisms (see below for the calculation of carrying capacity dominance). The density dependence parameters were not assumed to vary with time. It may be argued that regional carrying capacities in particular should be able to fluctuate with changing availability of marine resources, but this level of complexity would best be investigated with the use of covariate information on, for example, prey availability, as part of future studies with this framework (e.g., see [Caillat et al., 2019; Matthiopoulos et al., 2014] for a similar extension of an initial framework of a harbor seal population model).

Population harvest

In total, 12 of the 53 colonies were harvested for eggs or chicks over different periods of time (Table 1). The quality of the data on the number of harvested gannets was variable. Precise numbers were only available for the Icelandic colonies of the Westman Islands (Brandur, Geldungur, Hellisey, and Sulnasker) and Eldey (Einarsson, 1987), Mykines on the Faroe Islands (Olsen, 2008), and only for parts of the time series. We therefore implemented *harvest* ($H_{n,t}$) as a binary covariate of mortality, indicating whether a colony was harvested (1) or not (0) in any given year. Because harvest focuses on gannet chicks or “gugas,” we implemented the term with a time lag of 4 years. We estimated a harvest parameter h representing the proportion of female gugas surviving the harvest:

$$Y_{n,t} = s_i b_{n,t-4} P_{n,t-4} h^{H_{n,t-4}}. \tag{10}$$

Multicolony dynamics: immigration

To model connectivity between colonies, we extended the closed population model by an immigration term ι that represented the proportion of female immigrants into

each receiver colony n . We extended Equation (5) to a metapopulation version that captured immigration into the n^{th} colony as a weighted function of the total number of immigrants:

$$R_{n,t} = (1 - \iota) r_{n,t} Y_{n,t} + \iota \sum_{i=1}^n Y_{i,t} W_{n,t} \text{ where} \tag{11}$$

$$W_{n,t} = \frac{w_{n,t}}{\sum_j w_{n,t}}.$$

The local philopatric young female birds are represented by the complement of ι and both together form the pool of recruits R in each colony n at time t . Once adult gannets have decided on a breeding site, breeding site fidelity is very high (Nelson, 2002) that makes it appropriate to implement this choice only once, upon entry of young birds into the pool of breeders.

The function $W_{n,t}$ distributed immigrants to each colony n in each year t in the colony network, based solely on the attractiveness of that colony compared with all others (hence the normalization operation in the definition of $W_{n,t}$). We were interested in comparing different mechanisms that influence dispersal to a breeding colony and therefore ran models with differently weighted redistribution functions W . The simpler scenario of indiscriminate colony choice (models 2 and 4) can be considered as a null model and assumed that each extant colony n in year t in the network received an equal share of the globally available immigrants:

$$w_{n,t} = \begin{cases} 1 & \text{if } P_{n,t} \geq 1 \\ 0 & \text{otherwise} \end{cases}. \tag{12}$$

The alternative scenario assumed that immigrants are attracted to larger colonies (models 3 and 5) thus we modeled conspecific attraction according to colony size:

$$w_{n,t} = P_{n,t}. \tag{13}$$

In addition, we also explored two more complex scenarios, an “attraction to local recruits” scenario:

$$w_{n,t} = R_{n,t}, \tag{14}$$

a mechanism that has been shown for common terns (Szostek et al., 2014) and an “attraction to mega-colonies” scenario:

$$w_{n,t} = r_{n,t} P_{n,t}, \tag{15}$$

where the conspecific attraction was re-enforced by higher recruitment rates. The latter two scenarios, although easy to specify within our framework, are essentially very strong positive feedback loops within the recruitment process and led to numerical overflow problems during fitting. Although this is not a direct refutation of these two redistribution mechanisms, it nevertheless indicates that their mathematical formulation needs to be re-examined in a more biological light.

Model parameterization and priors

We encountered convergence problems when developing the models with unbounded prior distributions, as others have reported for fairly complex models with large numbers of parameters (Matthiopoulos et al., 2014). Following the approach taken by Matthiopoulos et al. (2014), we used rescaled beta distributions for the informative priors for adult survival (s_a), immature survival (s_j) and immigration (i). Below, we describe our selection of priors and biological rationale for the derivation of minimum and maximum values for different prior distributions.

Fecundity (b)

To inform the fecundity parameter b we derived average fecundity estimates from the compilation of all available fecundity data collated from the literature and the UK Seabird Monitoring Program run by the JNCC, accessed through its database (<http://archive.jncc.gov.uk/smp>). The mean breeding success, defined as the proportion of chicks fledged, was 0.72 ± 0.12 , based on 345 annual means from 15 colonies widely distributed across the metapopulation and spanning the years 1961–2018 in a noncontinuous way. We generated a random normal distribution of 1000 samples based on these parameters, halved this to calculate the breeding probability for the female breeders, transformed it to a log scale and used the mean of -0.58 representing a fixed fecundity rate a_0 and the standard deviation σ_e of 15.4 to incorporate annual stochastic variation in fecundity.

Immature and adult survival (s_j and s_a)

We used published survival estimates for immatures and adults based on ring recovery data from the British Trust for Ornithology (BTO) for gannets, mainly ringed as chicks from 1959 to 2002 (Wanless et al., 2006) to inform the priors for immature and adult survival parameters. Wanless et al. (2006) reported survival estimates as mean

and confidence interval around the mean, and stated separate estimates for each of the 4 years of immaturity. We converted these estimates into mean and standard deviation for adults (0.918 ± 0.023) and compounded mean and standard deviation over the first 4 years of life for immatures (0.279 ± 0.05), respectively, and used those as limits for bounded prior distributions (see above).

Harvest (h)

Gannet chicks or eggs were harvested at 12 of the 53 colonies throughout the time series, or for part of it (Table 1), but precise information on the number of harvested individuals as a proportion of the colony size was limited (see above). We therefore used an uninformative uniform prior based on a beta distribution with parameter values of 1.

Immigration (i)

We used all ringing and recovery records from the BTO ring recovery database for the Northeast Atlantic metapopulation between 1924 (the earliest ringed gannet chick) and 24 February 2015 to derive a prior for i , the proportion of immigrants. We limited the dataset to birds ringed as chicks (age code 1, 92.2% of the data) and reported again when aged 4 years or older during the breeding season (April to September, $n = 910$, 22.7% of the data, omitting 10 birds that were recorded twice). We matched the exact spatial location of gannet breeding colonies to the ringing data using the function “st_nearest_feature” in the package *sf* (the coordinates in the ringing database are recorded with an imprecision between 1 and 10 km). We then calculated a distance matrix between all gannet colonies and all ring recovery data ($n = 910$) using the function “st_distance” in the R package *sf*, and appended a column stating that of the colonies associated with each distance record for each bird was the natal colony based on matching colony ID. We filtered this dataset using the minimum distance (in kilometers) between the ring recovery location and the breeding colony for each bird. We deemed birds recovered closest to their breeding colony and within a distance of 10 km philopatric, and birds recovered within a distance of 10 km to a colony that was not their natal colony emigrants. We cross-checked that each recovery colony existed at the time of recovery, based on the foundation year of each breeding colony. Based on these criteria, 58% of recovered birds were philopatric and 42% were immigrants. We therefore assumed that 42% of recruits were immigrants and used a maximum of 52% and a minimum of 32% to constrain the prior distribution for i .

