Metapopulation dynamics of Roseate Terns: sources, sinks and implications for conservation management decisions

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Abstract

1. Habitat management to restore or create breeding sites may allow metapopulations to increase in size and reduce the risk of demographic stochasticity or disasters causing metapopulation extinction. However, if newly restored or created sites are of low quality, they may act as sinks that draw individuals away from better quality sites to the detriment of metapopulation size.
2. Following intensive conservation effort, the metapopulation of roseate tern (*Sterna dougallii*) in NW Europe is recovering from a large crash in numbers, but most former colonies remain unoccupied and hence are potential targets for restoration. To inform conservation efforts, we studied the dynamics of this metapopulation with a multistate integrated population model to assess each of the three main colonies for important demographic contributors to population growth rate, source/sink status and possible density dependence.
3. All three study colonies are managed for roseate terns (and other tern species) in similar ways but the demographic processes vary considerably between colonies. The largest colony is a source involved in almost all dispersal, and its growth is determined by survival rates and productivity.
4. Productivity and juvenile apparent survival at the largest colony appear to be density dependent. Although the mechanisms are unclear, this may provide an increasing impetus for emigration of recruits to other colonies in the future.
5. The smallest of the three colonies is a sink, relying on immigration for its growth. Simulation models suggest the metapopulation would be ~10 % larger in the absence of dispersal to the sink colony.
6. This work indicates that, due to variable site quality, aims to enhance both distribution and size of metapopulations may be mutually exclusive. In this case, before future attempts to encourage recolonisation of former sites, assessments of site suitability should be undertaken,

focusing on food availability and isolation from predators to maximise the likelihood of attaining levels of productivity and survival that avoid creation of a sink population to the detriment of the overall metapopulation size.

Key-words: demography, density dependence, dispersal, immigration, integrated population model, metapopulation dynamics, roseate tern, seabirds

Introduction

It is generally accepted that expanding the range of a species through the creation or restoration of suitable habitat will increase population size by increasing the carrying capacity, thereby relaxing density dependent regulation (MacArthur & Wilson, 1967). In addition, within a metapopulation, the creation or restoration of additional, discrete sites may buffer the whole population against the effects of localised events or demographic stochasticity (Hanski & Gyllenberg, 1993).Within a metapopulation there may be both source populations and sink populations (Pulliam, 1988). Newly created or restored sites that are of lower quality than those in the core of the range may act as sinks that draw animals away from better quality sites, leading to a reduction in total metapopulation size (Battin, 2004; Kristan, 2003; Robertson & Hutto, 2006). Sinks may, however, aid persistence of a metapopulation by providing refugia if catastrophic events cause major population reductions at source sites. Investigations of demographic processes operating within a metapopulation should seek to identify and understand source and sink populations in order to help the development of effective management strategies that make best use of limited conservation resources to ensure metapopulation persistence (Furrer & Pasinelli, 2016).

Almost all seabirds aggregate into discrete colonies during their breeding seasons (Rolland, Danchin, & de Fraipont, 1998). There is typically some dispersal of individuals between colonies, which differ in their demographic rates (Clobert, Danchin, Dhondt, & Nichols, 2001). Thus, an entire population of breeding seabirds displays many of the fundamental characteristics of a metapopulation and this may have important implications when devising effective seabird conservation strategies (Esler, 2000). Events such as coastal erosion (Casey et al., 1995) or the introduction of predators (Craik, 1997; Oro, Pradel, & Lebreton, 1999) can lead to large reductions in colony size and even site abandonment (Cabot, 1995; Heubeck, Mellor, Harvey, Mainwood, & Riddington, 1999; Whittam & Leonard, 1999). When some of the individual colonies are very small, there is the additional challenge that demographic stochasticity increases the risk of local colony extinction (Hanski, 1998).

While seabirds generally display high fidelity to breeding sites (Coulson, 2001), terns (Laridae: Sternini) can show relatively high rates of dispersal (Breton, Nisbet, Mostello, & Hatch, 2014) and can move to new colonies readily in response to disturbance or changes in habitat quality (Brindley et al., 1999; Jennings, McGlashan, & Furness, 2012; Spendelow et al., 2016). Removal of large gulls (Laridae: Lari), management of habitat and deployment of decoys and recordings can be used to restore or create new tern colonies (Dunlop, Blokpoel, & Jarvie, 1991; Kress, 1983; Kress, Borzik, & Hall, 2008; Wanless, 1988). Tern colonies have also been successfully relocated by increasing the suitability of receptor sites while discouraging them from their original sites. For example, a colony of 9,000 pairs of Caspian terns (*Hydroprogne caspia*) were encouraged to move (using disturbance and streamer lines) from an estuary where they were eating endangered salmon smolts to an offshore island where they ate marine prey (Roby et al., 2002). Conservationists have the power to manipulate tern distribution, but this power needs to be wielded with caution to avoid undesirable consequences of these actions upon the overall size, structure and functioning of the metapopulation.

The NW Europe metapopulation of roseate tern (*Sterna dougallii*) has been the focus of intensive conservation activity since the late 1980s, following a steep decline from 3,812 pairs in 1968 to 561 pairs in 1987 (Avery, Green, & del Nevo, 1991; Cabot, 1995). The decline has been attributed to several factors acting at the breeding grounds – human disturbance, depredation by gulls and rats, displacement from nesting sites by gulls and high tides and coastal erosion – as well as trapping in the African wintering grounds (Avery et al., 1995). The loss of the largest colony at the time (Tern Island, Co. Wexford, Republic of Ireland) in the 1970s due to erosion meant that the birds had to relocate, but as there was a population crash at the same time it is difficult to ascertain their dispersal from counts alone. Conservation measures to enhance the status of roseate terns in NW Europe (discouraging gulls from nesting, provision of breeding terraces and nest boxes and reducing human disturbance) have been implemented at Rockabill and Lady’s Island Lake in the Republic of Ireland, Coquet Island in England and several sites in Northern Ireland, Wales and Brittany, France (Avery et al., 1991). Management has been most successful at Rockabill: an offshore islet that is isolated from mainland predators and located in an area of high food availability. Following removal of gulls and nesting habitat management that started in 1989, numbers of roseate terns increased rapidly, fuelled by immigration from colonies in Northern Ireland and Wales that were subject to higher levels of predation and disturbance and which were ultimately abandoned (Cabot, 1995). Since 1987, the metapopulation has recovered to 1,921 breeding pairs in 2016, with most pairs breeding at Rockabill. While numbers have partially recovered, the range has not; in 1968 roseate terns bred at 15 colonies (12 with more than 10 pairs) in NW Europe (Cabot, 1995), while in 2016 they bred at just seven colonies, only three with more than 10 pairs.

An ongoing EU LIFE project (LIFE14 NAT/UK/000394 Roseate Tern) aspires to restore roseate tern colonies at previously occupied sites in the belief this will increase the range and size of the metapopulation. However, we need further information on metapopulation dynamics to inform decisions on whether sites should be restored and, if so, which ones. Without this information, restoration attempts may create ecological traps that lure birds to sites at which they fail to produce sufficient surviving offspring due to predation and poor food availability (Kristan, 2003).

We studied the population dynamics of the main NW European colonies of roseate tern to inform the conservation strategy for this species in Europe. The objectives of this study were to (1) estimate the demographic rates (productivity, survival, immigration and emigration) at each colony, (2) identify the demographic rates contributing most to temporal variance in population growth rate at each colony and of the whole metapopulation and (3) compare the population dynamics between the different colonies, assessing whether density dependence is limiting any of the demographic rates. We combined population counts, data on productivity and capture-mark-resight data to construct a multi-state integrated population model (IPM) to help to understand the demographic drivers of temporal variability in population growth rate of roseate terns in NW Europe.

