Modeling population dynamics of roseate terns (*Sterna dougallii*) in the Northwest Atlantic Ocean

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ABSTRACT

The endangered population of roseate terns (*Sterna dougallii*) in the Northwestern Atlantic Ocean consists of a network of large and small breeding colonies on islands. This type of fragmented population poses an exceptional opportunity to investigate dispersal, a mechanism that is fundamental in population dynamics and is crucial to understand the spatio-temporal and genetic structure of animal populations. Dispersal is difficult to study because it requires concurrent data compilation at multiple sites. Models of population dynamics in birds that focus on dispersal and include a large number of breeding sites are rare in literature. In this work, we propose a stochastic simulation model that captures the dispersal dynamics of this population of roseate terns. The colonization and decolonization (abandonment) of breeding colonies are modeled as discrete events that follow different dynamics than dispersal. We show that our model reproduces the properties of this population that have been observed in field data. We also analyzed the sensitivity of our model to alterations in different variables, and study the impact of these alterations in the model dynamics. Our results suggest that large colony population size exhibits a threshold sensitivity to adult survival, and that regional persistence is maintained by the larger populations.

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1. Introduction

Understanding the dynamics of populations is central to assessments of extinction risk, invasion, and community dynamics, as well as other topics (Rhodes et al., 1996). Dispersal is an important mechanism in population dynamics, and is fundamental to understanding metapopulation structure, source-sink dynamics, population synchrony, gene flow and genetic structure, as well as colonization, range shifts and species conservation (e.g. Hanski, 2001; Saura et al., 2014; Whitlock, 2001). However, dispersal is a difficult demographic parameter to study, especially in continuous habitats, because it requires detecting individuals at multiple locations (e.g. Jønsson et al., 2016; Koenig et al., 1996). Dispersal can be somewhat easier to study in discontinuous populations, such as those formed by colonial seabirds nesting on islands, but it still requires data collection at multiple sites, and large samples at each site may be required to estimate rates and dynamics of dispersal if

these are small (Crespin et al., 2006; Dolman, 2012; Opdam, 1991; Serrano et al., 2005).

Comprehensive models of populations in fragmented landscapes are uncommon for bird populations, particularly those distributed among a large number of breeding sites. Here, we present a population dynamics model for the population of roseate terns (*Sterna dougallii*; Aves, Laridae) that breeds on islands distributed along about 300 km of the Atlantic coast of the USA south and west of Cape Cod, Massachusetts. Although roseate terns have nested on 32 islands in recent decades, only 5–10 have been occupied in any one year (see Fig. 1, Tables 1 and 2). A few of the islands are occupied every year by large populations, while other islands contain small populations that persist for a while, disappear, and are later recolonized (Tables 1 and 2). This fits Dolman's categorization of a mainland-island metapopulation (where the 'mainland' in this case is the set of islands with large populations), and of a fragmented population having regional population effects (Dolman, 2012); for convenience, we will refer to our system as being a metapopulation (Harrison and Taylor, 1997; Stith et al., 1996). This metapopulation of terns has been studied intensively since 1988 (e.g. Nisbet et al., 2016; Spendelow et al., 2016), with

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Table 1
Site coordinates.

Colony site	Latitude	Longitude
Bird Island, Marion, MA	41°40′ N	70°43′ W
Dead Neck-Sampsons Island, MA	41°37′ N	70°25′ W
Ram Island, Mattapoisett, MA	41°37′ N	70°48′ W
Muskeget sandbars, Nantucket, MA	41°34′ N	70°30′ W
Muskeget Island, Nantucket, MA	41°34′ N	70°31′ W
Penikese Island, Gosnold, MA	41°27′ N	70°56′ W
Nashawena Island, Gosnold, MA	41°26′ N	70°52′ W
Little Beach, MV, MA	41°24′ N	70°30′ W
Haystack Point, MV, MA	41°24′ N	70°32′ W
Norton Point, MV, MA	41°21′ N	70°29′ W
Menemsha Pond, MV, MA	41°20′ N	70°46′ W
Shore Rock, Ocean Point., CT	41°18′ N	72°06′ W
Smith Point, Nantucket, MA	41°17′ N	70°13′ W
Tuxis Island, CT	41°16′ N	72°36′ W
Duck Island, CT	41°15′ N	72°28′ W
Falkner Island, CT	41°13′ N	72°39′ W
Great Gull Island, NY	41°12′ N	72°07′ W
Gardiners Point Island (Fort Tyler), NY	41°08′ N	72°09′ W
Gardiners Island, NY	41°06′ N	72°07′ W
Hicks Island, East Hampton, NY	41°01′ N	72°04′ W
Gardiners Island-Cartwright Point, NY	41°01′ N	72°06′ W
Young's Island, Smithtown, NY	40°55′ N	73°11′ W
Warner Island, Southampton, NY	40°51′ N	72°30′ W
Lanes Island, Southampton, NY	40°50′ N	72°31′ W
Greater Greenbacks Island, Southampton, NY	40°50′ N	72°32′ W
East Inlet Island, Brookhaven, NY	40°47′ N	72°45′ W
Pattersquash Island, Brookhaven, NY	40°45′ N	73°50′ W
Sexton Island, Islip, NY	40°39′ N	73°14′ W
Cedar Beach, Babylon, NY	40°38′ N	73°20′ W
Goose Flat, Babylon, NY	40°38′ N	73°23′ W
West End Jones Beach, Hempstead, NY	40°35′ N	73°33′ W
Breezy Point, Queens City, NY	40°33′ N	73°57′ W

