

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

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19 **Abstract**

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

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

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

49 **Introduction**

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

64 Almost all seabirds aggregate into discrete colonies during their breeding seasons (Rolland, Danchin,
65 & de Fraipont, 1998). There is typically some dispersal of individuals between colonies, which differ
66 in their demographic rates (Clobert, Danchin, Dhondt, & Nichols, 2001). Thus, an entire population
67 of breeding seabirds displays many of the fundamental characteristics of a metapopulation and this
68 may have important implications when devising effective seabird conservation strategies (Esler,
69 2000). Events such as coastal erosion (Casey et al., 1995) or the introduction of predators (Craik,
70 1997; Oro, Pradel, & Lebreton, 1999) can lead to large reductions in colony size and even site
71 abandonment (Cabot, 1995; Heubeck, Mellor, Harvey, Mainwood, & Riddington, 1999; Whittam &
72 Leonard, 1999). When some of the individual colonies are very small, there is the additional
73 challenge that demographic stochasticity increases the risk of local colony extinction (Hanski, 1998).

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

87 The NW Europe metapopulation of roseate tern (*Sterna dougallii*) has been the focus of intensive
88 conservation activity since the late 1980s, following a steep decline from 3,812 pairs in 1968 to 561
89 pairs in 1987 (Avery, Green, & del Nevo, 1991; Cabot, 1995). The decline has been attributed to
90 several factors acting at the breeding grounds – human disturbance, depredation by gulls and rats,
91 displacement from nesting sites by gulls and high tides and coastal erosion – as well as trapping in
92 the African wintering grounds (Avery et al., 1995). The loss of the largest colony at the time (Tern
93 Island, Co. Wexford, Republic of Ireland) in the 1970s due to erosion meant that the birds had to
94 relocate, but as there was a population crash at the same time it is difficult to ascertain their dispersal
95 from counts alone. Conservation measures to enhance the status of roseate terns in NW Europe
96 (discouraging gulls from nesting, provision of breeding terraces and nest boxes and reducing human
97 disturbance) have been implemented at Rockabill and Lady's Island Lake in the Republic of Ireland,
98 Coquet Island in England and several sites in Northern Ireland, Wales and Brittany, France (Avery et

99 al., 1991). Management has been most successful at Rockabill: an offshore islet that is isolated from
100 mainland predators and located in an area of high food availability. Following removal of gulls and
101 nesting habitat management that started in 1989, numbers of roseate terns increased rapidly, fuelled
102 by immigration from colonies in Northern Ireland and Wales that were subject to higher levels of
103 predation and disturbance and which were ultimately abandoned (Cabot, 1995). Since 1987, the
104 metapopulation has recovered to 1,921 breeding pairs in 2016, with most pairs breeding at Rockabill.
105 While numbers have partially recovered, the range has not; in 1968 roseate terns bred at 15 colonies
106 (12 with more than 10 pairs) in NW Europe (Cabot, 1995), while in 2016 they bred at just seven
107 colonies, only three with more than 10 pairs.

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

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

123

124 **Materials and Methods**

125 **Study sites**

126 We studied the population processes of roseate terns at the major colonies in Britain and Ireland:
127 Rockabill, Lady's Island Lake (LIL) and Coquet Island (Coquet). Rockabill (Co. Dublin, Republic of
128 Ireland) comprises two granite islands separated by a channel approximately 20 m wide, with a
129 combined area of 0.9 ha and lying 6 km offshore. LIL (Co. Wexford, Republic of Ireland) is a
130 shallow coastal lagoon, within which roseate terns breed on the 3.1 ha sedimentary island Inish.
131 Coquet (Northumberland, England, United Kingdom) is an island of 7 ha lying 1.2 km offshore.
132 Each colony is a nature reserve and managed to enhance roseate tern conservation, with measures
133 including control of predators, competitors and human disturbance, nest box provision and
134 vegetation management. The proportion of the NW Europe metapopulation that these colonies
135 comprised ranged from 79.8% in 1992 to 97.3% in 2016. The next largest congregation of roseate
136 terns in the metapopulation breeds at several sites in Brittany, France, with the combined number of
137 breeding pairs at these sites during the study period ranging from 14.0% in 1992 to 2.6% in 2016.
138 We did not include the French colonies in our study due to the sparseness of the capture-mark-
139 recapture data collected there. There were 29 sightings of 23 individuals in French colonies between
140 2007 and 2014 of roseate terns ringed at the three study colonies (there is no resighting data before
141 this period). In comparison, the numbers of roseate terns seen at each study colony over the same
142 period that were ringed at a different colony were 869 for Rockabill, 1457 for LIL and 538 for
143 Coquet. There were 13 sightings of four individual French-ringed terns across the study sites
144 between 1996 and 2016. Since Isle aux Dames was abandoned in 2006 numbers there have been
145 small and of little importance. Ring resighting records within our system and in other
146 metapopulations in the Azores and eastern North America indicate that immigration and emigration
147 into and out of the NW Europe metapopulation is very rare.

148 **Demographic data**

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

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

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

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

174 **Statistical analysis**

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

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

188 To enable demographic stochasticity to be modelled, we used Poisson and binomial distributions to
189 describe the dynamics of the true population size over time with a pre-breeding projection model
190 (Schaub et al., 2012). Thus, the number of fledglings in year t depended on the number of breeding
191 (age 3+) females in year t and productivity in year t . The number of age 3, age 4 and age 5+ females
192 at each colony in each year depended on the numbers of each age group in the preceding year (or
193 three years before in the case of age 3 females), age- and colony-specific survival rate and age- and
194 intercolony-specific dispersal rate. The demographic parameters are defined in Table S1. The pre-
195 breeding projection model equations for each study site are given in Appendix S1. The projection
196 model equations for each site were constituents of the multistate IPM. The observation process
197 describes the relationship between the observed population counts and the true population size, using
198 a Poisson distribution. Productivity was analysed with random effects for time, with a normal

199 distribution and log link. Age- and colony-specific emigration and immigration rates were derived
200 parameters, based on the total number of age- and colony-specific emigrants or immigrants in year t
201 + 1 divided by the total breeding population of the colony in year t . Population growth rate (λ_t) was a
202 derived parameter, calculated from the total breeding population at the colony in year $t + 1$ divided by
203 the total breeding population at the colony in year t .