Materials and Methods

Study sites

We studied the population processes of roseate terns at the major colonies in Britain and Ireland: Rockabill, Lady's Island Lake (LIL) and Coquet Island (Coquet). Rockabill (Co. Dublin, Republic of Ireland) comprises two granite islands separated by a channel approximately 20 m wide, with a combined area of 0.9 ha and lying 6 km offshore. LIL (Co. Wexford, Republic of Ireland) is a shallow coastal lagoon, within which roseate terns breed on the 3.1 ha sedimentary island Inish. Coquet (Northumberland, England, United Kingdom) is an island of 7 ha lying 1.2 km offshore. Each colony is a nature reserve and managed to enhance roseate tern conservation, with measures including control of predators, competitors and human disturbance, nest box provision and vegetation management. The proportion of the NW Europe metapopulation that these colonies comprised ranged from 79.8% in 1992 to 97.3% in 2016. The next largest congregation of roseate terns in the metapopulation breeds at several sites in Brittany, France, with the combined number of breeding pairs at these sites during the study period ranging from 14.0% in 1992 to 2.6% in 2016. We did not include the French colonies in our study due to the sparseness of the capture-mark-recapture data collected there. There were 29 sightings of 23 individuals in French colonies between 2007 and 2014 of roseate terns ringed at the three study colonies (there is no resighting data before this period). In comparison, the numbers of roseate terns seen at each study colony over the same period that were ringed at a different colony were 869 for Rockabill, 1457 for LIL and 538 for Coquet. There were 13 sightings of four individual French-ringed terns across the study sites between 1996 and 2016. Since Isle aux Dames was abandoned in 2006 numbers there have been small and of little importance. Ring resighting records within our system and in other metapopulations in the Azores and eastern North America indicate that immigration and emigration into and out of the NW Europe metapopulation is very rare.

Demographic data

From 1992 to 2016, we collected three types of demographic data on roseate tern at each colony: population survey data consisting of counts of breeding pairs, data on productivity and capture-mark-recapture data.

Data on population size are derived from annual nest counts at each colony in the metapopulation. A breeding survey was performed each year at each colony from 1992 until 2016, except for 2000 at LIL. The breeding survey attempted to count all pairs of roseate terns present at each colony and did not include unpaired individuals or juveniles.

Productivity in our study consists of the number of offspring fledged per monitored pair. Daily monitoring (weather permitting) of breeding roseate terns was carried out by wardens. For the number of fledged offspring we use the number of chicks of monitored pairs ringed minus any that were recorded dead before fledging age (reasons included depredation, chilling or starvation). For Coquet, the number of monitored pairs equals the number of pairs counted in the census. In most years at Rockabill and some years at LIL a sample of pairs, considered representative of each colony were monitored, while in other years all pairs were monitored. These efforts were designed to estimate as accurately as possible the number of chicks surviving to fledging after ringing. In the population model, all breeding is assumed to be by adults aged 3 years or over.

Each year from 1992 to 2016, attempts were made to capture all roseate tern chicks at each colony. All captured chicks were marked with uniquely numbered national metal rings and field-readable rings marked with an individual code of four alphanumeric characters stamped on both sides. Only chicks marked from 1992 until 2013 were included in the study because we assume an age of first breeding of three years (Ratcliffe, Nisbet, & Newton, 2004) and exclude sightings of birds at one and two years old. Chicks which died before fledging were not included in the dataset. The unique ring codes of marked individuals were read by observers using telescopes from fixed and mobile hides at each colony throughout each breeding season, except for 1995, 2000 and 2001 at LIL, when access restrictions were in place.

Statistical analysis

We developed a multistate IPM (Schaub & Abadi, 2011) with age classes and time variation using the general structure outlined by Kéry & Schaub (2012) to estimate population size and demographic rates of the three roseate tern colonies in Britain and Ireland. Within our IPM, the likelihoods of the three data sets (breeding population counts, productivity and capture-mark-resighting (CMR) data) were formulated jointly. The model assumes an equal sex ratio amongst chicks hatched, no sex differences for survival, movement only occurs between the three study colonies (except for migration to and from the wintering grounds) and birds start breeding at age 3 (Ratcliffe et al., 2004).

The analysis of the time series of population counts was conducted with a state-space model consisting of a set of state process equations that describe the development of the number of individuals in different states as a function of demographic rates. We built a pre-breeding census model with a total of 36 states, each of which described a combination of age, colony in the previous time step and colony in the current time step. Table S1 (Supporting Information) provides the state definitions. In our models, birds of age 3+ are considered part of the breeding population.

To enable demographic stochasticity to be modelled, we used Poisson and binomial distributions to describe the dynamics of the true population size over time with a pre-breeding projection model (Schaub et al., 2012). Thus, the number of fledglings in year *t* depended on the number of breeding (age 3+) females in year *t* and productivity in year *t*. The number of age 3, age 4 and age 5+ females at each colony in each year depended on the numbers of each age group in the preceding year (or three years before in the case of age 3 females), age- and colony-specific survival rate and age- and intercolony-specific dispersal rate. The demographic parameters are defined in Table S1. The pre-breeding projection model equations for each study site are given in Appendix S1. The projection model equations for each site were constituents of the multistate IPM. The observation process describes the relationship between the observed population counts and the true population size, using a Poisson distribution. Productivity was analysed with random effects for time, with a normal distribution and log link. Age- and colony-specific emigration and immigration rates were derived parameters, based on the total number of age- and colony-specific emigrants or immigrants in year *t* + 1 divided by the total breeding population of the colony in year *t*. Population growth rate (λ_t) was a derived parameter, calculated from the total breeding population at the colony in year *t* +1 divided by the total breeding population at the colony in year *t*.

We estimate survival of individuals using multistate models of CMR data. Our CMR data set consists of 20,702 individuals initially marked as chicks and which were not recorded as dying before fledging (17,636 at Rockabill, 1,707 at LIL and 1,359 at Coquet). We analysed the CMR data with a multistate model (Kéry & Schaub, 2012; J.-D. Lebreton, Burnham, Clobert, & Anderson, 1992) with a multinomial likelihood. We used this model to estimate the parameters *S* (survival probability: annual or from fledging to age 3, dependent on subscript as described below), ψ (dispersal probability) and *p* (resighting probability). We based the model on age-structured models described by Kéry & Schaub (2012: chapter 9) and (Weegman et al., 2016). While goodness of fit (GOF) tests for IPMs remain unavailable (Lee et al., 2015), it is recommended that component datasets are assessed for GOF to the model (Kéry & Schaub, 2012; Schaub & Abadi, 2011). Goodness of fit tests with programme U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) indicated the existence of 'trap dependence' and transience within the data (Table S3). Following Ratcliffe, Newton, et al., (2008), we dealt with transience by considering three age classes for *S* and ψ: juvenile (the period fledging to age 3; subscript juv, reported in the text as annual juvenile survival after calculating the cube-root), age 3 (subscript age3) and age 4+ (subscript age4+). We included six parameters for p, which consisted of age since last recorded (age 0, age 3 or age 4+) and, to account for 'trap dependence', time since last recorded (previous year or before previous year; for birds last recorded as age 0, the previous year was three years previous because birds are not resighted at age 1 and 2 in our model). We considered it possible that birds in their first year of breeding may have a lower resighting probability than older birds for reasons including breeding failure, later arrival and less optimal nesting locations. Any sightings of age 1 or 2 birds were discarded and we assume that no birds of age 1 or 2 return to the breeding colonies. To enable fast analysis times, we summarised the data in the m-array format, with separate m-arrays for each age class. The parameters S_{juv}, S_{age3+}, ψ_{juv} and ψ_{age3+} were modelled with random effects for time, with normal distributions and logit links. S_{juv} was used to derive juvenile annual survival probability during the model run for the purposes of presentation. We estimated resighting probability for each colony and year independently of each other (i.e. with fixed effects).

We used Markov chain Monte Carlo (MCMC) methods within a Bayesian framework to estimate the model parameters. We used uninformative priors for all parameters as we did not want to influence them with prior knowledge (see Appendix S2). The uniform priors for mean productivity were bounded between zero and two because roseate terns lay a maximum of two eggs in a clutch and are single brooded. IPM analysis was conducted with JAGS 4.2.0 (Plummer, 2003) called via jagsUI (Kellner, 2016), a package for program R 3.2.5 (R Development Core Team, 2016). We ran 3 chains with 800,000 iterations, of which 600,000 iterations were discarded as a burn-in and used a thinning rate of 50. This yielded a total of 12,000 posterior samples for each parameter. The chains were well-mixed and converged satisfactorily ($\hat{R} < 1.05$). The JAGS code for running the model is provided in Appendix S2.