some historical information dating back to 1870 (see Supplementary Material). It is thought to be demographically isolated from other metapopulations of the species in the North Atlantic region, with negligible rates of interchange of individuals (U.S. Fish and Wildlife Service, 2010). One of the challenging aspects of modeling its demography is that there exists a time lag of 3–4 years between the time chicks hatch, and the time they start breeding (Lebreton et al., 2003). Monitoring and Capture-Mark-Recapture (CMR) studies have yielded estimates of numbers of breeding pairs, breeding productivity, adult and juvenile survival and dispersal rates, and ages at first breeding, for all the large colonies and most of the medium-sized colonies in this metapopulation for all or part of the 28-year period (see Supplementary Material, Tables 2–10). However, estimates of demographic parameters are incomplete for some of the medium-sized colonies and for all the small colonies; the small colonies have been occupied transitorily, with frequent colonizations and decolonizations.

We developed a model based on stochastic estimates of the missing demographic parameters that aims to reproduce the observed statistical behavior of the actual metapopulation. Our model is based on assumptions about the spatio-temporal dynamics that describe the allocation of dispersing individuals (adults that do not return to the same site in successive years, and juveniles that do not return to their natal site when they recruit to the breeding population) among the breeding colonies within the system. Our goal was to construct a model that conforms to the following observed properties of the metapopulation: (1) total numbers remain within the range of 3000–8000 pairs over long periods of time (>50 years); (2) about 90% of the total numbers breed in 2–4 large colonies (500–2000 pairs), which remain large for periods of 20–50 years; (3) small colonies (≤10 pairs) are occupied and abandoned intermittently, and the majority of them do not reach medium nor large size; (4) the frequency of formation of a new large colony is about once every 30 years; (5) at about the same fre-

quency, one new medium-sized colony becomes established and persists for a long period (>30 years). A model that reproduces these features of the wild population could be used realistically for population viability analyses and for assessing potential effects of perturbations (e.g., climate change, predator introductions) and management actions.

2. Methods

To capture the dynamics of this system, we propose a population model consisting of a set of finite difference equations (FDEs). Our model reproduces the fecundity, survival and dispersal of a population distributed among M sites over T years. In this discrete-time model, each time step t, $1 \leq t \leq T$, represents a year in the system, and each site is denoted by an index i, $1 \leq i \leq M$. The number of breeding pairs in site i and year t is represented as $N_{i,t}$. Before describing the model equations, the following definitions are introduced:

Definition 1. We define the *annual proportion* $a_{i,t}$ of birds at site i at year t $1 \leq i \leq M$, $1 \leq t \leq T$ as the fraction of the total population in year t that breed at site i in that year: $a_{i,t} = N_{i,t}/\sum_{j=1}^{M} N_{j,t}$. We consider that adults that bred at site i in year t, and juveniles that were raised at the same site in year $t-4$, are 'attached' to site i. The time lag for returning juveniles is driven by the species' biology, where hatch-year birds migrate, stay in the non-breeding grounds for 1.5 years, visit breeding sites at age 2 years, and breed for the first time at ages 3 or 4 years (Lebreton et al., 2003; Nisbet, 2014). Our model ignores birds that breed at age 3 because these usually breed late in the season and raise few young (Nisbet, 2014). We also assume that 'unattached' birds, defined as those that emigrated from other breeding sites, are attracted to site i in proportion to the number of breeding pairs at site i relative to proportions at other sites.