204 We estimate survival of individuals using multistate models of CMR data. Our CMR data set
205 consists of 20,702 individuals initially marked as chicks and which were not recorded as dying
206 before fledging (17,636 at Rockabill, 1,707 at LIL and 1,359 at Coquet). We analysed the CMR data
207 with a multistate model (Kéry & Schaub, 2012; J.-D. Lebreton, Burnham, Clobert, & Anderson,
208 1992) with a multinomial likelihood. We used this model to estimate the parameters S (survival
209 probability: annual or from fledging to age 3, dependent on subscript as described below), ψ
210 (dispersal probability) and p (resighting probability). We based the model on age-structured models
211 described by Kéry & Schaub (2012: chapter 9) and (Weegman et al., 2016). While goodness of fit
212 (GOF) tests for IPMs remain unavailable (Lee et al., 2015), it is recommended that component
213 datasets are assessed for GOF to the model (Kéry & Schaub, 2012; Schaub & Abadi, 2011).

214 Goodness of fit tests with programme U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel,
215 2009) indicated the existence of ‘trap dependence’ and transience within the data (Table S3).

216 Following Ratcliffe, Newton, et al., (2008), we dealt with transience by considering three age classes
217 for S and ψ : juvenile (the period fledging to age 3; subscript *juv*, reported in the text as annual
218 juvenile survival after calculating the cube-root), age 3 (subscript *age3*) and age 4+ (subscript
219 *age4+*). We included six parameters for p , which consisted of age since last recorded (age 0, age 3 or
220 age 4+) and, to account for ‘trap dependence’, time since last recorded (previous year or before
221 previous year; for birds last recorded as age 0, the previous year was three years previous because
222 birds are not resighted at age 1 and 2 in our model). We considered it possible that birds in their first
223 year of breeding may have a lower resighting probability than older birds for reasons including

224 breeding failure, later arrival and less optimal nesting locations. Any sightings of age 1 or 2 birds
225 were discarded and we assume that no birds of age 1 or 2 return to the breeding colonies. To enable
226 fast analysis times, we summarised the data in the m-array format, with separate m-arrays for each
227 age class. The parameters S_{juv} , S_{age3+} , ψ_{juv} and ψ_{age3+} were modelled with random effects for time,
228 with normal distributions and logit links. S_{juv} was used to derive juvenile annual survival probability
229 during the model run for the purposes of presentation. We estimated resighting probability for each
230 colony and year independently of each other (i.e. with fixed effects).

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

241 To assess the impact of the demographic parameters on λ , we computed the posterior distributions of
242 the correlation coefficients (Schaub et al., 2012). The strength of these correlations indicate the
243 strength of the contribution of the temporal variation in demographic parameters to the temporal
244 variation in λ over the study period (Freeman, Robinson, Clark, Griffin, & Adams, 2007; Robinson,
245 Green, Baillie, Peach, & Thomson, 2004). We used the mode to describe the posterior distributions
246 of the correlation coefficients because most of them were very skewed. We also calculated the
247 probability that the correlation coefficients were greater than zero [$P(r > 0)$]. We performed

248 equivalent correlations with the same set of demographic parameters and population size instead of λ
249 to assess whether there was evidence for density dependence (Schaub, Jakober, & Stauber, 2013).
250 The source or sink status of a colony can be determined by calculating its contribution to the wider
251 population network and this depends on productivity, (apparent) survival and emigration rates
252 (Runge, Runge, & Nichols, 2006). To investigate the source-sink dynamics between the colonies, we
253 used the posterior samples of demographic rates obtained from the IPM to re-run the population
254 process equations described above 12,000 times (the number of posterior samples), but without any
255 emigration or immigration between colonies. In this projection without dispersal, the states consist of
256 age groups at each colony. The breeding population size at each colony for the first three years in the
257 projection are copies of the posterior samples from the IPM. For each subsequent time-step, the
258 number of individuals in each state is determined by the posterior samples of productivity, S_{juv} , S_{age3}
259 and S_{age4+} from the IPM. We make the assumption that mean productivity (and survival) at the
260 colonies remains unchanged when dispersal was fixed to 0. A colony was determined to be a source
261 if its population increased in the absence of dispersal and a sink if its population decreased in the
262 absence of dispersal.

263

264 **Results**

265 **Temporal patterns in demographic parameters**

266 The number of pairs of the three colonies combined increased from an estimate of 496 (95% CRI:
267 454-540) pairs in 1992 to an estimate of 1,844 (95% CRI: 1,768-1,922) pairs in 2016. The
268 populations of all three colonies increased over the study period (Rockabill: from 373 (95% CRI:
269 338-411) breeding pairs in 1992 to 1,538 (95% CRI: 1,466-1,611) breeding pairs in 2016; LIL: 85
270 (95% CRI: 68-104) to 203 (95% CRI: 181-226); Coquet: 38 (95% CRI: 27-51) to 103 (95% CRI: 88-
271 118)) (Fig. 1).

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

275 Productivity was highest at Rockabill (Table 1, Fig. 1). Productivity varied considerably at Rockabill
276 and LIL but varied little at Coquet (Table 1, Fig. 1). Annual survival rates were higher for age 3 and
277 4+ than juvenile birds and varied by colony (Table 1, Fig. 1). Juvenile annual survival fluctuated
278 moderately at Rockabill and LIL (Fig. 1). From 1995 to 2010, juvenile survival at Coquet was
279 particularly low (0.59 (95% CRI: 0.43-0.73)) compared to the other colonies; the average for the
280 remaining years at Coquet was 0.72 (95% CRI: 0.45-0.81) (Fig. 1). Age 3 and age 4+ survival were
281 higher at Rockabill and LIL than Coquet (Table 1, Fig. 1). Rates of emigration and immigration were
282 highest at LIL and Coquet (Table 1, Fig. 2; note different y-axis scales). At Rockabill, juvenile
283 emigration generally exceeded immigration with the opposite occurring at LIL and Coquet (Table 1,
284 Fig. 2). At Rockabill and LIL, age 3 and 4+ emigration balanced relatively with immigration overall,
285 although not on an annual basis (Table 1, Fig. 2). At Coquet, age 3 and 4+ immigration exceeded
286 emigration in several years, with balance between emigration and immigration in other years (Fig. 2).
287 The estimated actual number of annual emigrants from and immigrants to each colony, on which the
288 emigration and immigration rates are based, are illustrated in Fig. S2.