To assess the impact of the demographic parameters on λ, we computed the posterior distributions of the correlation coefficients (Schaub et al., 2012). The strength of these correlations indicate the strength of the contribution of the temporal variation in demographic parameters to the temporal variation in λ over the study period (Freeman, Robinson, Clark, Griffin, & Adams, 2007; Robinson, Green, Baillie, Peach, & Thomson, 2004). We used the mode to describe the posterior distributions of the correlation coefficients because most of them were very skewed. We also calculated the probability that the correlation coefficients were greater than zero [$P(r > 0)$]. We performed equivalent correlations with the same set of demographic parameters and population size instead of λ to assess whether there was evidence for density dependence (Schaub, Jakober, & Stauber, 2013).

The source or sink status of a colony can be determined by calculating its contribution to the wider population network and this depends on productivity, (apparent) survival and emigration rates (Runge, Runge, & Nichols, 2006). To investigate the source-sink dynamics between the colonies, we used the posterior samples of demographic rates obtained from the IPM to re-run the population process equations described above 12,000 times (the number of posterior samples), but without any emigration or immigration between colonies. In this projection without dispersal, the states consist of age groups at each colony. The breeding population size at each colony for the first three years in the projection are copies of the posterior samples from the IPM. For each subsequent time-step, the number of individuals in each state is determined by the posterior samples of productivity, S_{juv}, S_{age3} and S_{age4+} from the IPM. We make the assumption that mean productivity (and survival) at the colonies remains unchanged when dispersal was fixed to 0. A colony was determined to be a source if its population increased in the absence of dispersal and a sink if its population decreased in the absence of dispersal.

Results

Temporal patterns in demographic parameters

The number of pairs of the three colonies combined increased from an estimate of 496 (95% CRI: 454-540) pairs in 1992 to an estimate of 1,844 (95% CRI: 1,768-1,922) pairs in 2016. The populations of all three colonies increased over the study period (Rockabill: from 373 (95% CRI: 338-411) breeding pairs in 1992 to 1,538 (95% CRI: 1,466-1,611) breeding pairs in 2016; LIL: 85 (95% CRI: 68-104) to 203 (95% CRI: 181-226); Coquet: 38 (95% CRI: 27-51) to 103 (95% CRI: 88-118)) (Fig. 1).

Resighting probability was higher at age 4+ than age 3, when birds had been observed the preceding year. (Fig. S1, Supporting Information). Resighting probability also varied by colony and year (Fig. S1).

Productivity was highest at Rockabill (Table 1, Fig. 1). Productivity varied considerably at Rockabill and LIL but varied little at Coquet (Table 1, Fig. 1). Annual survival rates were higher for age 3 and 4+ than juvenile birds and varied by colony (Table 1, Fig. 1). Juvenile annual survival fluctuated moderately at Rockabill and LIL (Fig. 1). From 1995 to 2010, juvenile survival at Coquet was particularly low (0.59 (95% CRI: 0.43-0.73)) compared to the other colonies; the average for the remaining years at Coquet was 0.72 (95% CRI: 0.45-0.81) (Fig. 1). Age 3 and age 4+ survival were higher at Rockabill and LIL than Coquet (Table 1, Fig. 1). Rates of emigration and immigration were highest at LIL and Coquet (Table 1, Fig. 2; note different y-axis scales). At Rockabill, juvenile emigration generally exceeded immigration with the opposite occurring at LIL and Coquet (Table 1, Fig. 2). At Rockabill and LIL, age 3 and 4+ emigration balanced relatively with immigration overall, although not on an annual basis (Table 1, Fig. 2). At Coquet, age 3 and 4+ immigration exceeded emigration in several years, with balance between emigration and immigration in other years (Fig. 2). The estimated actual number of annual emigrants from and immigrants to each colony, on which the emigration and immigration rates are based, are illustrated in Fig. S2.

Source-sink dynamics

There were striking differences in the dispersal of pre-breeding and breeding terns (Fig. 3). There was relatively high dispersal of pre-breeding terns from Rockabill to LIL and to Coquet. There was considerably lower dispersal of pre-breeders towards Rockabill, although the numbers as a proportion of the source colony sizes were higher than from Rockabill (Fig. 3). The average number of age 3 and age 4+ birds dispersing from Rockabill to LIL and Coquet was similar to the numbers moving in the opposite direction, despite the much greater source population of Rockabill.

Population growth rate (λ) at all three colonies tended to be positive (mean λ calculated as the regression of population size over time) (Table 1). The population of Rockabill grew quite steadily while the populations of LIL and Coquet experienced more fluctuations (Fig. 1). Fixing dispersal probability to 0 resulted in a λ above 1 at Rockabill and LIL, and a λ below 1 at Coquet (Table 1), demonstrating that Rockabill and LIL have been self-sufficient and population sources while the internal demographic rates of Coquet have been insufficient to sustain its population, which has acted as a sink. Fixing dispersal probability to 0 resulted in a higher projected λ at Rockabill and a lower projected λ at Coquet, with no change at LIL (Table 1, Fig. 4). λ with and without emigration and immigration at Rockabill fluctuated similarly over time, although the population size was predicted to be larger in the absence of emigration and immigration, with a probability of 1 (2,441 (95% CRI: 2,072-2,794) pairs vs 1,538 (95% CRI: 1,466-1,611) pairs modelled with emigration and immigration). In contrast, at the two smaller colonies of LIL and Coquet, fixing dispersal probability at 0 resulted in a great reduction in annual fluctuations in predicted λ (Fig. 4), showing the large effect of emigration and immigration on population dynamics at these colonies. The number of pairs at LIL with dispersal fixed at 0 was projected to reach 253 (95% CRI: 122-417) by 2016, with a 0.70 probability that this is larger than the 202 (95% CRI: 181-226) pairs modelled with emigration/immigration. At Coquet, fixing dispersal to 0 resulted in a continual decline in predicted population size, showing that Coquet has relied on immigration for population growth. Without emigration/immigration, the Coquet colony was projected to fall to 10 pairs (95% CRI: 5-16) by 2016, with a probability of 1.0 that this was lower than the 102 (95% CRI: 88-118) pairs modelled with emigration/immigration. In summary, by 2016, net migration appears to have reduced the population size at Rockabill, had little impact at LIL and led to an increase in the population size at Coquet, while fixing dispersal to 0 within the model resulted in a greater projected metapopulation size of 2,703 (95% CRI: 2,344-3,026) compared to 1,844 (95% CRI: 1,768-1,922) in the original model, with a probability of 1 that the population size was larger without dispersal.

Correlations of demographic parameters and annual population growth rate

At Rockabill, the strongest positive correlations with annual population growth rate, λ, were with juvenile survival [$r = 0.59$; $P(r > 0) = 1$] and age 4+ survival [$r = 0.66$; $P(r > 0) = 0.97$] and productivity [$r = 0.42$; $P(r > 0) = 1$] (Table 2, Fig. 5). λ at Rockabill also correlated positively with age 4+ immigration [$r = 0.31$; $P(r > 0) = 0.96$], but less strongly (Table 2, Fig. 5). At LIL, the strongest positive correlation with λ was with age 4+ immigration [$r = 0.52$; $P(r > 0) = 1$; Table 2, Fig. 5]. λ at LIL also correlated positively with juvenile survival [$r = 0.36$; $P(r > 0) = 1$], juvenile immigration [$r = 0.32$; $P(r > 0) = 0.98$] and age 3 immigration [$r = 0.35$; $P(r > 0) = 1$] (Table 2, Fig. 5). At Coquet, λ correlated strongly and positively with juvenile immigration [$r = 0.72$; $P(r > 0) = 1$], age 3 immigration [$r = 0.56$; $P(r > 0) = 1$] and age 4+ immigration [$r = 0.53$; $P(r > 0) = 0.99$] (Table 2, Fig. 5).