Local density dependence (ν) and carrying capacity (K)

To inform the prior distribution of local density dependence, we used expert opinion (Albert et al., 2012) to assess local carrying capacities cc in AOS from colleagues responsible for local or regional gannet censuses. Experts supplied estimates of how much potentially suitable nesting habitat was available at each colony and hence how many AOS the colony could accommodate. The prior for the local carrying capacity K was derived from these data, using a beta distribution and the confidence interval around the cc estimates to calculate the minimum and maximum values to constrain the prior distribution.

To specify a prior for the estimated parameter ν for local density dependence, we considered the population without the influence of regional density dependence that simplifies Equation (6) to:

$$r_{n,t} = \text{logit}^{-1}(\alpha - \nu_n P_{n,t}). \quad (16)$$

As a deterministic model, without the influence of immigration and harvest the population in year $t + 1$ can be expressed as:

$$P_{n,t+1} = s_a P_{n,t} + r_{n,t} s_i b_{n,t-4} P_{n,t-4}. \quad (17)$$

At equilibrium, where P_t , P_{t+1} and P_{t-4} are the same and equal to the local carrying capacity K_n , the baseline recruitment rate r_e is then:

$$r_e = \frac{1 - s_a}{s_i b_e}, \quad (18)$$

where b_e is the baseline fecundity calculated as:

$$b_e = \text{logit}^{-1}(a_0) \quad (19)$$

We can therefore write the relationship between ν_n and any given prior value of K_n as

$$\nu_n = \frac{1}{K_n} \left(\alpha - \ln \left(\frac{r_e}{1 - r_e} \right) \right) \quad (20)$$

Regional density dependence (η_{k_n}) and carrying capacity (K_{reg})

We used the same principle as above to formulate K_{reg} , the regional carrying capacity,

$$K_{\text{reg}} = \frac{1}{\eta_{k_n}} \left(\alpha - \ln \left(\frac{r_e}{1 - r_e} \right) \right), \quad (21)$$

where η_{k_n} was the parameter for regional density dependence per colony, for all colonies within each region for which we implemented an uninformative gamma prior with a mean of 0.05 and a standard deviation of 0.02. Within the model, during the process of model fitting to the data, the parameter values for ν and η were considered relative to each other to determine the dominating spatial scale of density dependence in each colony (see above). In intuitive terms, the model used information from the strong (expert-driven) priors on local density dependence, to determine regional carrying capacities. Thus, when the local carrying capacity of individual populations was expected to be higher than their observed equilibrium levels, the model would conclude that a regional bottleneck was constraining their growth. Corroborative evidence from other colonies in the region that settled at similarly low levels was used to determine the value of regional K . We estimated K and K_{reg} in the unit of population census data (AOS), thus as the number of female breeders the region can sustain as a common upper limit to each colony in the region, thus absolute numerical values of K and K_{reg} were important.

Overdispersion (s) and shrinkage (θ)

Although our implementation of the Poisson–Gamma overdispersed stochasticity acknowledges the fact that interannual variation accumulates stochasticity from multiple demographic processes, we still wanted to make sure that the magnitude of this term did not overshadow the deterministic components of our model (i.e., the signal in the population time series). We therefore implemented a shrinkage tendency toward Poisson dispersion by assigning the following prior to θ , the extra-Poisson dispersion parameter:

$$\theta = \max(10,000 - \theta^*, 1000) \text{ where } \theta^* \sim \exp(1/200). \quad (22)$$

We ran several iterations of model 5 with different fixed values for θ to determine the suitable truncation values for the prior distribution (Appendix S3). Briefly, a value of $\theta = 10,000$ was equivalent to a Poisson model (see Appendix S3) and values below 1000 led to limited model convergence as a result of too much stochasticity in the process. We also explored several ways of deriving the prior for θ and Equation (19) emerged as the most suitable form (Appendix S3).

Forecast

We were interested in evaluating the differences in projected metapopulation size for each of the different regulatory scenarios. We therefore included a 20-year forecast by projecting the population size in each gannet colony from the end of the data time series in 2016 forward until 2036.

Model fitting and prediction

We fit the population model to the historical census data for 53 gannet colonies using the program JAGS (Plummer, 2003) interfaced with R via the *runjags* package (Denwood, 2016).

We consistently ran four parallel MCMC chains, each lasting 20,000 iterations with a burn-in stage of 15,000 and thinned to retain each 10th sample. We assessed and confirmed the convergence of the four chains visually and by analyzing the Gelman–Rubin diagnostic for each model run. We evaluated the model by exploring different model specifications and by investigating its sensitivity to priors. We calculated pairwise correlation coefficients between all parameters in the model to assess parameter identifiability (Appendix S2: Figure S1).

We assessed the fit of all five models by calculating the $R_{P,\text{dev}}^2$, for each colony as a measure of model fit based on deviance residuals:

$$R_{P,\text{dev}}^2 = 1 - \frac{\sum_{i=1}^n \left\{ y_i \log\left(\frac{y_i}{\bar{y}}\right) - (y_i - \hat{y}_i) \right\}}{\sum_{i=1}^n y_i \log\left(\frac{y_i}{\bar{y}}\right)} \quad (23)$$

where y_i are the colony census data for each colony for each year i when census data were collected, \bar{y} is the mean of the colony census data for each colony and \hat{y}_i is

the posterior colony size estimates for each year i when census data were collected, for each colony. $R_{P,\text{dev}}^2$ has been shown to be the best-behaved measure of fit for count data (Cameron & Windmeijer, 1996).

To assess the predictive ability, we fitted the models with the highest $R_{P,\text{dev}}^2$ (models 1, 3 and 5) to a reduced time series (10 years shorter, i.e., data time series supplied to the models ending in 2006) and calculated the standardized residuals between the posterior colony size estimate and the colony census data for the period between 2006 and 2016 (Figure 4B; Appendix S6: Figures S2–S5).

Model selection

We fitted five alternative models that represented different and increasingly complex scenarios of the influence of local, regional and global density dependence on metapopulation regulation on gannets (Table 2). In the simplest scenario, the “null model” represents a system of closed populations with local negative density dependence contributing to the regulation of the population. Even though this scenario might appear biologically unrealistic, it is relevant for comparison with more complex scenarios because assumptions of closed populations have been used to estimate population-level effects on gannets (Deakin et al., 2019; Lane et al., 2020) and for environmental impact assessments, for example of offshore wind farms on seabird populations (Green et al., 2016). Because the models were constructed in nested form, each complex model would have been able to revert to a simpler mechanistic form during fitting. For example, in model 5, recruitment was dampened by either local or regional density dependence (Equation 9), but if regional dynamics were not the limiting factor, the model would have consistently selected only local dynamics as limiting

TABLE 2 The five nested models listing the five different regulatory scenarios and relevant parameters.