289

290 **Source-sink dynamics**

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

297 Population growth rate (λ) at all three colonies tended to be positive (mean λ calculated as the
298 regression of population size over time) (Table 1). The population of Rockabill grew quite steadily
299 while the populations of LIL and Coquet experienced more fluctuations (Fig. 1). Fixing dispersal
300 probability to 0 resulted in a λ above 1 at Rockabill and LIL, and a λ below 1 at Coquet (Table 1),
301 demonstrating that Rockabill and LIL have been self-sufficient and population sources while the
302 internal demographic rates of Coquet have been insufficient to sustain its population, which has acted
303 as a sink. Fixing dispersal probability to 0 resulted in a higher projected λ at Rockabill and a lower
304 projected λ at Coquet, with no change at LIL (Table 1, Fig. 4). λ with and without emigration and
305 immigration at Rockabill fluctuated similarly over time, although the population size was predicted
306 to be larger in the absence of emigration and immigration, with a probability of 1 (2,441 (95% CRI:
307 2,072-2,794) pairs vs 1,538 (95% CRI: 1,466-1,611) pairs modelled with emigration and
308 immigration). In contrast, at the two smaller colonies of LIL and Coquet, fixing dispersal probability
309 at 0 resulted in a great reduction in annual fluctuations in predicted λ (Fig. 4), showing the large
310 effect of emigration and immigration on population dynamics at these colonies. The number of pairs
311 at LIL with dispersal fixed at 0 was projected to reach 253 (95% CRI: 122-417) by 2016, with a 0.70
312 probability that this is larger than the 202 (95% CRI: 181-226) pairs modelled with
313 emigration/immigration. At Coquet, fixing dispersal to 0 resulted in a continual decline in predicted
314 population size, showing that Coquet has relied on immigration for population growth. Without
315 emigration/immigration, the Coquet colony was projected to fall to 10 pairs (95% CRI: 5-16) by
316 2016, with a probability of 1.0 that this was lower than the 102 (95% CRI: 88-118) pairs modelled
317 with emigration/immigration. In summary, by 2016, net migration appears to have reduced the
318 population size at Rockabill, had little impact at LIL and led to an increase in the population size at
319 Coquet, while fixing dispersal to 0 within the model resulted in a greater projected metapopulation
320 size of 2,703 (95% CRI: 2,344-3,026) compared to 1,844 (95% CRI: 1,768-1,922) in the original
321 model, with a probability of 1 that the population size was larger without dispersal.

322

323 **Correlations of demographic parameters and annual population growth rate**

324 At Rockabill, the strongest positive correlations with annual population growth rate, λ , were with
325 juvenile survival [$r = 0.59$; $P(r > 0) = 1$] and age 4+ survival [$r = 0.66$; $P(r > 0) = 0.97$] and
326 productivity [$r = 0.42$; $P(r > 0) = 1$] (Table 2, Fig. 5). λ at Rockabill also correlated positively with
327 age 4+ immigration [$r = 0.31$; $P(r > 0) = 0.96$], but less strongly (Table 2, Fig. 5). At LIL, the
328 strongest positive correlation with λ was with age 4+ immigration [$r = 0.52$; $P(r > 0) = 1$; Table 2,
329 Fig. 5]. λ at LIL also correlated positively with juvenile survival [$r = 0.36$; $P(r > 0) = 1$], juvenile
330 immigration [$r = 0.32$; $P(r > 0) = 0.98$] and age 3 immigration [$r = 0.35$; $P(r > 0) = 1$] (Table 2, Fig.
331 5). At Coquet, λ correlated strongly and positively with juvenile immigration [$r = 0.72$; $P(r > 0) =$
332 1], age 3 immigration [$r = 0.56$; $P(r > 0) = 1$] and age 4+ immigration [$r = 0.53$; $P(r > 0) = 0.99$]
333 (Table 2, Fig. 5).

334 λ of the metapopulation (all three colonies combined) correlated positively and significantly with
335 juvenile and age 4+ survival at Rockabill [$r = 0.51$ (95% CRI: 0.27, 0.65); $P(r > 0) = 1$ and $r = 0.34$
336 (95% CRI: 0.07, 0.56); $P(r > 0) = 0.98$] and productivity at Rockabill [$r = 0.43$ (95% CRI: 0.24,
337 0.59); $P(r > 0) = 1$] (Fig. 6). The demographic parameters are plotted against λ at each colony in Figs
338 S3-S5 and for each colony against λ for the three colonies combined in Fig S6.

339

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

341 Population size was negatively correlated with juvenile survival [$r = -0.26$; $P(r > 0) = 0.99$] and
342 productivity [$r = -0.32$; $P(r > 0) = 0$] at Rockabill (Table 3). Population size was negatively
343 correlated with emigration and immigration for several age classes at all the colonies (Table 3). The
344 decrease in immigration rates with increasing population size reflects the reduced number of
345 dispersing individuals relative to overall population size. Population size correlated positively with

346 the number of juvenile emigrants and age 3 immigrants at Rockabill, age 3 emigrants and juvenile
347 immigrants at LIL and juvenile, age 3 and age 4+ immigrants at COQ (Table S2). Population size
348 did, however, correlate negatively with number of age 4+ immigrants at Rockabill and age 4+
349 emigrants at LIL (Table S2). The demographic parameters are plotted against population size at each
350 colony in Fig S7-S9.

351

352 **Discussion**

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

361 Resighting probability varied annually and between sites, which can be explained by variation in
362 effort devoted to tern ring reading by site and year. Resighting probability at Rockabill declined over
363 time, which may be due to ring reading effort not increasing in proportion to population size. The
364 lower resighting of age 3 birds could be due to them: (1) being absent from the colonies, (2) being at
365 a colony but not breeding and therefore spending less time there, (3) breeding but failing early and
366 therefore having fewer chances to be seen and (4) breeding at the edge of the colony, where the
367 likelihood of detection is lower. The former two of these reasons relate to non-breeding and the latter
368 two do not, ruling out possible use of resighting probability as a proxy for breeding propensity.

369 Breeding propensity is assumed to be 100% for all birds of age three and over in the model, which is
370 a necessary assumption because only a minority of tern detections were confirmed as breeders (c.f.