λ of the metapopulation (all three colonies combined) correlated positively and significantly with juvenile and age 4+ survival at Rockabill [$r = 0.51$ (95% CRI: 0.27, 0.65); $P(r > 0) = 1$ and $r = 0.34$ (95% CRI: 0.07, 0.56); $P(r > 0) = 0.98$] and productivity at Rockabill [$r = 0.43$ (95% CRI: 0.24, 0.59); $P(r > 0) = 1$] (Fig. 6). The demographic parameters are plotted against λ at each colony in Figs S3-S5 and for each colony against λ for the three colonies combined in Fig S6.

Correlations of demographic parameters and population size (assessing density dependence)

Population size was negatively correlated with juvenile survival [$r = -0.26$; $P(r > 0) = 0.99$] and productivity [$r = -0.32$; $P(r > 0) = 0$] at Rockabill (Table 3). Population size was negatively correlated with emigration and immigration for several age classes at all the colonies (Table 3). The decrease in immigration rates with increasing population size reflects the reduced number of dispersing individuals relative to overall population size. Population size correlated positively with the number of juvenile emigrants and age 3 immigrants at Rockabill, age 3 emigrants and juvenile immigrants at LIL and juvenile, age 3 and age 4+ immigrants at COQ (Table S2). Population size did, however, correlate negatively with number of age 4+ immigrants at Rockabill and age 4+ emigrants at LIL (Table S2). The demographic parameters are plotted against population size at each colony in Fig S7-S9.

Discussion

Our IPM of the three major roseate tern colonies comprising the NW Europe metapopulation confirmed that the largest colony, Rockabill (1,538 pairs in 2016; 83% of the total), is self-sustaining and a source of terns for the other colonies. The smallest and most remote colony, Coquet (103 pairs in 2016; 6% of the total), has depended on immigration for much of its growth and has acted as a sink. Here, immigration has exceeded emigration, and mortality has exceeded local recruitment over much of the study period. Immigration was a major factor behind population growth of the third colony, LIL (203 pairs in 2016; 11% of the total), but overall this colony has been a migration neutral.

Resighting probability varied annually and between sites, which can be explained by variation in effort devoted to tern ring reading by site and year. Resighting probability at Rockabill declined over time, which may be due to ring reading effort not increasing in proportion to population size. The lower resighting of age 3 birds could be due to them: (1) being absent from the colonies, (2) being at a colony but not breeding and therefore spending less time there, (3) breeding but failing early and therefore having fewer chances to be seen and (4) breeding at the edge of the colony, where the likelihood of detection is lower. The former two of these reasons relate to non-breeding and the latter two do not, ruling out possible use of resighting probability as a proxy for breeding propensity. Breeding propensity is assumed to be 100% for all birds of age three and over in the model, which is a necessary assumption because only a minority of tern detections were confirmed as breeders (c.f.

Lebreton et al. 2003; Szostek et al. 2014). The existence of age 3+ non-breeders would lead to an over-estimation of the number of fledglings produced which could bias population size estimates upwards or juvenile survival rates downwards. Since the productivity data were very close to the modelled estimates, breeding population estimates tracked population count data very closely and juvenile survival compared well to roseate terns in the NW Atlantic (Nisbet, Monticelli, Spendelow, & Szczys, 2016; Spendelow, Nichols, Hines, Lebreton, & Pradel, 2002), any bias in the model caused by non-breeding amongst age 3+ females appears negligible.

Our modelling suggests that dispersal within the metapopulation has limited the increase in the number of breeding pairs. These population projections do not, however, account for the possibility that density dependence of certain demographic parameters may have imposed stronger constraints on the size of source colonies in the absence of dispersal. We found evidence of density dependent regulation of productivity and juvenile survival at Rockabill. Density dependence acting on juvenile survival at larger colonies has also been reported for roseate terns in the NW Atlantic metapopulation (García-Quismondo, Nisbet, Mostello, & Reed, 2018). The likely mechanism for density dependent productivity and survival at Rockabill is increased competition for limited food supplies, leading to poorer chick and fledging condition and/or poorer food availability for young birds post-fledging, with consequent carryover effects (O'Connor, Norris, Crossin, & Cooke, 2014) into the non-breeding season. The higher dispersal of pre-breeders from Rockabill compared to breeders may also reflect density dependence. With the increasing size of the Rockabill population, young, inexperienced individuals may gain fitness benefits by moving from Rockabill to lower quality sites with reduced competition (Hamilton, 1964a, 1964b; Morris, Lundberg, & Ripa, 2001).

From 1960 to 1981 only a small proportion of the metapopulation bred on Rockabill, where large gulls displaced and predated on terns (Cabot, 1995). Since then, management has reduced the level of predation and the roseate tern numbers at Rockabill increased; unpublished ring resighting data indicates that this rise in the 1980s was due to terns moving there from abandoned former colonies.

Our results confirm that the colony has been a source since at least 1992 (the start of this study), with the average productivity of 1.22 considerably higher than at the other colonies in this metapopulation, as well as higher than NW Atlantic colonies, where average productivity ranges from 1.06 to 1.17 (Burger *et al.* 1996; Nisbet & Ratcliffe 2008; Hays 2017). Tern breeding success is sensitive to variation in food supply (Crawford, 2009; Dänhardt & Becker, 2011; Safina, Burger, Gochfeld, & Wagner, 1988) and the high mean productivity at Rockabill indicates high food availability near the colony.

Since 2009 there has been an almost continual fall in productivity at Rockabill while the colony grew by ~600 pairs (Fig. 1). Relatively high predation of tern chicks by large gulls, noted by Rockabill field staff in some years between 2009 and 2016, could be a factor. Increased foraging competition or depletion of fish stocks due to the increase in breeding terns may also have contributed to the decline in productivity, as found in other seabirds (Birt, Birt, Goulet, Cairns, & Montevecchi, 1987; Hunt, Eppley, & Schneider, 1986; Lewis, Sherratt, Hamer, & Wanless, 2001). Nesting habitat creation and provision of boxes at Rockabill has, by design, outpaced population expansion, removing an alternative candidate mechanism by which breeding density might negatively affect productivity.

Despite intensive efforts since 2000 to improve conditions for roseate terns at Coquet, this colony has been a cryptic sink (Weegman et al., 2016). Increasing numbers have been fuelled by immigration and counts of the breeding numbers alone would not have detected this. The average productivity of 1.02 is similar to LIL (1.03) and both of these colonies are at the low end of productivity recorded at the main colonies in the NW Atlantic. Possibly more significantly, from 1995-2010, the average annual survival of juveniles at Coquet was 0.59: lower than at Rockabill and LIL. Exploration of the reasons for low demographic rates at Coquet should include comparative studies of provisioning rates, diet and fledging weights. The period of low juvenile annual survival at Coquet is not accompanied by low age 3 and age 4+ survival, suggesting a higher risk of mortality for birds in the interval from 0 to 3 years old than for birds 3 years and older. Most young birds remain in their African wintering grounds until at least age 2 and could therefore be disproportionately affected by variation in food availability or hunting there. However, neither juvenile nor age 3 and age 4+ survival rates were correlated between any pair of colonies and, as we believe the birds to winter in the same areas (Ratcliffe & Merne, 2002), we would expect such correlations if factors in the wintering grounds had strong impacts on annual variability of survival rates. It should be noted that the figures for juvenile survival are likely to be biased downwards – and productivity upwards – to some extent as although we removed those ringed chicks known to have died before fledging from analysis, some will inevitably have been overlooked.

Productivity at LIL was highly variable, which likely reflects sporadically heavy predation by mammals such as rats (*Rattus norvegica*) and stoats (*Mustela erminea*), which do not have far to travel to this inshore colony, as well as various avian predators. While productivity did not correlate with annual population growth rate at LIL, high predation (which reduces productivity) may have been a cue for roseate terns to disperse from LIL and may have resulted in the sporadically high emigration from LIL to Rockabill (Fig. 2), as has been documented in seabirds previously (Oro et al., 1999). Rockabill and Coquet, by contrast, are offshore and safe from mammalian predators.