Definition 2. We define the *intrinsic quality* q_i of site i as the average annual proportion of the population found at this site over all years. Intrinsic quality is calculated as $q_i = \sum_{t=k_1}^{k_{T_{max}}} a_{i,k_t}/(\sum_{j=1}^{M} \sum_{l=k_1}^{k_{T_{max}}} a_{j,k_l})$, where $k_1, \ldots, k_{T_{max}}$, $k_1 \leq k_{T_{max}}$ is the population size across the range of years for which historical data on the number of pairs on each site are available. In our case, this range spans from 1988 to 2015, i.e., $k_1 = 1988$ and $k_{T_{max}} = 2015$.

Definition 3. We define a 'small' site as one for which the maximum number of pairs found in the historical data is 10 (see Supplementary Material, Appendix S1). We define that a 'small' site i in year t is in *colonization mode* ($col_{i,t} = 1$) if it can receive immigrants from other sites in year $t+1$ and its productivity in the following year $t+1$ ($H_{i,t+1}$, see below) can be greater than 0. Likewise, we define that a small site is in *decolonization mode* ($decol_{i,t} = 1$) if it is not in colonization mode and cannot enter colonization mode in year $t+1$. It is important to note that a site cannot be simultaneously in colonization and decolonization modes, i.e., it is not possible that $col_{i,t} = 1 \wedge decol_{i,t} = 1$, for any $i, t | 1 \leq i \leq M, 1 \leq t \leq T$. However, it is possible that a site can be simultaneously in neither of these modes. As an example, a site may not receive immigrants nor produce juveniles at a given year t but may be eligible for colonization in year $t+1$. Large sites are always considered to be in colonization mode.

Both annual proportion and quality values were calculated from a dataset of nest counts at each site from 1988 to 2015 (see Supplementary Material, Table 2). We consider that $col_{i,1} = 0$ and $decol_{i,1} = 0$, $1 \leq i \leq M$ for small sites. In other words, in the initial state of the model, all small colonies are not in colonization mode but are susceptible to enter this mode from year 2 and on.

Table 2

Estimated numbers of breeding pairs of roseate terns (*Sterna dougallii*) at each site in each year, 1988–2015. Data were collected at each of 32 sites in the Northwest Atlantic metapopulation, 1988–2015 (see Table 1 for site coordinates). Each estimate is for the 'peak of season' and excludes late nests, many of which were established by first-time breeders.

Colony site	1988	1989	1990	1991	1992
Bird Island, Marion, MA	1572	1473	1547	1728	1375
Dead Neck-Sampsons Island, MA	13	27	0	0	0
Ram Island, Mattapoisett, MA	0	0	0	0	0
Muskeget sandbars, Nantucket, MA	0	0	0	0	0
Muskeget Island, Nantucket, MA	0	0	0	0	0