Model	Relevant parameters	Description	DIC
M.1	ν, θ	Null model; system of closed populations; local DD	21,033
M.2	ν, ι, θ $w_{n,t} = \min(1, P_{n,t})$	Metapopulation; local DD; equal redistribution of immigrants	21,094
M.3	ν, ι, θ $w_{n,t} = r_{n,t} P_{n,t}$	Metapopulation; local DD; conspecific attraction	21,032
M.4	ν, η, ι, θ $w_{n,t} = \min(1, P_{n,t})$	Metapopulation; local and regional DD; equal redistribution of immigrants	21,748
M.5	ν, η, ι, θ $w_{n,t} = r_{n,t} P_{n,t}$	Metapopulation; local and regional DD; conspecific attraction	21,020

Abbreviation: DD, density dependence; DIC, deviance information criterion.

colony carrying capacities (i.e., the parameter estimates for η would have been small for all regions). In addition, we also estimated a more customary model selection criterion for each model, the deviance information criterion (DIC) (Spiegelhalter et al., 2002) where a lower DIC is an indication of a more parsimonious model.

Metapopulation capacity and saturation

We calculated the metapopulation carrying capacity, conceptually related “metapopulation capacity” of Hanski and Ovaskainen (2000). This quantity essentially represents an estimate of the number of female breeders the metapopulation can sustain, as the sum of the posterior estimates of the colony carrying capacities (i.e., whichever posterior estimate of local or regional carrying capacity was lower indicating that form of density dependence was relevant in each colony) for each colony in 2016, at the end of the data time series. We also calculated the size of the metapopulation as the sum of the posterior mean colony size estimates of all colonies that existed in 2016, and the metapopulation saturation as the percentage ratio of the metapopulation carrying capacity and the metapopulation size.

RESULTS

Mechanistic form of metapopulation regulation

We compared five increasingly complex metapopulation models with a Poisson growth term and the same five models with a negative binomial growth term to account for overdispersion (e.g., due to missing covariates or aspects of model misspecification). Models that accounted for overdispersion fitted the data better than models with a simple Poisson growth term (Appendix S3: Table S3), thus we focus our presentation on the negative binomial models only for further comparisons.

All model scenarios fit the data well (mean $R_{P,dev}^2$ between 0.962 and 0.975). However, models 3 and 5, in which immigrants were attracted to larger colonies, fitted better (both mean $R_{P,dev}^2 = 0.976$) than models 2 and 4 in which immigrants were distributed evenly between receiver colonies (both mean $R_{P,dev}^2 = 0.962$; Table 2; Appendix S4: Figure S1B). Incorporating regional density dependence improved the model, as model 5 estimated this regulatory form to dominate in more than half of the colonies (Figure 6) instead of reverting to the simpler scenario represented by the nested model 3. Model 5 also had the lowest DIC (Table 2). However, the DIC values

did not differ dramatically (Table 2) and the differences in fit between model 5, model 3, and model 1 were slight (mean $R_{P,dev}^2 = 0.976, 0.976, \text{ and } 0.975$ for model 5, model 3, and model 1, respectively).

Forecast

Despite the small difference in fit and DIC between the models, the future projections for colony trajectories varied markedly between model 5, model 3, and model 1, in particular for colonies in which regional density dependence dominated. Once released from the data, the projected future trajectories for these colonies based on model 1 or 3 (which did not consider regional density dependence) increased drastically compared with the forecast based on model 5 (Figure 3A,B). Consequently, the projected size of the metapopulation at the end of the forecast period in 2036 varied considerably, giving projections of 768,308 and 839,824 female gannets, respectively, under models 1 and 3, compared with 521,449 females projected under model 5. Based on model 5, but not on models 3 or 1, the growth trajectories of most colonies were projected to have leveled off by 2036, the end of the forecast period (Figure 3A,B; Appendix S4: Figure S1).

Out-of-sample predictive ability

The three best-fitting models were able to predict reasonably well when leaving out the last 10 years of the data time series (Figure 4; Appendix S6). The spread of standardized residuals was slightly tighter around zero for model 5, in particular for regionally regulated colonies (Figure 4C) and for older colonies (Appendix S6: Figures S4 and S5), while the distribution of standardized residuals for models 1 and 3 showed slightly more bias and less precision. For all three models, the predictive ability was more variable for the youngest colonies (Appendix S6: Figure S1), and for those showing sudden increases or decreases in size (e.g., Troup Head, Bempton Cliff; Figure 4B) which led to a wider spread in the distribution of residuals for the group of most recently founded colonies (Appendix S6: Figure S2). This may indicate a missing biological feature in the formulation of our growth model for young colonies.

Metapopulation carrying capacity and saturation

Models 1, 3, and model 5 differed considerably in the posterior estimates of the colony carrying capacities, due