Dispersal rates within the metapopulation exhibited substantial annual variation and correlated with population growth rates of each colony. The finding that immigration rates were the most important correlates with population growth rate at Coquet and LIL is consistent with the closely-related common terns at the Banter See colony (Szostek et al., 2014). Rockabill differed in that survival and productivity were the most important determinants of population growth. Given the very large relative size of the Rockabill colony, large proportions of birds from LIL or Coquet would need to immigrate to have a significant impact on Rockabill's population growth. Greater numbers of terns that fledged on Rockabill recruited to LIL and Coquet than moved in the opposite direction, which could reflect density dependence at Rockabill and/or attractiveness of LIL and Coquet to younger birds. Availability of local recruits was suggested to be the main driver of immigration in common terns at Banter See, also in the NE Atlantic (Szostek et al., 2014), but of our three colonies of roseate terns, the most local recruits are found at the very large Rockabill colony, which received fewer recruiting immigrants than the smaller colonies (Fig. 3).

Our data suggest that the colony at Coquet would disappear without immigration from Rockabill. LIL is the only other source colony in the metapopulation, but the threat from predation is higher than at Rockabill or Coquet. The availability of multiple potential breeding locations (hosting other breeding tern species) within a region allows colonies of roseate terns to respond to changing levels of predation or disturbance by moving to alternative sites (Cabot, 1995; Spendelow et al., 2016). While Rockabill is safe from erosion and flooding, and management reduces predation and almost eliminates nest site competition by gulls, a catastrophic stochastic event here is not impossible and would likely be devastating for the overall roseate tern metapopulation. Sink sites such as Coquet can act as refugia for terns that have lost former breeding colonies, either temporarily or permanently, to a catastrophic event, thereby helping the metapopulation to survive.

Variable site quality can affect the success of efforts to restore animal populations within a metapopulation. In the case of roseate terns, our results highlight the importance of choosing sites for restoration work where assessment suggests a high likelihood of attaining sufficiently high levels of productivity and survival to avoid creation of further sink colonies. Identifying such sites is challenging in the absence of current breeding roseate terns, but colonisation apparently requires an established common tern (*Sterna hirundo*) colony (Nisbet & Spendelow, 1999), while the risk of incursions by most mammalian predators from the mainland can be assessed relatively easily by considering the distance from the mainland shore (Ratcliffe, Craik, Helyar, Roy, & Scott, 2008; Ratcliffe, Mitchell, Varnham, Verboven, & Higson, 2009). Distance from shore (and hence water depth) tends to be inversely related to food availability for terns (e.g. Monaghan 1996), however, so managers need to trade-off these conflicting demands when selecting sites for restoration. Studying the foraging success and productivity of common terns at candidate sites may help to identify those with sufficient food availability within foraging range and without significant predation. Conservationists have considerable power to manipulate tern distributions (Dunlop et al., 1991; Kress, 1983; Roby et al., 2002) and could for example remove nest boxes at Rockabill to increase density dependent competition for nesting sites, with the ultimate goal of encouraging emigration of young birds to new sites that have been prepared for them. Our study indicates that such an approach may lead to a reduction in metapopulation size because of the high productivity achieved by roseate terns on Rockabill and the low productivity and survival elsewhere i.e. at Coquet. However, with the appearance of density dependent regulation at Rockabill it is possible a growing number of individual terns will gain fitness benefits by emigrating to other colonies, which could also be beneficial for the size of the overall metapopulation, provided conditions at receptor colonies are sufficiently favourable.

In conclusion, habitat management to restore or create breeding sites may allow metapopulations to increase in size and reduce the risk of extinction caused by demographic stochasticity or disasters. However, it is not always straightforward and considerable resources may also be spent unwittingly managing sink populations, to the detriment of overall metapopulation size. To avoid this, we recommend that the suitability of potential sites for colony restoration should be evaluated prior to attempts to restore colonies. In the case of roseate terns, evaluations should include assessments of: safety from mainland-based predators, the risk of site loss due to coastal erosion, the diet, provisioning rate, fledging weight and ideally also the productivity and juvenile survival of any other tern species already nesting at potential recolonization sites. The insights gained from our integrated population model suggest that effective management of other small metapopulations of conservation concern would be enhanced by investigations of this kind, and highlight the importance of collecting long-term, multi-site demographic data that allow such insights.

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Authors' Contributions

AS, NR, SN, RC, PM and MB conceived the ideas and designed methodology; NR, SN, PM, TC and WD collected the data; AS analysed the data; AS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

The roseate tern population data presented here will be available from the Dryad Digital Repository https://doi.org/xxxx/dryad.xxxx (Seward *et al*, 2018). These data include the population counts, fledgling counts and number pairs for which productivity was monitored, and capture–mark-recapture data.

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Table 1. Posterior means and 95% credible intervals (in parentheses) of demographic rates at the three colonies, averaged over the whole study period (1992-2016).

	Colony		
Demographic rate	Rockabill	LIL	Coquet
Productivity	1.223 (0.673, 1.706)	1.032 (0.129, 1.708)	1.018 (0.767, 1.283)
Survival juvenile	0.772 (0.658, 0.899)	0.751 (0.64, 0.842)	0.628 (0.448, 0.808)
Survival age 3	0.846 (0.763, 0.915)	0.883 (0.583, 0.998)	0.807 (0.631, 0.943)
Survival age 4+	0.84 (0.754, 0.916)	0.82 (0.687, 0.923)	0.782 (0.667, 0.876)
Emigration juvenile	0.024 (0, 0.061)	0.068 (0, 0.304)	0.032 (0, 0.24)
Immigration juvenile	0.01 (0, 0.039)	0.098 (0, 0.337)	0.167 (0, 0.6)
Emigration age 3	0.007 (0, 0.034)	0.033 (0, 0.149)	0.034 (0, 0.167)
Immigration age 3	0.006 (0, 0.026)	0.033 (0, 0.235)	0.058 (0, 0.321)
Emigration age 4+	0.011 (0, 0.044)	0.074 (0, 0.479)	0.055 (0, 0.196)
Immigration age 4+	0.016 (0, 0.098)	0.072 (0, 0.6)	0.072 (0, 0.294)
Population growth rate	1.055 (1.05, 1.061)	1.038 (1.017, 1.06)	1.057 (1.042, 1.072)
Projected population growth rate without dispersal	1.080 (1.074–1.087)	1.036 (1.010-1.062)	0.930 (0.908, 0.952)

Table 2. Posterior modes and 95% credible intervals (in parentheses) of correlation coefficients between demographic rates and population growth rate at the three colonies. Correlations with a probability >0.95 of being positive or negative are marked with *.

	Correlation with population growth rate		
Demographic rate	Rockabill	LIL	Coquet
Juvenile survival	0.585 (0.453, 0.683)*	0.356 (0.004, 0.584)*	0.062 (-0.195, 0.331)
Age 3 survival	0.144 (-0.280, 0.414)	0.073 (-0.347, 0.346)	0.009 (-0.358, 0.368)
Age 4+ survival	0.365 (0.058, 0.565)*	0.272 (-0.204, 0.548)	0.147 (-0.229, 0.465)
Productivity	0.422 (0.281, 0.541)*	0.217 (-0.085, 0.415)	0.141 (-0.189, 0.430)
Juvenile emigration rate	-0.001 (-0.211, 0.550)	0.304 (-0.005, 0.558)	-0.322 (-0.482, 0.108)
Age emigration rate	-0.169 (-0.397, 0.124)	-0.345 (-0.545, 0.196)	-0.171 (-0.428, 0.201)
Age 4+ emigration rate	-0.497 (-0.696, -0.288)*	-0.704 (-0.781, -0.538)*	-0.154 (-0.368, 0.244)
Juvenile immigration rate	0.163 (-0.178, 0.640)	0.319 (0.076, 0.536)*	0.721 (0.437, 0.839)*
Age 3 immigration rate	0.146 (-0.189, 0.370)	0.351 (0.172, 0.625)*	0.563 (0.236, 0.762)*
Age 4+ immigration rate	0.307 (0.015, 0.488)*	0.707 (0.523, 0.819)*	0.529 (0.160, 0.781)*

Table 3. Posterior modes and 95% credible intervals (in parentheses) of correlation coefficients between demographic rates and population size at the three colonies. Correlations with a probability >0.95 of being positive or negative are marked with *.