Penikese Island, Gosnold, MA	0	0	0	0	0
Nashawena Island, Gosnold, MA	3	0	3	0	4
Little Beach, MV, MA	0	0	0	0	0
Haystack Point, MV, MA	0	4	0	0	0
Norton Point, MV, MA	0	0	0	0	0
Menemsha Pond, MV, MA	0	0	0	2	0
Shore Rock, Ocean Point., CT	0	1	0	0	0
Smith Point, Nantucket, MA	0	0	0	0	0
Tuxis Island, CT	0	4	0	0	0
Duck Island, CT	2	5	0	0	0
Falkner Island, CT	157	96	150	149	107
Great Gull Island, NY	1004	960	1026	1204	964
Gardiners Point Island (Fort Tyler), NY	0	0	0	0	0
Gardiners Island, NY	0	0	0	0	0
Hicks Island, East Hampton, NY	0	0	2	4	4
Gardiners Island-Cartwright Point, NY	0	0	0	0	0
Young's Island, Smithtown, NY	0	0	0	0	0
Warner Island, Southampton, NY	0	6	17	40	39
Lanes Island, Southampton, NY	0	0	0	6	16
Greater Greenbacks Island, Southampton, NY	0	2	0	0	0
East Inlet Island, Brookhaven, NY	2	40	20	6	1
Pattersquash Island, Brookhaven, NY	0	0	0	0	0
Sexton Island, Islip, NY	0	0	0	0	0
Cedar Beach, Babylon, NY	93	66	94	120	80
Goose Flat, Babylon, NY	0	0	0	0	0
West End Jones Beach, Hempstead, NY	13	2	0	0	0
Breezy Point, Queens City, NY	0	0	0	0	0
Colony site	1993	1994	1995	1996	1997
Bird Island, Marion, MA	1319	1238	1250	996	1179
Dead Neck-Sampsons Island, MA	0	0	0	0	0
Ram Island, Mattapoisett, MA	0	76	197	719	253
Muskeget sandbars, Nantucket, MA	0	0	0	0	0
Muskeget Island, Nantucket, MA	0	0	0	0	0
Penikese Island, Gosnold, MA	0	0	0	0	0
Nashawena Island, Gosnold, MA	0	0	0	0	0
Little Beach, MV, MA	0	0	0	0	0
Haystack Point, MV, MA	0	0	0	0	0
Norton Point, MV, MA	0	0	0	0	0
Menemsha Pond, MV, MA	0	0	0	0	0
Shore Rock, Ocean Point., CT	0	0	0	0	0
Smith Point, Nantucket, MA	0	0	0	0	0
Tuxis Island, CT	0	1	0	0	0
Duck Island, CT	0	0	0	0	0
Falkner Island, CT	130	123	125	135	136
Great Gull Island, NY	1040	1138	1056	1064	1455
Gardiners Point Island (Fort Tyler), NY	0	0	157	4	23
Gardiners Island, NY	0	0	0	0	0
Hicks Island, East Hampton, NY	0	0	0	0	0
Gardiners Island-Cartwright Point, NY	4	14	0	1	5
Young's Island, Smithtown, NY	0	0	0	0	0
Warner Island, Southampton, NY	28	53	34	24	41
Lanes Island, Southampton, NY	12	35	59	36	16
Greater Greenbacks Island, Southampton, NY	0	0	0	0	2
East Inlet Island, Brookhaven, NY	12	0	0	0	0
Pattersquash Island, Brookhaven, NY	0	0	0	0	0
Sexton Island, Islip, NY	0	0	0	0	0
Cedar Beach, Babylon, NY	51	58	37	0	0
Goose Flat, Babylon, NY	0	0	0	0	9
West End Jones Beach, Hempstead, NY	0	0	0	0	0
Breezy Point, Queens City, NY	2	2	2	2	4
Colony site	1998	1999	2000	2001	2002
Bird Island, Marion, MA	1113	1148	1130	1062	505
Dead Neck-Sampsons Island, MA	0	0	0	0	0
Ram Island, Mattapoisett, MA	543	630	988	626	952
Muskeget sandbars, Nantucket, MA	0	0	0	0	0
Muskeget Island, Nantucket, MA	0	5	0	0	0
Penikese Island, Gosnold, MA	0	0	0	0	0
Nashawena Island, Gosnold, MA	0	0	0	0	0