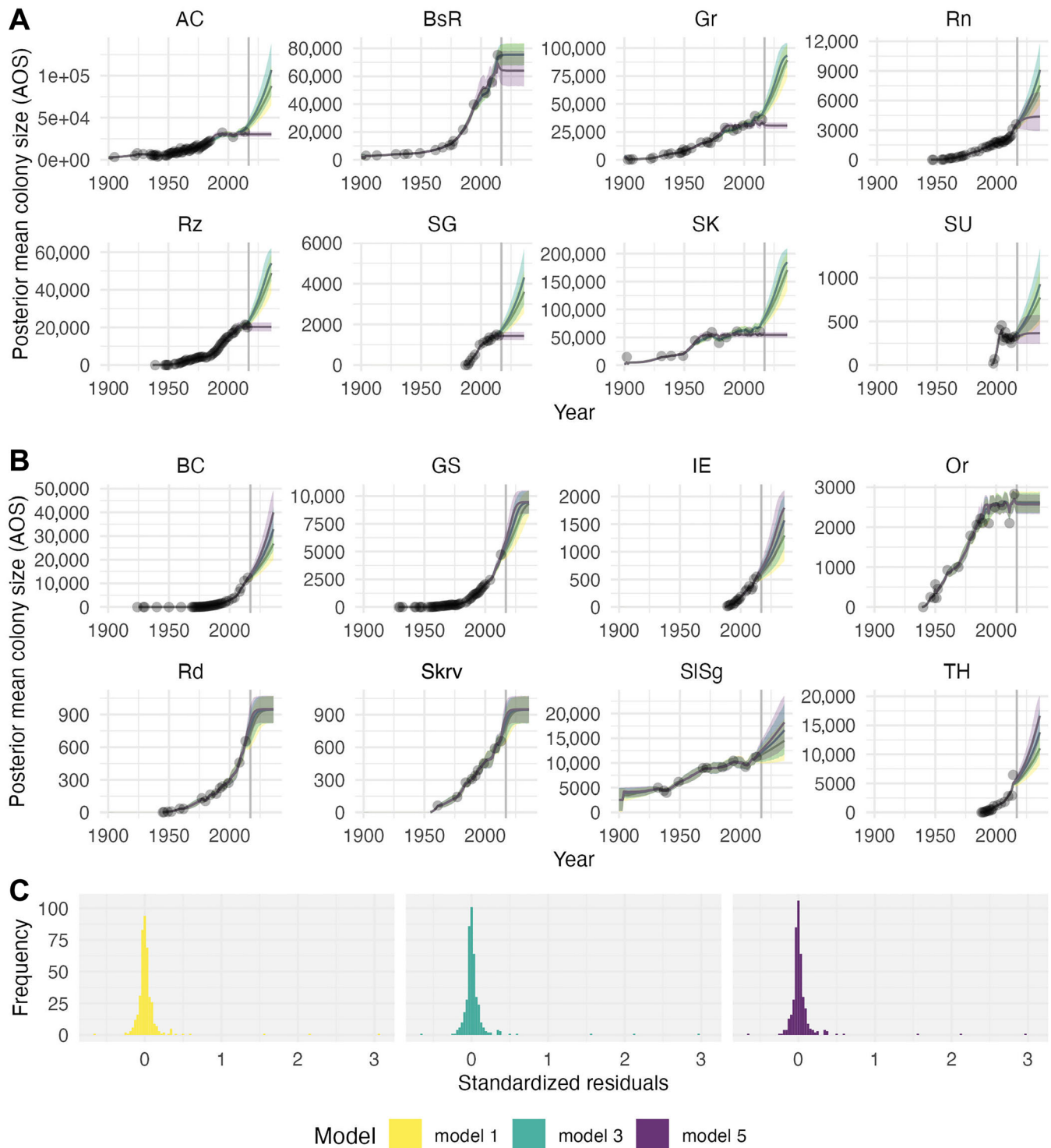


FIGURE 3 Colony time series based on posterior mean colony size estimates for model 1 (closed populations), 3 (conspecific attraction), and 5 (conspecific attraction and regional density dependence) for (A) eight regionally regulated colonies and (B) eight locally regulated colonies. Shaded areas are credible intervals, black dots are colony count data. In each subpanel, colonies appear in increasing order of colony foundation from top left (oldest colony) to bottom right (youngest colony). (C) Frequency distribution of standardized residuals of the census data and the posterior mean colony size estimated by models 1, 3, and 5 for the selected colonies. Appendix S4, Figure S1 shows trajectories and the frequency distributions of standardized residuals for all colonies. AC, Ailsa Craig; AOS, Apparently Occupied Site; BC, Bempton Cliff; BsR, Bass Rock; Gr, Grassholm; GS, Great Saltee; IE, Ireland's Eye; Or, Ortag; Rd, Raudinupur; Rn, Runde; Rz, Rouzic; SG, Storstappen, Gjesvaer; SISg, Sula Sgeir^h; SK, St Kilda^h; Skrv, Skorvikurbjarg; SU, St Ulvøyholmen; TH, Troup Head.

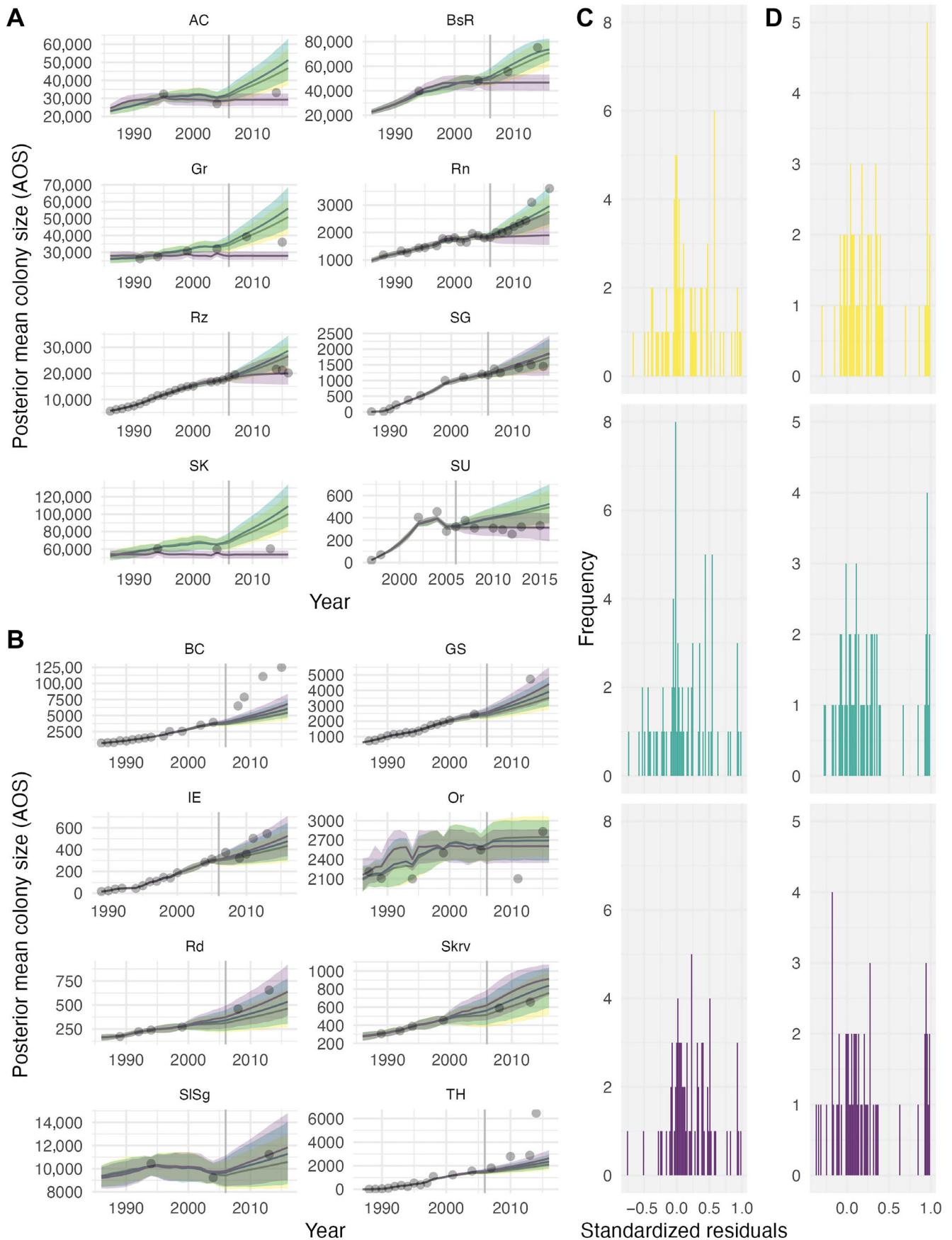


FIGURE 4 Legend on next page.

to the inclusion of joined dynamics of colonies within regions in model 5 (Figure 5). In 2016, approximately one-third of the colonies had reached or exceeded their carrying capacity, and most of these were dampened through regional density dependence (based on model 5; Figure 5C) while under models 3 or 1, very few or none of the colonies had reached the estimated local carrying capacity (Figure 5A,B).