	Correlation with population size		
Demographic rate	Rockabill	LIL	Coquet
Juvenile survival	-0.261 (-0.414, -0.079)*	0.162 (-0.158, 0.446)	-0.087 (-0.33, 0.130)
Age 3 survival	-0.062 (-0.429, 0.332)	0.101 (-0.269, 0.393)	-0.026 (-0.36, 0.346)
Age 4+ survival	0.148 (-0.119, 0.351)	-0.019 (-0.319, 0.313)	-0.035 (-0.351, 0.332)
Productivity	-0.320 (-0.417, -0.204)*	0.005 (-0.261, 0.203)	0.026 (-0.262, 0.309)
Juvenile emigration rate	0.055 (-0.247, 0.209)	-0.400 (-0.525, -0.166)*	-0.445 (-0.572, -0.193)*
Age 3 emigration rate	-0.253 (-0.385, -0.044)*	0.432 (-0.035, 0.629)	-0.039 (-0.342, 0.335)
Age 4+ emigration rate	-0.234 (-0.382, -0.075)*	0.110 (-0.006, 0.207)	-0.141 (-0.363, 0.260)
Juvenile immigration rate	-0.431 (-0.554, -0.204)*	0.088 (-0.093, 0.258)	-0.313 (-0.523, -0.145)*
Age 3 immigration rate	0.159 (-0.161, 0.390)	-0.280 (-0.403, -0.075)*	-0.245 (-0.438, 0.022)
Age 4+ immigration rate	-0.376 (-0.436, -0.287)*	-0.369 (-0.537, -0.291)*	-0.368 (-0.534, -0.039)*

Fig. 1. Estimates of change in population size (a-c; raw count data indicated with dashed line), population growth rate (d-f), productivity (g-i; raw productivity data indicated with dashed line) and juvenile (j-l), age 3 (m-o) and age 4+ (p-r) survival obtained from the integrated population model for Rockabill, LIL and Coquet, with 95% credible intervals. Note different y-axis scales for population size for each colony.

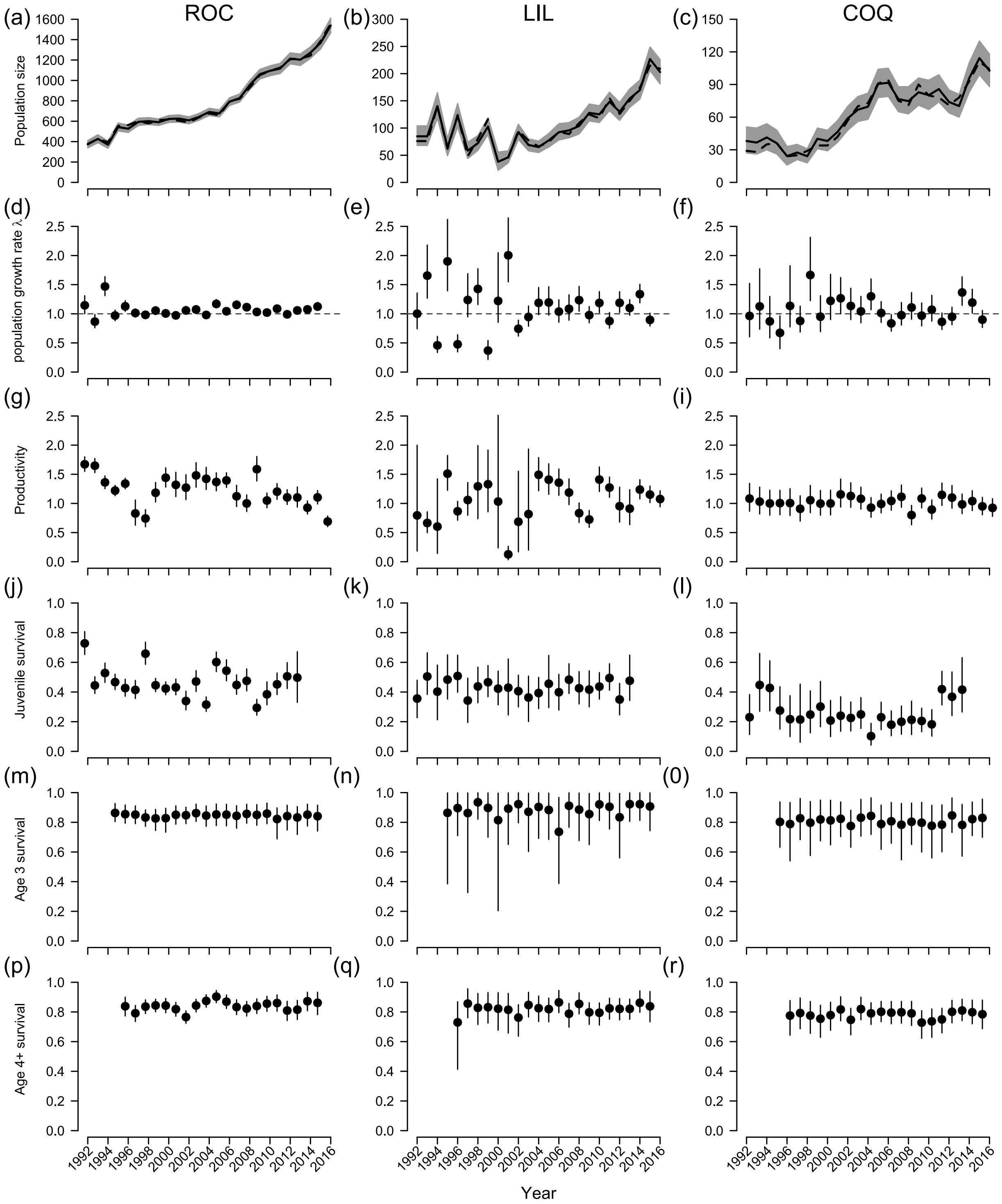

Fig. 2. Estimates of juvenile (a-c), age 3 (d-f) and age 4+ (g-i) emigration and immigration obtained from the integrated population models for Rockabill, LIL and Coquet, with 95% credible intervals. Note different y-axis scales for each colony.