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

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

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

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

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

412 Despite intensive efforts since 2000 to improve conditions for roseate terns at Coquet, this colony
413 has been a cryptic sink (Weegman *et al.*, 2016). Increasing numbers have been fuelled by
414 immigration and counts of the breeding numbers alone would not have detected this. The average
415 productivity of 1.02 is similar to LIL (1.03) and both of these colonies are at the low end of
416 productivity recorded at the main colonies in the NW Atlantic. Possibly more significantly, from
417 1995-2010, the average annual survival of juveniles at Coquet was 0.59: lower than at Rockabill and
418 LIL. Exploration of the reasons for low demographic rates at Coquet should include comparative
419 studies of provisioning rates, diet and fledging weights. The period of low juvenile annual survival at
420 Coquet is not accompanied by low age 3 and age 4+ survival, suggesting a higher risk of mortality

421 for birds in the interval from 0 to 3 years old than for birds 3 years and older. Most young birds
422 remain in their African wintering grounds until at least age 2 and could therefore be
423 disproportionately affected by variation in food availability or hunting there. However, neither
424 juvenile nor age 3 and age 4+ survival rates were correlated between any pair of colonies and, as we
425 believe the birds to winter in the same areas (Ratcliffe & Merne, 2002), we would expect such
426 correlations if factors in the wintering grounds had strong impacts on annual variability of survival
427 rates. It should be noted that the figures for juvenile survival are likely to be biased downwards – and
428 productivity upwards – to some extent as although we removed those ringed chicks known to have
429 died before fledging from analysis, some will inevitably have been overlooked.

430 Productivity at LIL was highly variable, which likely reflects sporadically heavy predation by
431 mammals such as rats (*Rattus norvegica*) and stoats (*Mustela erminea*), which do not have far to
432 travel to this inshore colony, as well as various avian predators. While productivity did not correlate
433 with annual population growth rate at LIL, high predation (which reduces productivity) may have
434 been a cue for roseate terns to disperse from LIL and may have resulted in the sporadically high
435 emigration from LIL to Rockabill (Fig. 2), as has been documented in seabirds previously (Oro et al.,
436 1999). Rockabill and Coquet, by contrast, are offshore and safe from mammalian predators.

437 Dispersal rates within the metapopulation exhibited substantial annual variation and correlated with
438 population growth rates of each colony. The finding that immigration rates were the most important
439 correlates with population growth rate at Coquet and LIL is consistent with the closely-related
440 common terns at the Banter See colony (Szostek et al., 2014). Rockabill differed in that survival and
441 productivity were the most important determinants of population growth. Given the very large
442 relative size of the Rockabill colony, large proportions of birds from LIL or Coquet would need to
443 immigrate to have a significant impact on Rockabill's population growth. Greater numbers of terns
444 that fledged on Rockabill recruited to LIL and Coquet than moved in the opposite direction, which
445 could reflect density dependence at Rockabill and/or attractiveness of LIL and Coquet to younger

446 birds. Availability of local recruits was suggested to be the main driver of immigration in common
447 terns at Banter See, also in the NE Atlantic (Szostek et al., 2014), but of our three colonies of roseate
448 terns, the most local recruits are found at the very large Rockabill colony, which received fewer
449 recruiting immigrants than the smaller colonies (Fig. 3).

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

460 Variable site quality can affect the success of efforts to restore animal populations within a
461 metapopulation. In the case of roseate terns, our results highlight the importance of choosing sites for
462 restoration work where assessment suggests a high likelihood of attaining sufficiently high levels of
463 productivity and survival to avoid creation of further sink colonies. Identifying such sites is
464 challenging in the absence of current breeding roseate terns, but colonisation apparently requires an
465 established common tern (*Sterna hirundo*) colony (Nisbet & Spendelow, 1999), while the risk of
466 incursions by most mammalian predators from the mainland can be assessed relatively easily by
467 considering the distance from the mainland shore (Ratcliffe, Craik, Helyar, Roy, & Scott, 2008;
468 Ratcliffe, Mitchell, Varnham, Verboven, & Higson, 2009). Distance from shore (and hence water
469 depth) tends to be inversely related to food availability for terns (e.g. Monaghan 1996), however, so
470 managers need to trade-off these conflicting demands when selecting sites for restoration. Studying

471 the foraging success and productivity of common terns at candidate sites may help to identify those
472 with sufficient food availability within foraging range and without significant predation.
473 Conservationists have considerable power to manipulate tern distributions (Dunlop et al., 1991;
474 Kress, 1983; Roby et al., 2002) and could for example remove nest boxes at Rockabill to increase
475 density dependent competition for nesting sites, with the ultimate goal of encouraging emigration of
476 young birds to new sites that have been prepared for them. Our study indicates that such an approach
477 may lead to a reduction in metapopulation size because of the high productivity achieved by roseate
478 terns on Rockabill and the low productivity and survival elsewhere i.e. at Coquet. However, with the
479 appearance of density dependent regulation at Rockabill it is possible a growing number of
480 individual terns will gain fitness benefits by emigrating to other colonies, which could also be
481 beneficial for the size of the overall metapopulation, provided conditions at receptor colonies are
482 sufficiently favourable.

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

495

496 **Acknowledgements**

497 This study was made possible by the efforts of banders and wardens who marked and resighted birds:
498 Oscar Merne, Nik Aspey, Jo Hulsman, Nicola Reddy, Julia Baer, Vicky Jones, Mary Robinson,
499 Claire Bailly, Ashling Kelly, Ben Stammers, Graham Barker, Aleks Maljkovic, Jeff Stenning,
500 Dominic Berridge, James Millett, Alyn Walsh, Adam Cowles, Rick Mundy, Chris Watts, Olivia
501 Crowe, Veronica Neves, Yvonne White, Dave Daly, Anne Newton, Chris Wilson, Maggie Hall,
502 Gearoid O’Sullivan, Cathryn Hannon, David Patrick, Rob Lidstone-Scott, James Robinson, Alastair
503 Boulton, Liz Giddings, Dave Fletcher, Sarah Lowe, Zoe Tapping, Bill Ashby, Arthur Jones and
504 Mark Oksien. The work was funded by the LIFE Programme of the European Union as part of the
505 project "Improving the conservation prospects of the priority species roseate tern throughout its
506 range in the UK and Ireland" (LIFE14 NAT/UK/000394) and Natural England and conducted under
507 the auspices of long-term ringing and monitoring work funded by BirdWatch Ireland, RSPB and
508 NPWS. Mark Avery, Adrian del Nevo and John Coveney initiated the special ringing programme
509 and managed the project during its early years. Ian Nisbet kindly provided comments on an earlier
510 draft of the paper.