Model scenarios that did not consider regional dynamics thus estimated a much higher metapopulation capacity (summed posterior carrying capacities at the end of the data time series in 2016). The metapopulation carrying capacity in 2016 was estimated at 1,367,352 female gannets (model 3) compared with 645,655 female gannets (model 5). Consequently, the saturation of the metapopulation (the metapopulation size as the proportion of the metapopulation carrying capacity) also differed such that model 3 estimated the metapopulation to be 34% saturated, compared with 65% saturation for model 5.

Density dependence at different spatial scales

We used the posterior local and regional carrying capacity estimates for each colony based on model 5 to illustrate the variation in regulation between colonies and regions, and the relative importance of the regulatory form. By subtracting the local carrying capacity estimate from the regional carrying capacity estimate, we determined which regulatory form dominated in each colony. Both forms of density-dependent regulation were important (Figure 6). More than half of the colonies were regionally regulated, that is, the posterior regional carrying capacity was smaller than the posterior local carrying capacity (Figure 6). Regionally regulated colonies included most of the largest colonies, for example, St. Kilda, Ailsa Craig, the Bass Rock, Grassholm, and Eldey and most of the very small Norwegian colonies. Most colonies on the

Scottish Continental Shelf (Sule Stack, Noss Westray, Hermaness, Fair Isle) and smaller colonies in the Irish Sea, the Western Channel, and Iceland were found to be locally regulated. The strength of the dominance (the magnitude of the numerical difference between regional and local carrying capacity) varied between colonies, for example for St. Kilda the difference between both carrying capacities was >100,000 female gannets, while for Helgoland it was <500 female gannets (Figure 6). The biogeographic regions varied in their composition of colonies with local or regional regulations. Regional regulation dominated in most regions, but the Irish Sea and the Scottish Continental Shelf contained predominantly locally regulated colonies (Figure 6).

DISCUSSION

We developed a mechanistic metapopulation model for a long-lived, colonially breeding seabird species. Novel features of the model included accommodation of more complex life history characteristics and behavior such as targeted dispersal, density dependence, and the integration of multiple spatial scales over which regulatory feedback can operate, thus substantially advancing our understanding of metapopulation structure in seabirds. We based our model on data covering an unprecedented temporal and spatial scale of more than 100 years of colony census data of the entire Northeast Atlantic metapopulation, that covers the area from northern France and northern Germany to Iceland, northern Norway and Western Russia and in 2014 contained 80% of the global breeding population of the Northern gannet (Murray et al., 2015). By constructing and comparing a set of nested models of increasing complexity based on biologically relevant hypotheses of metapopulation connectivity and density-dependent regulation, we illustrate an exemplary process of investigating metapopulation regulation in a colonial seabird that is easily transferable to other colonial species.

FIGURE 4 (A) Predictive ability of model 1 (closed populations), model 3 (conspecific attraction), and 5 (conspecific attraction and regional density dependence), illustrated by (A) eight regionally regulated representative colonies and (B) eight locally regulated representative colonies. We fitted each model to a reduced time series by omitting 10 years of data. Time-series data, posterior estimates of colony size and credible intervals are depicted for the period 1986–2016 for context. A gray vertical line indicates the start of the forecast in 2006. (C) Frequency distributions of standardized residuals for regionally regulated colonies, calculated as the difference between the colony count data for the period between 2006 and 2016 and the posterior mean colony sizes based on model 1, model 3, and model 5, respectively. (D) Frequency distributions of standardized residuals for locally regulated colonies, calculated as the difference between the colony count data for the period between 2006 and 2016 and the posterior mean colony sizes based on model 1, model 3, and model 5, respectively. Note that the frequency distributions in (C) and (D) are truncated to values <−1 for better visibility. The full distribution that includes a very small number of residuals >−1 for all three models is shown in Appendix S6, together with the trajectories of all colonies, and residuals plots categorized by colony foundation year. AC, Ailsa Craig; AOS, Apparently Occupied Site; BC, Bempton Cliff; BsR, Bass Rock; Gr, Grassholm; GS, Great Saltee; IE, Ireland's Eye; Or, Ortag; Rd, Raudinupur; Rn, Runde; Rz, Rouzic; SG, Storstappen, Gjesvaer; SISg, Sula Sgeir^h; SK, St Kilda^h; SU, St Ulvøyholmen; TH, Troup Head.