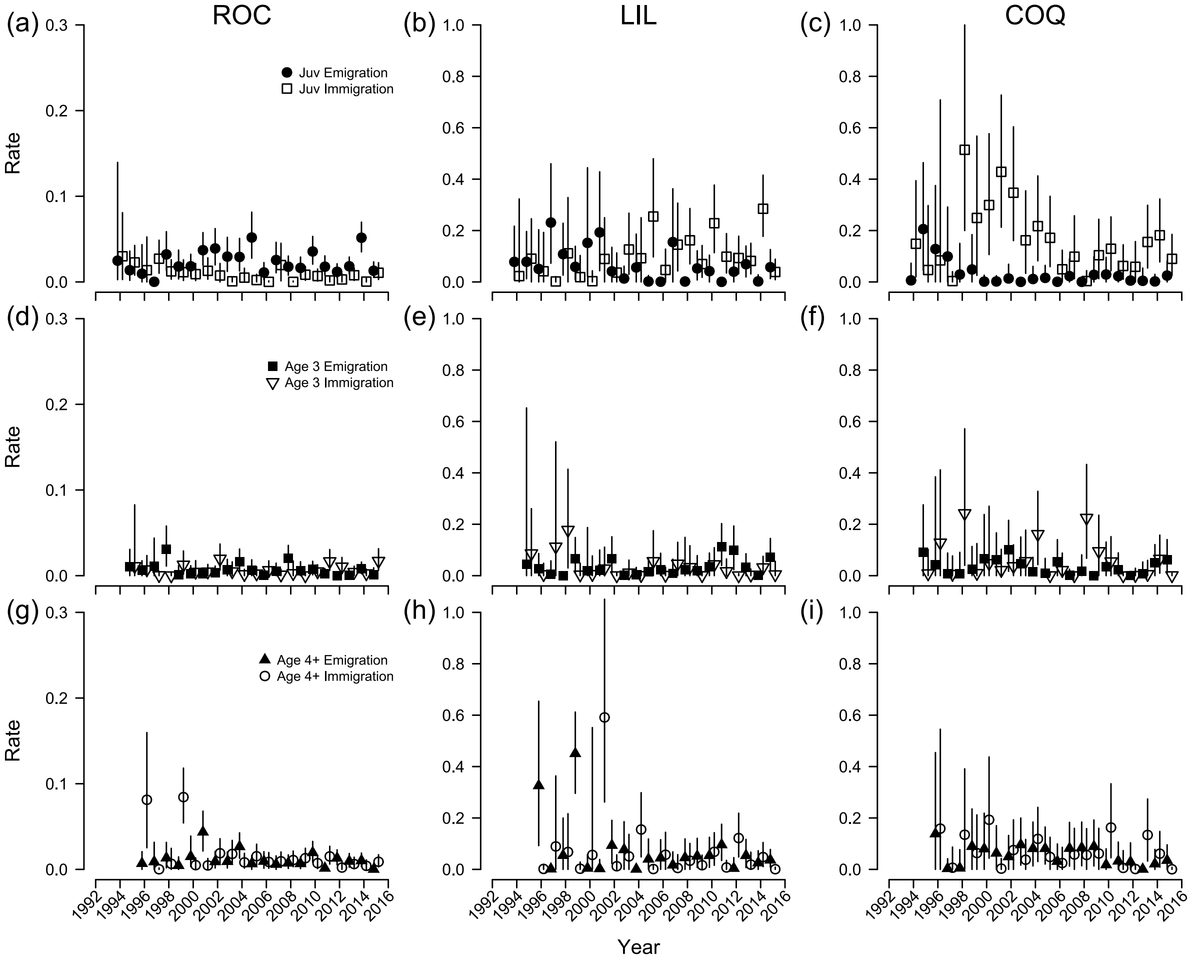

Fig. 3. Average movement rates and numbers of juvenile (age 0-3) (a), age 3 (b) and age 4+ (c) birds moving per annum among the three study colonies. The size of circles and length of the arrows represent colony size and inter-colony distance, respectively. Annual movement rates are represented by unenclosed figures and schematically with arrow thickness. Numbers in parentheses are credible intervals of the movement rates and figures in boxes represent the average number of birds moving in each year.

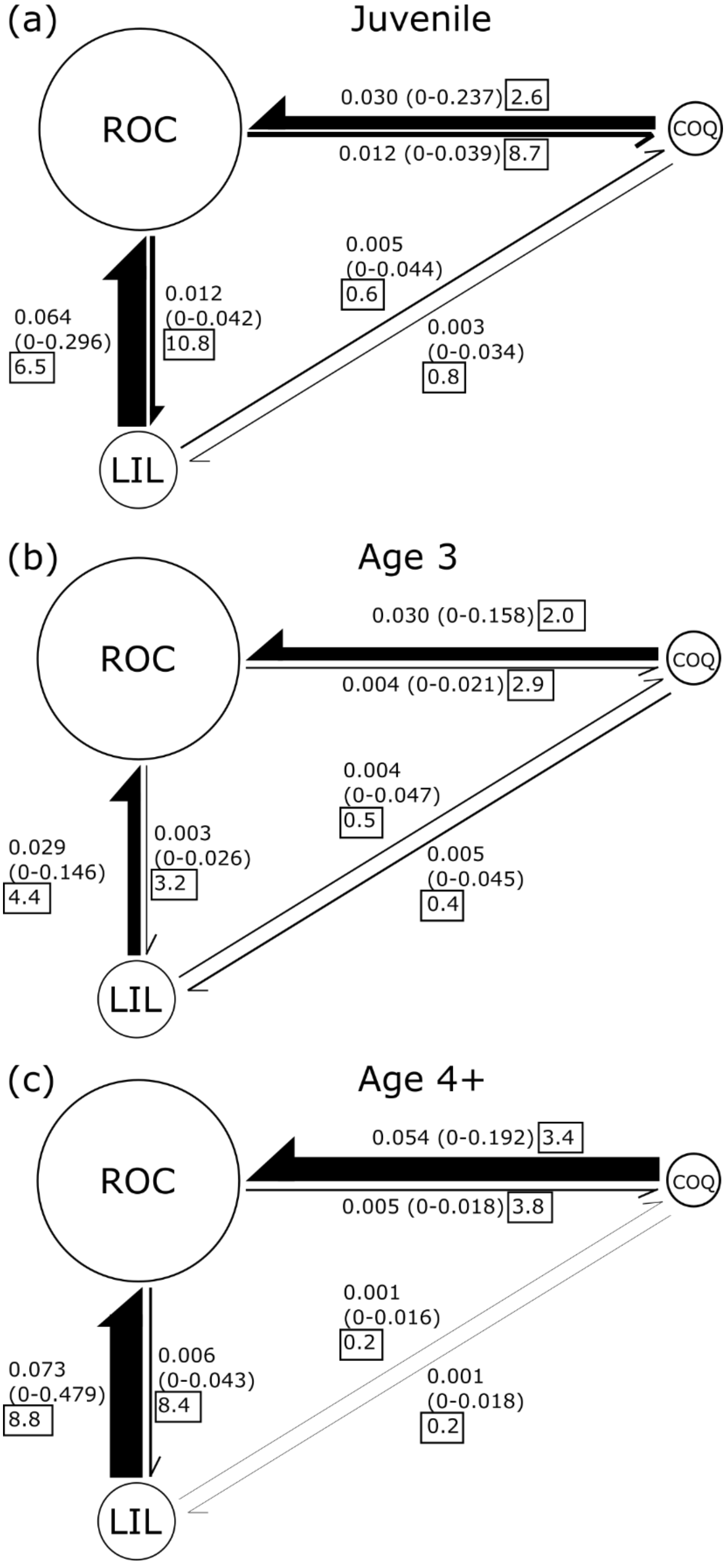

Fig. 4. Comparisons of population growth rate (a-c) and population size (d-e) with and without observed levels of emigration and immigration at the three colonies, with 95% credible intervals (bars in upper row, red (with dispersal) and blue (no dispersal) shading in lower row). Note different y-axis scales for each colony.

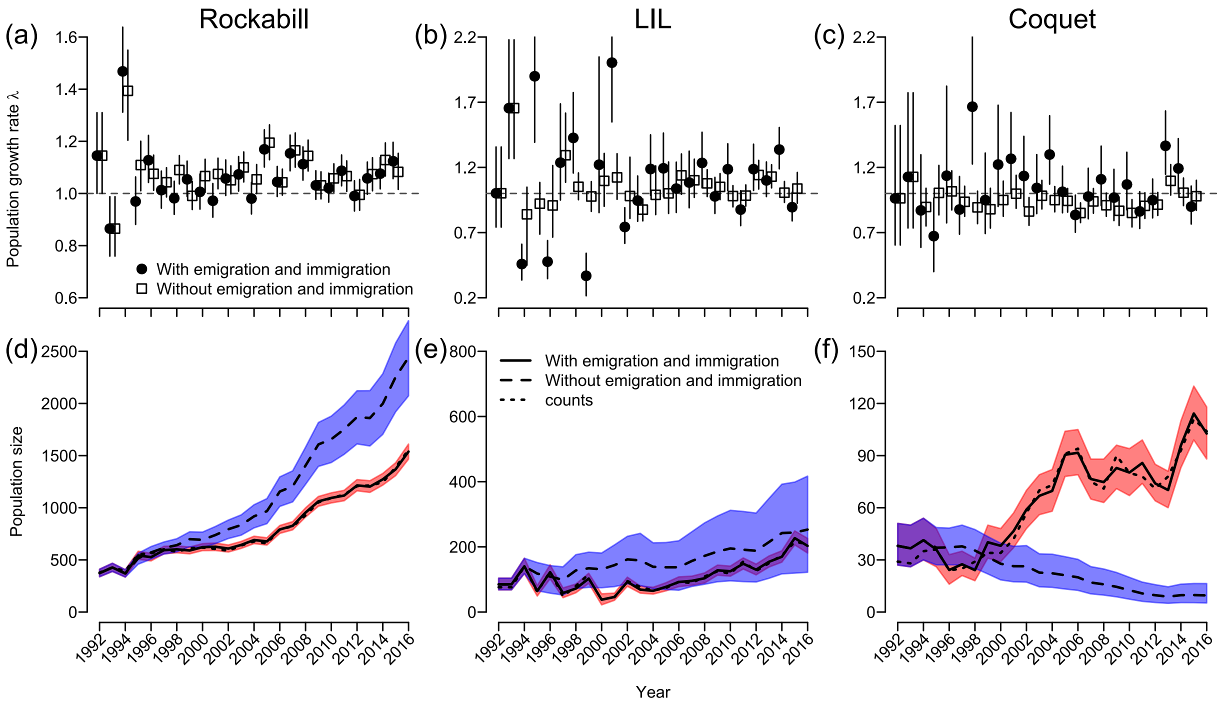

Fig. 5. Violin plots of correlation coefficients between demographic parameters and population growth rate λ at Rockabill (a), LIL (b) and Coquet (c). The probability of the coefficient being greater or lower than zero is indicated above and below each plot, respectively.