511

512 **Authors’ Contributions**

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

516

517 **Data Accessibility**

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

522

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

Demographic rate	Colony		
	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)

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

Demographic rate	Correlation with population growth 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)*

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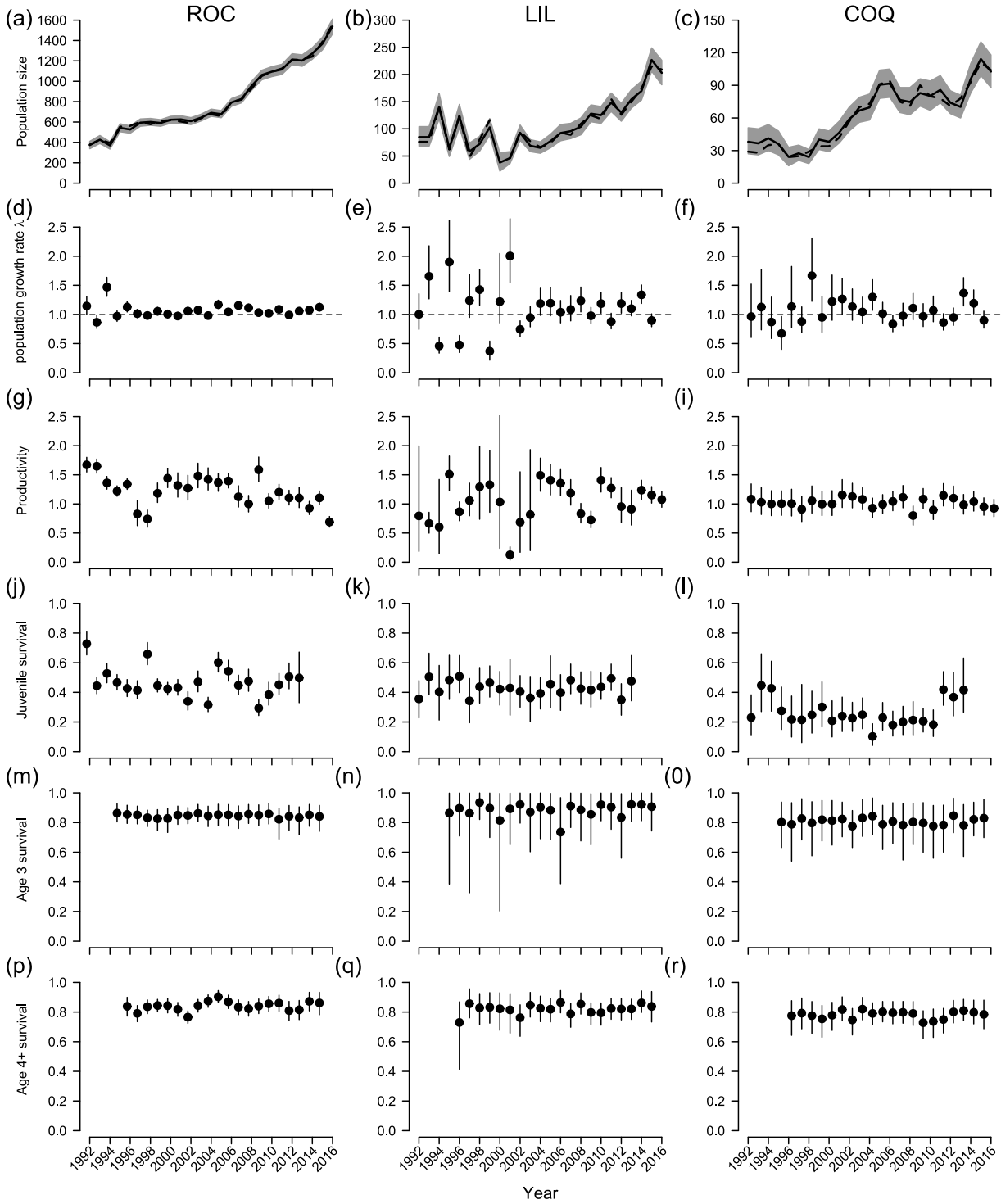
711 **Table 3.** Posterior modes and 95% credible intervals (in parentheses) of correlation coefficients
712 between demographic rates and population size at the three colonies. Correlations with a probability
713 >0.95 of being positive or negative are marked with *.

Demographic rate	Correlation with population size		
	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)*

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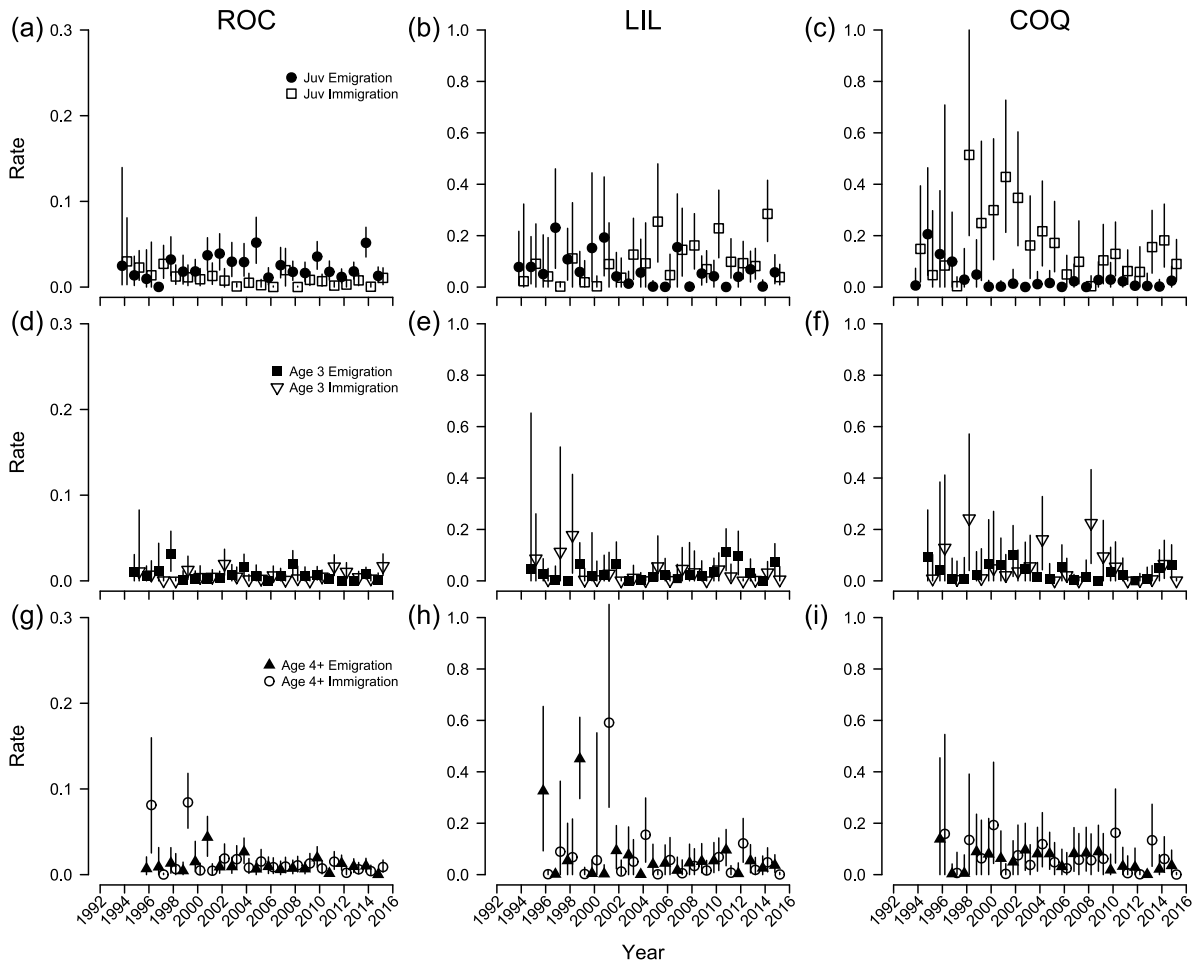
716 **Fig. 1.** Estimates of change in population size (a-c; raw count data indicated with dashed line),
 717 population growth rate (d-f), productivity (g-i; raw productivity data indicated with dashed line) and
 718 juvenile (j-l), age 3 (m-o) and age 4+ (p-r) survival obtained from the integrated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