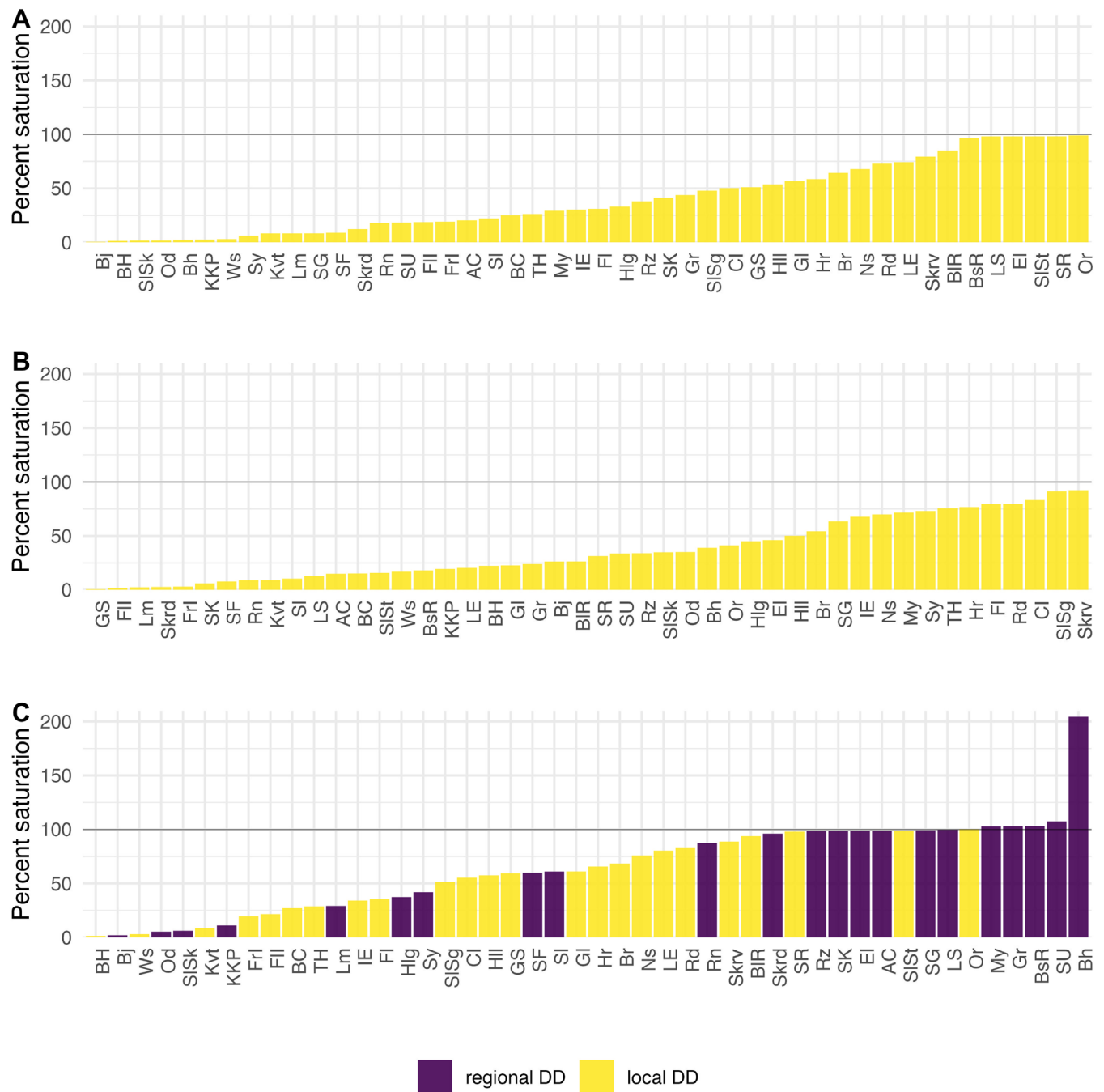


FIGURE 5 Percentage saturation indicates how closely a colony had approached the carrying capacity in 2016 at the end of the time series. The dominant form of density-dependent regulation in each colony was determined by selecting the lower posterior estimates for regional and local carrying capacity, respectively. (A) Posterior estimates based on model scenario 1 (local and regional density-dependent regulation), (B) posterior estimates based on model scenario 3 (local density-dependent regulation), (C) posterior estimates based on model scenario 5 (closed populations, local density-dependent regulation). For colony names associated with abbreviations see Table 1. DD, density dependence.

Generally, we found that our models fitted the data well, as evidenced by high deviance R^2 values for all five scenarios and by a generally similar narrow distribution of standardized residuals around zero. This suggests that the model we developed by closely following the biology of the gannet, for example, the implementation of fecundity, lagged maturity, harvest, and the dampening effect of

density dependence on recruitment, as well as the prior information associated with these parameters, is compatible with the extensive colony census data. However, all model scenarios struggled to predict sudden increases or decreases in the growth of younger and smaller colonies (Appendix S6: Figure S2). This might be because our model did not contain Allee effects (Courchamp et al.,

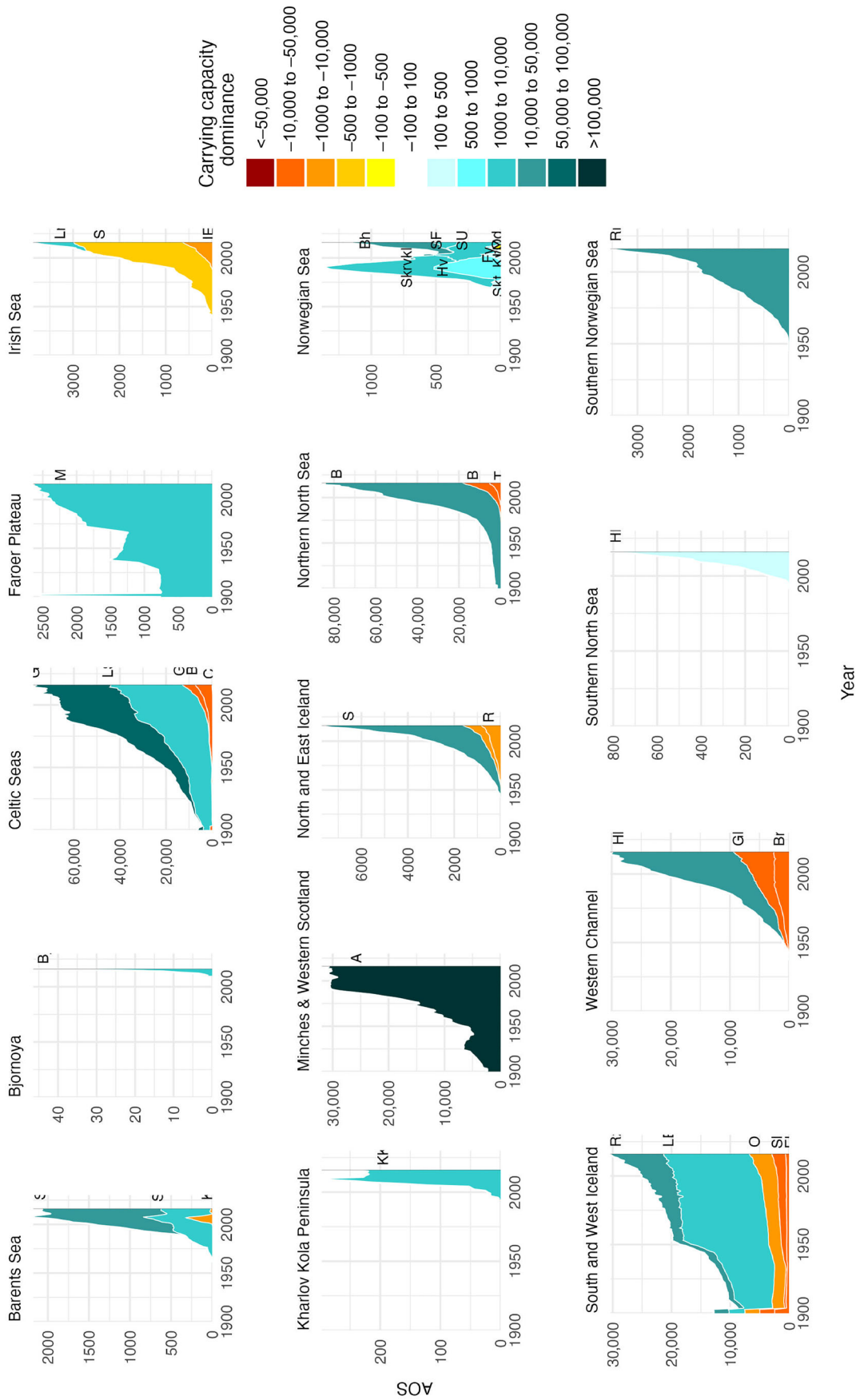


FIGURE 6 Stacked time series of posterior mean colony size estimates based on model 5, for each biogeographic region. The total height of the colored area in each year indicates the number of female gannets in each region, the height within each colored area indicates the number of female gannets in each colony. We calculated the dominance of one of the two forms of density-dependent regulation by subtracting the posterior local carrying capacity estimate from the posterior regional carrying capacity and we used the difference as color gradient for the colony trajectories. Local density-dependent regulation dominates in colonies colored in shades of orange-red, regional density dependence dominates in colonies colored in shades of blue. More saturated colors indicate more pronounced differences (see legend). For colony names associated with abbreviations see Table 1. Note that the y-axis scales vary for better illustration of small colonies. AOS, Apparently Occupied Site.