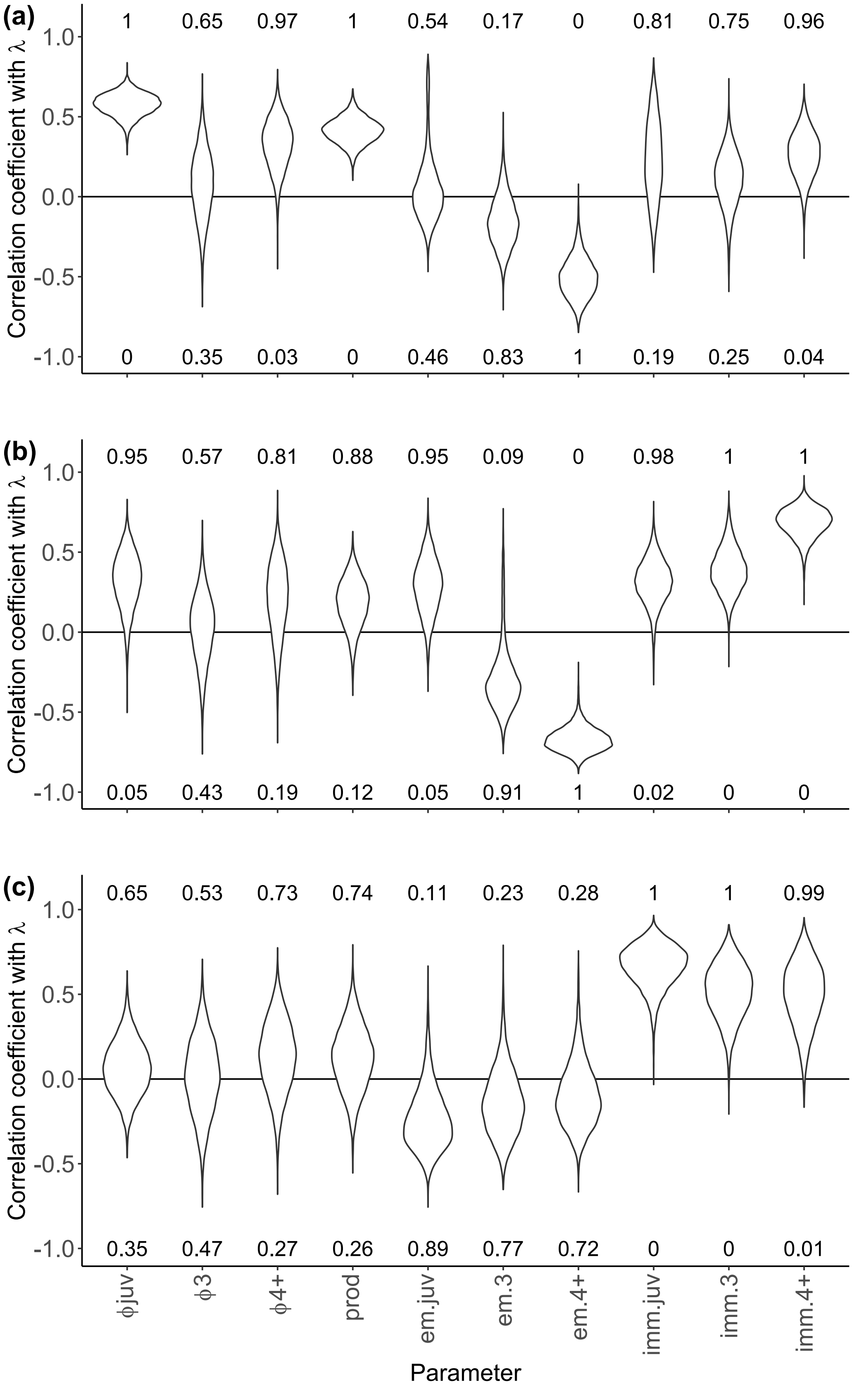

Fig. 6. Violin plots of correlation coefficients between juvenile survival, age 3+ survival and productivity at Rockabill, LIL and Coquet and total population growth rate λ (for all three colonies combined). The probability of the coefficient being greater or lower than zero is indicated above and below each plot, respectively.

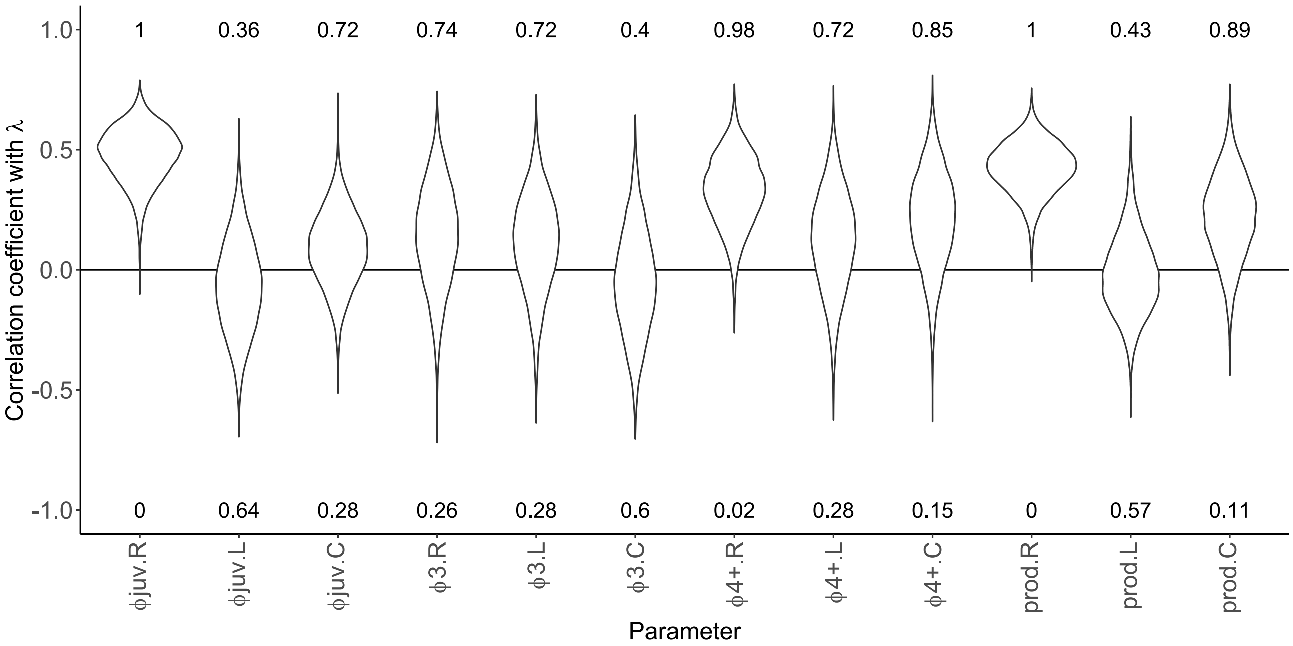

Fig. 7. Violin plots of correlation coefficients between demographic parameters and number of breeding females Ntot at Rockabill (a), LIL (b) and Coquet (c). The probability of the coefficient being greater or lower than zero is indicated above and below each plot, respectively.