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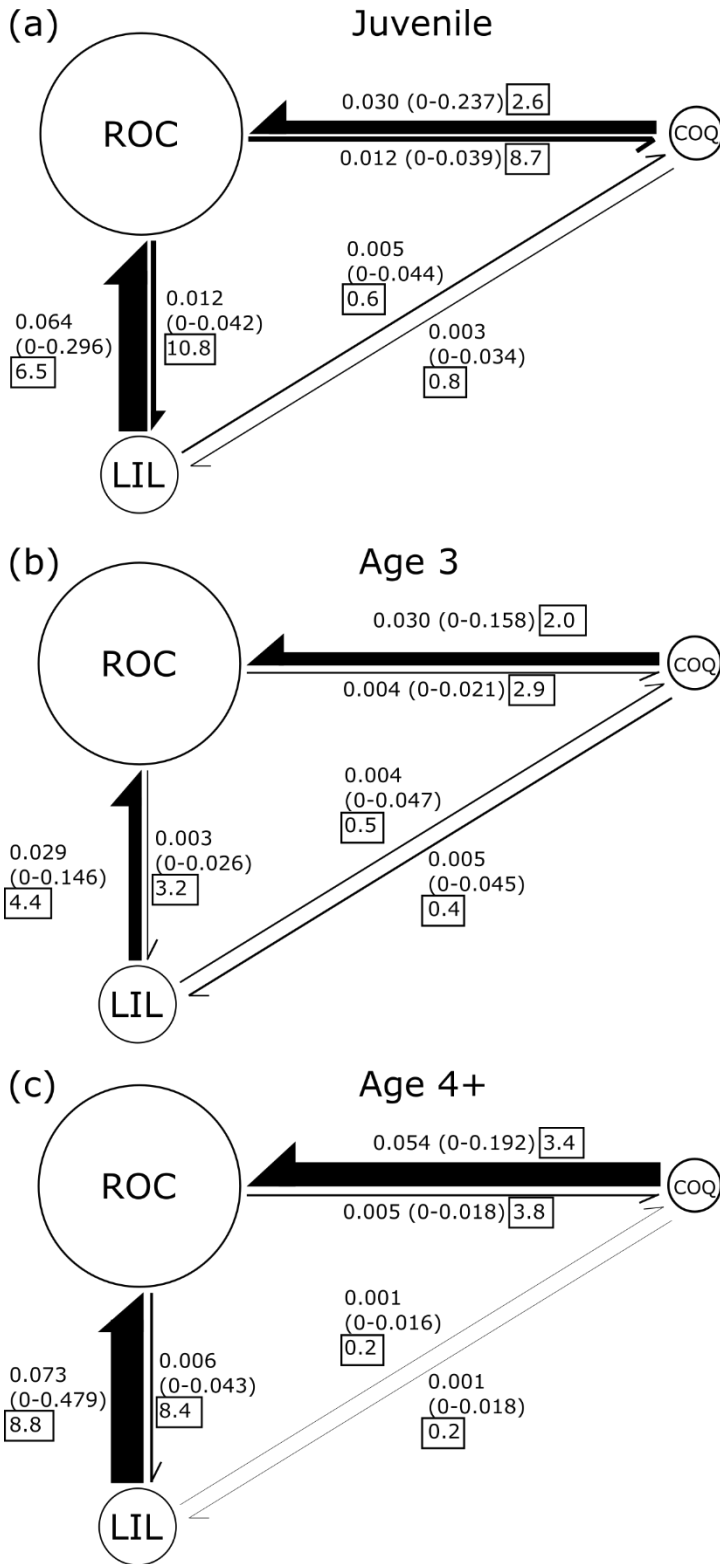
723 **Fig. 2.** Estimates of juvenile (a-c), age 3 (d-f) and age 4+ (g-i) emigration and immigration obtained
 724 from the integrated population models for Rockabill, LIL and Coquet, with 95% credible intervals.
 725 Note different y-axis scales for each colony.