1999, 2008; Kramer et al., 2018), which would allow modeling reduced growth at low densities and colony extinction below a critical threshold. Such dynamics might dominate the fluctuating growth and extinction patterns of the small colonies in the Norwegian Sea (Figure 6). For instance, Allee-type density-dependent dynamics have been shown to explain slow colonization times of empty patches in metapopulations of the common tern, *Sterna hirundo* (Schippers et al., 2011). Another interesting colony growth model in gannets suggests a contrasting pattern, namely that small colonies might experience a phase of accelerated growth, predominantly fueled by immigrants (Moss et al., 2002). Such “attraction to a recently colonized patch” would not have been modeled by our redistribution function, which redistributed immigrants preferentially to larger colonies (see below). Both these refinements can easily be added to our framework for example, by adding a parameter that impedes recruitment at low densities to implement the Allee effect, and would contribute to improving the ability of the model to predict the more volatile dynamics of younger colonies.

Underappreciated connectivity in seabird metapopulations

Hanski (2004) highlighted the need for a family of models incorporating different mechanistic hypotheses for more complex redistribution forms that govern the connectivity between patches in metapopulations. Here, we compared three different mechanistic hypotheses of the existence and shape of connectivity in the gannet metapopulation, a scenario of closed populations (model 1), equal redistribution of immigrants to all colonies (models 2 and 4) and redistribution of immigrants proportional to the size of the receiver colony (models 3 and 5). We found that models with a simple redistribution function that allocated immigrants equally to all colonies in the network fitted the data less well than models that redistributed immigrants in proportion to the size of the receiver colony or the model of closed populations. Thus, conspecific attraction, where animals use the presence of conspecifics as a cue (Stamps, 1988), played a role in gannet metapopulation dynamics. This mechanism permeates seabird evolution, ecology and behavior, from the evolution of coloniality (Clode, 1993) to the transmission of information on the distribution of food resources (Ward & Zahavi, 1973; Weimerskirch et al., 2010) and the facilitation of pair formation (Szostek et al., 2014). Our findings align with earlier empirical and modeling studies that have highlighted the role of conspecific attraction in coloniality breeding bird species (Breton

et al., 2006; Fernández-Chacón et al., 2013; Podolsky & Kress, 1989; Tenan et al., 2017). In practice, this mechanism explains the persistence of a skewed colony size distribution, with few very large colonies and many smaller ones, that appears characteristic of the gannet.

However, while the model that implemented conspecific attraction fitted the data better than the model of closed populations, as assessed by the DIC, deviance R^2 , and predictive ability, the difference in fit was not pronounced. This underwhelming improvement in the fit of the model with conspecific attraction suggests that immigrants might display more sophisticated behavioral choices than many metapopulation models assume (Hanski & Gaggiotti, 2004), including ours, and thus that there is more specificity required to better capture the complexity of dispersal and immigration in the gannet. There is evidence for more refined mechanisms in some coloniality breeding birds: for example individuals may use patch reproductive success, for example, the number of chicks fledged, as a cue to inform their breeding habitat selection (“performance-based conspecific attraction,” Danchin et al., 1998; Doligez et al., 2002). Alternatively, the presence of prebreeders and recruits may guide the choice of a suitable breeding site (Szostek et al., 2014). Perhaps most importantly, the redistribution function we implemented might be modulated by the spatial scales at which immigrants are likely to move. Connectivity between colonies is, at least partly, influenced by distance in other seabirds. For example, evidence based on mitochondrial DNA from the Northern fulmar, *Fulmarus glacialis*, suggests that the metapopulation is structured in an “isolation by distance” pattern in which first-time breeders return to their natal colony or neighboring colonies, despite high individual mobility (Burg et al., 2003). Distance to the receiver colony also contributed to a reduced probability of settlement for Audouin’s gulls in a study based on detailed mark–recapture histories (Fernández-Chacón et al., 2013) and influenced the dispersal patterns observed in European shags, *Phalacrocorax aristotelis*, and Black-legged kittiwakes (Barlow et al., 2013; Coulson, 2011).

Multiple spatial scales in density dependence

We compared models that included several spatial scales on which density dependence might operate in the gannet metapopulation, addressing calls for process-based predictions of regional population dynamics in the light of the pressing need to understand the direct (i.e., local and immediate) as well as indirect (i.e., regional and delayed) impacts of environmental and anthropogenic change (Lasky et al., 2020). We found support for the

most complex model (model 5) that considered both local and regional density dependence as evidenced by its lowest DIC, however the difference in DIC compared with model 3, the model that considered only local density dependence, was small and the fit of the models to the data was very similar. Interestingly, model 5 had the flexibility to revert to the simpler mechanism of local regulation but estimated that more than half of the colonies were regulated by regional density dependence. Therefore, a scenario of local regulation alone might not capture the biological complexity of density-dependent regulation in the gannet. This suggestion is corroborated by the difference in out-of-sample predictive ability and forecast between the three relevant model scenarios. Model 5 was slightly better at out-of-sample prediction than model 1 and model 3, in particular for older and regionally regulated colonies. Comparing the forecasts, model 1 and model 3 projected steep colony growth increases, in particular for colonies that were regionally regulated under model 5. This suggests that the mechanistic form of the model with local density dependence, once released from the data, modeled a growth trajectory based on an estimated carrying capacity that did not agree with the data.

The lack of a more pronounced difference in fit between these models suggests that the implementation of regional density dependence in our model might not be sufficiently specific or geographically resolved to allow this scenario to distinguish itself more strongly from the simpler mechanistic form. For example, whereas we used a strong prior on local density dependence based on expert estimates of local carrying capacities (i.e., the maximum number of available nest sites in a colony), we did not have similarly informative prior information for the regional carrying capacity and thus regional density dependence. The collation and implementation of such prior information are more complex, since it would require an estimate of colony-specific foraging areas for each colony (Wakefield et al., 2013) that vary over time according to colony size (Furness & Birkhead, 1984; Lewis et al., 2001; Wakefield et al., 2013) so that it is possible to integrate relevant marine resources such as the abundance of forage fish or the distribution and strength of fronts (Scales et al., 2014) into the metapopulation model. Intercolony foraging segregation is characteristic of the gannet, and is common to many seabird species (Bolton et al., 2019). For the species in which such segregations have not been found, regional density dependence could be formulated as a function of joined foraging area and thus total regional population size, rather than the population size of the colony of interest.

Hanski (2004) warns that there is a temptation to impose structure on nature where there is none. This warning appears generally relevant when thinking about

continuous distributions of such things as marine resources in categorical terms. Future work on our framework may fruitfully replace the discrete allocation of colonies to regions, with an integrated statistical model of carrying capacity in terms of spatially and temporally continuous environmental covariates. This would allow evaluation and refined representation of these regional similarities and gradual changes in marine resource richness and composition across space and time.