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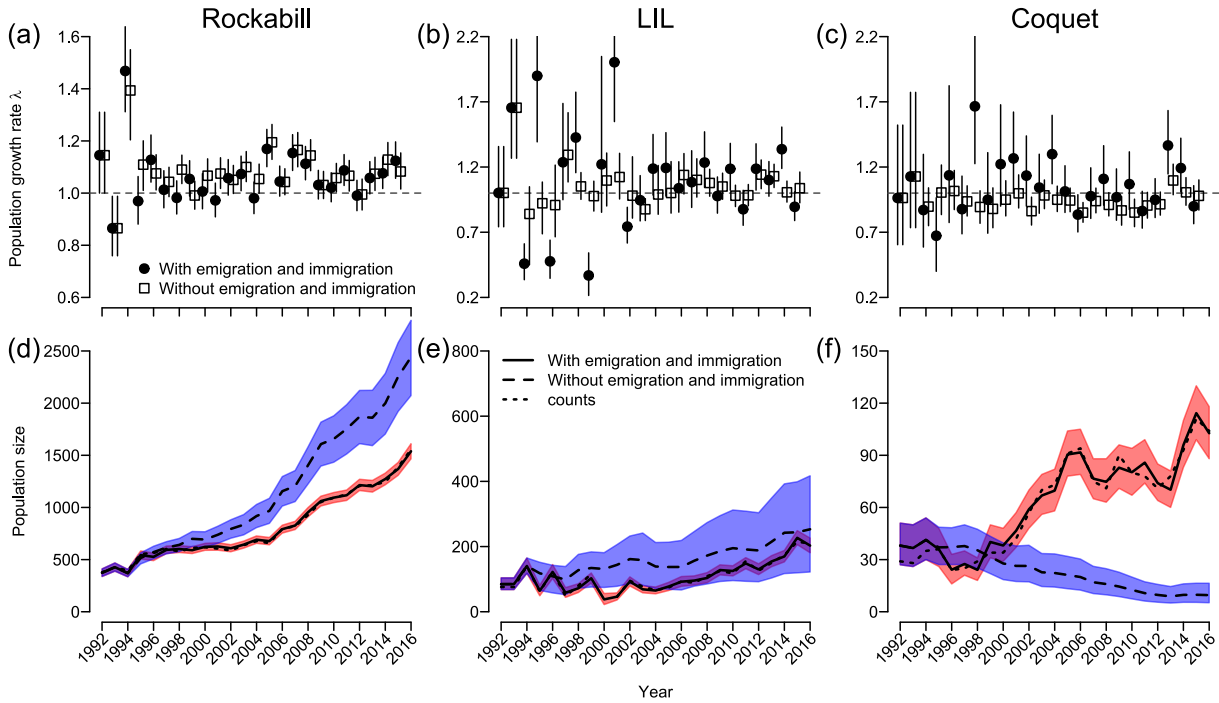
728 **Fig. 3.** Average movement rates and numbers of juvenile (age 0-3) (a), age 3 (b) and age 4+ (c) birds
 729 moving per annum among the three study colonies. The size of circles and length of the arrows
 730 represent colony size and inter-colony distance, respectively. Annual movement rates are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



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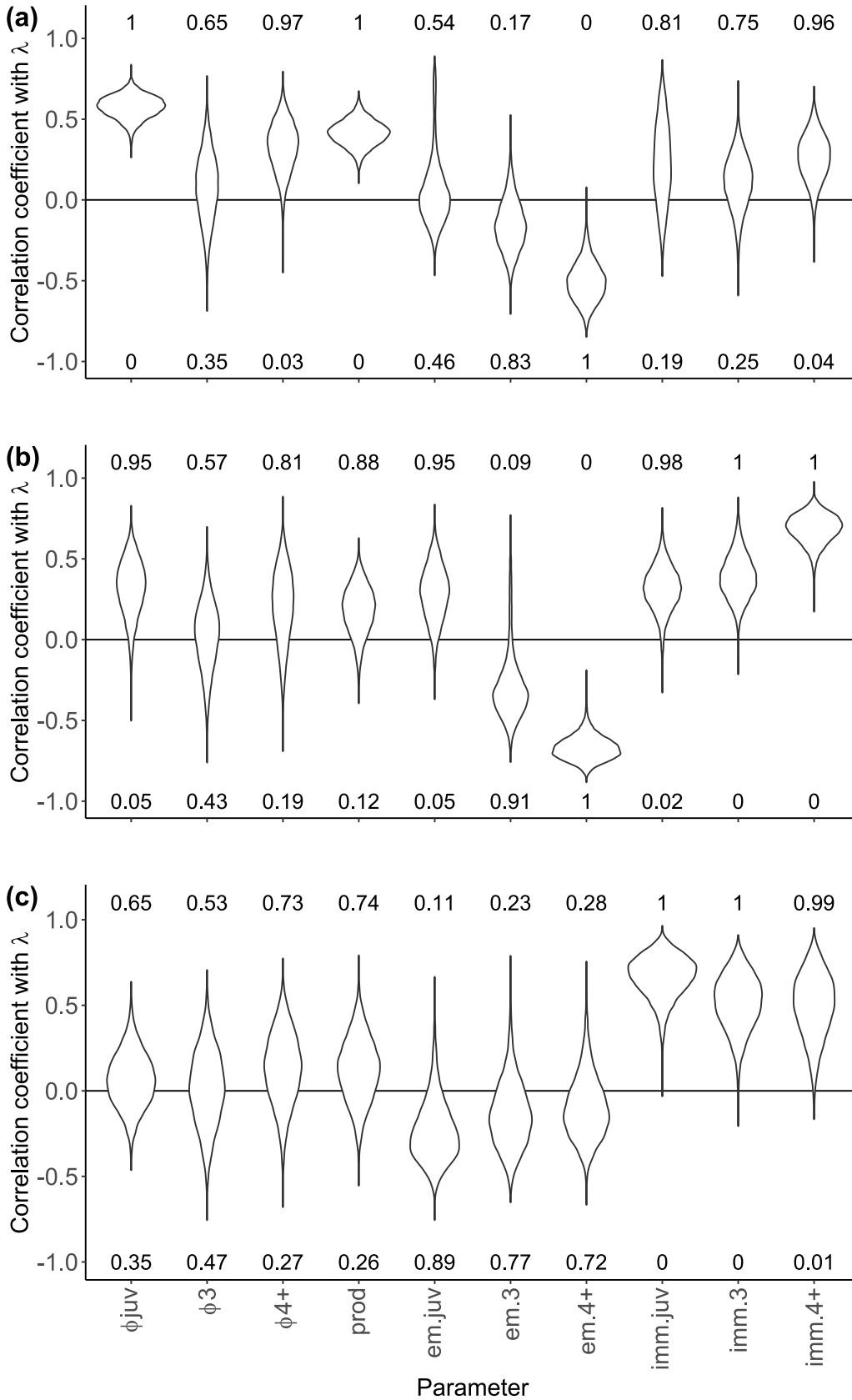
736 **Fig. 4.** Comparisons of population growth rate (a-c) and population size (d-e) with and without
 737 observed levels of emigration and immigration at the three colonies, with 95% credible intervals
 738 (bars in upper row, red (with dispersal) and blue (no dispersal) shading in lower row). Note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



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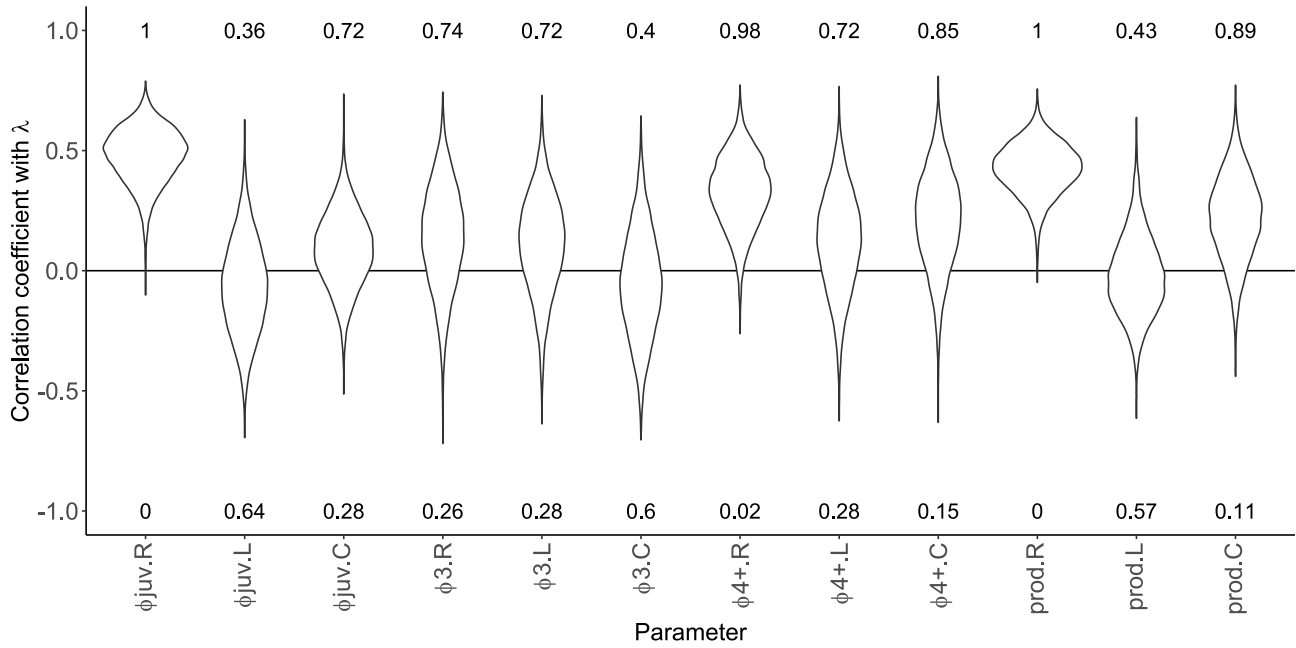
742 **Fig. 5.** Violin plots of correlation coefficients between demographic parameters and population
 743 growth rate λ at Rockabill (a), LIL (b) and Coquet (c). The probability of the coefficient being
 744 greater or lower than zero is indicated above and below each plot, respectively.



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

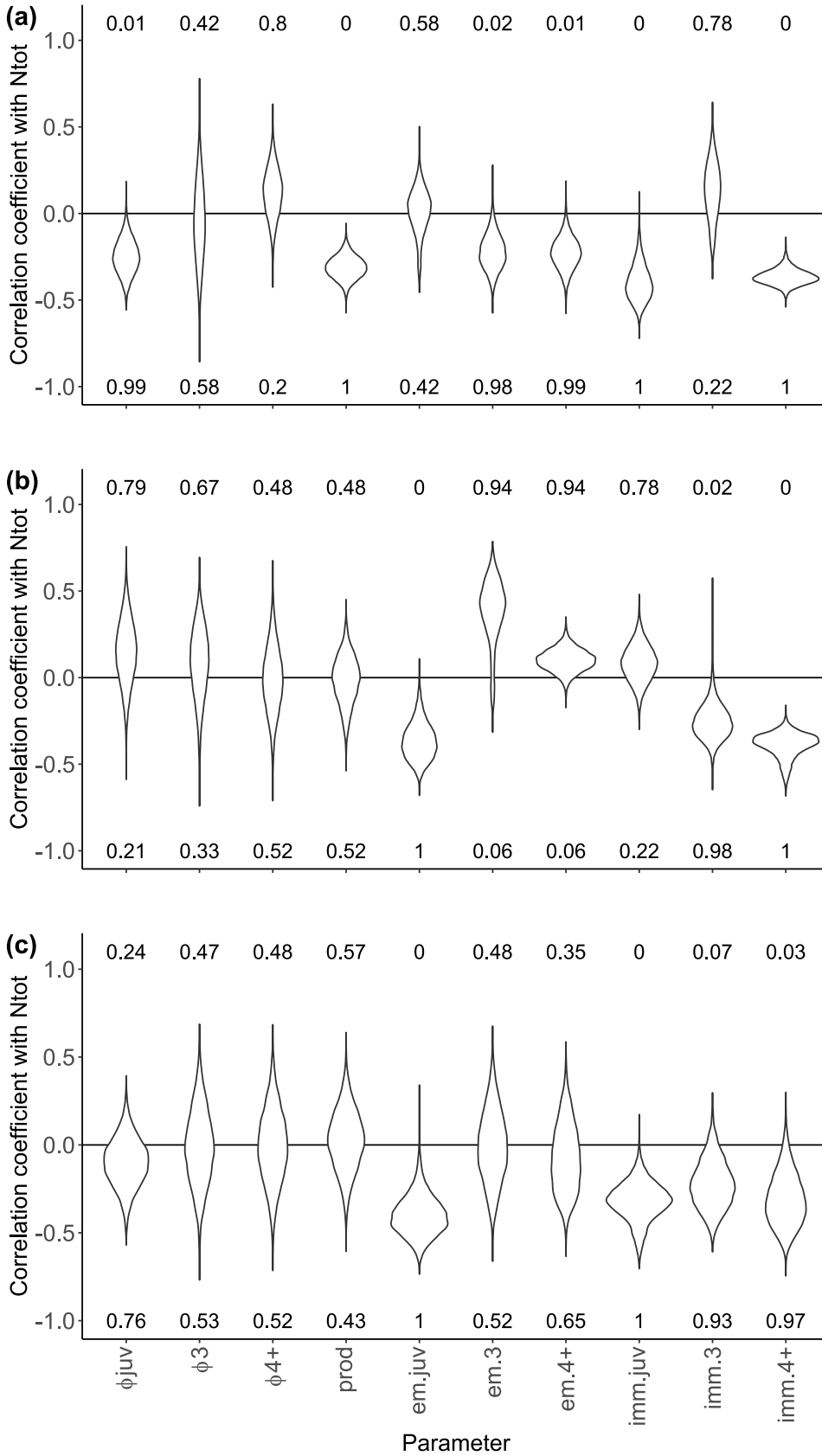


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754 **Fig. 7.** Violin plots of correlation coefficients between demographic parameters and number of
 755 breeding females Ntot at Rockabill (a), LIL (b) and Coquet (c). The probability of the coefficient
 756 being greater or lower than zero is indicated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



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