Methodological considerations—Strengths and limitations

State-space models are an increasingly popular framework for bringing diverse data together with realistic models of population dynamics. Because they distinguish between process variation and observation error, they enable us to estimate “hidden” (latent) states and parameters, formulate complex process models, and model incomplete time series (Auger-Méthé et al., 2021). Previous studies investigating density-dependent regulation in gannets required the use of unbroken time series (Lewis et al., 2001), a limitation that precludes the use of valuable, but intermittent count data. Collecting continuous time series data for entire metapopulations is particularly difficult for seabird species because colonies are often in remote locations and distributed across large geographic areas. These limitations increase survey effort and costs and may require multinational cooperation. From a modeling point of view, time series need to be long enough to detect population regulation. For example, the probability of detecting regulation in a 10-year time series is only ~10% (Turchin, 1995). Methodological work has also highlighted the influential role of the observation error on the resulting estimation of density dependence (Freckleton et al., 2006), much of which is accounted for by using Bayesian state-space methods that explicitly model the observation error as part of the observation model.

There are very few examples of data-driven metapopulation models for seabirds, that is models that consider the dynamics of all seabird colonies within a metapopulation or at least within a distinct region. The metapopulation model for the wandering albatross, *Diomedea exulans*, is an age structured, spatially explicit, stochastic model of the dynamics of three different islands containing 10 colonies in total (Inchausti & Weimerskirch, 2002). A metapopulation study on roseate terns, *Sterna dougallii*, used a multistate integrated population model based on population counts and mark–recapture data at three colonies for a time series of 24 years (Seward et al., 2019). An extensive metapopulation study on Audouin’s gulls built a multistate integrated population model for

69 “patches” based on population census data, individual capture re-encounter data and fertility data for a time series of 27 years (Genovart et al., 2018). The wandering albatross and Audouin’s gull studies used relatively large spatial scales, similar to our study, and all three models captured all or most of the colonies within the respective seabird metapopulation. However, our model added important novelty by estimating density dependence and carrying capacity as parameters, considering multiple spatial scales for regulatory feedback and incorporating mechanistic hypotheses for dispersal. These new features are important if we want to understand the impact of increasingly multifaceted and intensifying environmental change on the gannet and other seabird metapopulations and up-scale current efforts beyond single-colony dynamics.

Appropriate models for conservation

To address the increasingly pressing challenge of understanding the impact of environmental change on populations, we need to work with mechanistic models that consider the relevant processes and the relevant spatial scales to forecast population dynamics (Lasky et al., 2020). Here, we did not compare our models with a scenario that lacked density-dependent regulation, as the evidence for this important process is ubiquitous and strong. However, in practice, population models without density-dependent regulation are still being used in guiding seabird conservation and marine planning (Miller et al., 2019). For example, two recent population models for gannets for the Bass Rock and Grassholm colonies, respectively, used matrix models that did not consider density dependence or immigration (Deakin et al., 2019; Lane et al., 2020), and colony size projections for the Bass Rock and Grassholm were between ~80,000 and ~55,000 female gannets higher, respectively, than the mean posterior colony size estimate of our best-fitting metapopulation model for these colonies. The scale of these discrepancies highlights how important it is that impact assessments are based on biologically realistic models. The same is true for counterfactuals, for example the comparison of population growth scenarios with and without a particular impact, which can be used to inform conservation management decisions.

Our results also show that ignoring density dependence or implementing a form of density dependence that does not capture the complexity of the spatial scales in regulatory dynamics of a metapopulation does not lead to population size assessments that follow precautionary principles. Our three best models produced different estimates for the size and saturation of the individual colonies and the metapopulation as a whole, and they projected different future metapopulation sizes. The

discrepancy between the scenarios is clearly illustrated by the case of the southernmost gannet colony on the island of Rouzic in northern France. While the model considering local regulation only estimated the colony to be ~30% saturated (Figure 5), incorporating regional dynamics showed that this colony had exceeded the regional carrying capacity in the early 2000s, and is since fluctuating around it (Figure 3B). This finding is corroborated by empirical evidence of a disproportionately large foraging effort of gannets at the colony around the same time (Grémillet et al., 2006) and more recent reports of declining survival of adult birds concomitant with a decrease in breeding pairs at the colony (Grémillet et al., 2020; Le Bot et al., 2019). The authors presented evidence that gannets in this colony were limited by the depletion of fish resources through large-scale fisheries in the region (Grémillet et al., 2018; Le Bot et al., 2019).

Seabird metapopulations face a growing number of threats, many of which are linked to the increasing anthropogenic exploitation of the marine ecosystem (Lewison et al., 2012). Many gannet colonies are very remote, not allowing the detailed monitoring of demographic rates and foraging behavior that led to a comparably good understanding of the situation in Rouzic. We show here that for these colonies the information on their status (e.g., saturation) and future size can depend strongly on the mechanistic form of the model used to estimate it. We suggest that a careful mechanistic model comparison approach and identification of key features for model refinement such as presented here also constitute a helpful step toward developing better modeling tools for the challenging conservation management decisions ahead.

Conclusions

We developed a computationally economical metapopulation model that captured the specific characteristics of long-lived colonially breeding species such as seabirds and incorporated regulatory feedback across spatial scales. Ecologically motivated variants of this model produced good fits to the observational data of an exemplar seabird species. We highlighted key refinements for the mechanistic implementation of the spatial structure of regulatory feedback. Our model allowed us to impute long and intermittent time series of census data, discriminate between the different spatial scales and strength of density-dependent regulation at the different scales and make accurate and precise predictions of future population sizes. Our model accounts for some of the most important underlying processes (local and regional density dependence, and the attraction of conspecifics in the redistribution of recruits through the colony network). We consider this model as the basis for an iterative

process of empirical research and model refinement, where the collation of existing data or new research provides more detailed insights into metapopulation regulation in seabirds that can be used to mechanistically extend the current model. Such an iterative process will also help us to understand the processes we need to incorporate to robustly forecast regional scale population dynamics (Lasky et al., 2020).

AUTHOR CONTRIBUTIONS

Jana W. E. Jegliński, Sarah Wanless, and Jason Matthiopoulos conceived the ideas, Jana W. E. Jegliński and Jason Matthiopoulos designed the methodology; Sarah Wanless, Jana W. E. Jegliński, Stuart Murray, Mike P. Harris, Jochen Dierschke, Hallvard Strøm, Svein-Håkon Lorentsen, Arnthor Gardarsson, and Robert T. Barrett collected and collated the data; Jana W. E. Jegliński analyzed the data; Jana W. E. Jegliński led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The gannet colony census data (Jegliński et al., 2022) are available at the Enlighten database of the University of Glasgow at <https://doi.org/10.5525/gla.researchdata.1286>. The metapopulation model (JanaJeglińskiR, 2022) is available in Zenodo at <https://doi.org/10.5281/zenodo.7442402>. The fecundity data set that we used for prior information included all available breeding success data for each year in the United Kingdom, Ireland and the Channel Islands, was collated by the Seabird Monitoring Programme, and is available at <https://jncc.gov.uk/our-work/smp-report-1986-2019> (Joint Nature Conservation Committee (JNCC), 2021). The global classification of marine ecoregions and pelagic provinces spatial data that underlie our biogeographic regions classification is from the Nature Conservancy (2012) and is available at <http://data.unep-wcmc.org/datasets/38>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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