Table 2 (*Continued*)

Colony site	1988	1989	1990	1991	1992
Little Beach, MV, MA	0	0	0	0	0
Haystack Point, MV, MA	0	0	0	0	0
Norton Point, MV, MA	0	0	0	0	0
Menemsha Pond, MV, MA	0	0	0	0	0
Shore Rock, Ocean Point., CT	0	0	0	0	0
Smith Point, Nantucket, MA	0	0	0	0	0
Tuxis Island, CT	0	0	0	0	0
Duck Island, CT	0	0	0	0	0
Falkner Island, CT	115	110	110	95	65
Great Gull Island, NY	1690	1747	1762	1562	1505
Gardiners Point Island (Fort Tyler), NY	0	0	0	0	0
Gardiners Island, NY	46	2	0	0	0
Hicks Island, East Hampton, NY	0	0	0	0	0
Gardiners Island-Cartwright Point, NY	0	2	0.00	6	156
Young's Island, Smithtown, NY	0	0	0	0	0
Warner Island, Southampton, NY	31	28	9	0	0
Lanes Island, Southampton, NY	32	14	18	5	0
Greater Greenbacks Island, Southampton, NY	2	0	0	4	1
East Inlet Island, Brookhaven, NY	0	0	0	0	0
Pattersquash Island, Brookhaven, NY	0	0	0	0	0
Sexton Island, Islip, NY	0	0	0	0	0
Cedar Beach, Babylon, NY	0	0	0	0	0
Goose Flat, Babylon, NY	16	1	2	4	1
West End Jones Beach, Hempstead, NY	0	0	0	0	0
Breezy Point, Queens City, NY	5	0	0	0	0
Colony site	2003	2004	2005	2006	2007
Bird Island, Marion, MA	904	554	680	1111	919
Dead Neck-Sampsons Island, MA	0	0	0	0	0
Ram Island, Mattapoisett, MA	557	936	724	463	661
Muskeget sandbars, Nantucket, MA	0	0	0	0	0
Muskeget Island, Nantucket, MA	0	0	0	0	0
Penikese Island, Gosnold, MA	251	9	76	48	102
Nashawena Island, Gosnold, MA	0	0	0	0	0
Little Beach, MV, MA	0	0	0	0	0
Haystack Point, MV, MA	0	0	0	0	0
Norton Point, MV, MA	0	0	0	0	0
Menemsha Pond, MV, MA	0	0	0	0	0
Shore Rock, Ocean Point., CT	0	0	0	0	0
Smith Point, Nantucket, MA	0	0	0	0	0
Tuxis Island, CT	0	0	0	0	0
Duck Island, CT	0	0	0	0	0
Falkner Island, CT	45	37	44	62	54
Great Gull Island, NY	1613	1352	1195	1227	1546
Gardiners Point Island (Fort Tyler), NY	2	0	0	0	0
Gardiners Island, NY	0	0	0	0	0
Hicks Island, East Hampton, NY	0	nd	0	0	0
Gardiners Island-Cartwright Point, NY	155	248	90	80	216
Young's Island, Smithtown, NY	1	0	0	0	0
Warner Island, Southampton, NY	1	1	0	0	0
Lanes Island, Southampton, NY	4	4	2	0	2
Greater Greenbacks Island, Southampton, NY	0	0	0	2	2
East Inlet Island, Brookhaven, NY	0	0	0	0	0
Pattersquash Island, Brookhaven, NY	0	0	2	0	0
Sexton Island, Islip, NY	2	2	2	0	0
Cedar Beach, Babylon, NY	0	0	0	0	0
Goose Flat, Babylon, NY	0	11	11	25	2
West End Jones Beach, Hempstead, NY	0	0	0	0	0
Breezy Point, Queens City, NY	0	0	0	0	0
Colony site	2008	2009	2010	2011	2012
Bird Island, Marion, MA	747	708	735	937	814
Dead Neck-Sampsons Island, MA	0	0	0	0	0
Ram Island, Mattapoisett, MA	566	588	584	377	439
Muskeget sandbars, Nantucket, MA	0	0	0	0	0
Muskeget Island, Nantucket, MA	0	0	0	0	0
Penikese Island, Gosnold, MA	66	43	37	34	9
Nashawena Island, Gosnold, MA	0	0	0	0	0
Little Beach, MV, MA	0	0	0	0	0
Haystack Point, MV, MA	0	0	0	0	0
Norton Point, MV, MA	0	50	36	0	5
Menemsha Pond, MV, MA	0	0	0	0	0
Shore Rock, Ocean Point., CT	0	0	0	0	0
Smith Point, Nantucket, MA	0	0	0	0	0
Tuxis Island, CT	0	0	0	0	0
Duck Island, CT	0	0	0	0	0
Falkner Island, CT	32	28	45	48	36
Great Gull Island, NY	1288	1413	1303	1439	1596

Table 2 (Continued)

Colony site	1988	1989	1990	1991	1992
Gardiners Point Island (Fort Tyler), NY	0	0	0	0	0
Gardiners Island, NY	0	0	0	0	0
Hicks Island, East Hampton, NY	0	0	0	0	0
Gardiners Island-Cartwright Point, NY	27	27	0	0	0
Young's Island, Smithtown, NY	0	0	0	0	0
Warner Island, Southampton, NY	0	0	0	0	0
Lanes Island, Southampton, NY	0	0	0	0	0
Greater Greenbacks Island, Southampton, NY	2	2	0	0	0
East Inlet Island, Brookhaven, NY	0	0	0	0	0
Pattersquash Island, Brookhaven, NY	0	0	0	0	0
Sexton Island, Islip, NY	0	0	0	0	0
Cedar Beach, Babylon, NY	0	0	0	0	0
Goose Flat, Babylon, NY	1	0	0	0	0
West End Jones Beach, Hempstead, NY	0	0	0	0	0
Breezy Point, Queens City, NY	0	0	0	0	0
Colony site	2013	2014	2015		
Bird Island, Marion, MA	772	1121	1127		
Dead Neck-Sampsons Island, MA	0	0	0		
Ram Island, Mattapoisett, MA	535	682	735		
Muskeget sandbars, Nantucket, MA	0	0	0		
Muskeget Island, Nantucket, MA	0	0	0		
Penikese Island, Gosnold, MA	0	20	23		
Nashawena Island, Gosnold, MA	0	0	0		
Little Beach, MV, MA	0	0	7		
Haystack Point, MV, MA	0	0	0		
Norton Point, MV, MA	35	0	35		
Menemsha Pond, MV, MA	0	0	0		
Shore Rock, Ocean Point., CT	0	0	0		
Smith Point, Nantucket, MA	0	0	0		
Tuxis Island, CT	0	0	0		
Duck Island, CT	0	0	0		
Falkner Island, CT	26	21	36		
Great Gull Island, NY	1543	1459	1659		
Gardiners Point Island (Fort Tyler), NY	0	0	0		
Gardiners Island, NY	0	0	0		
Hicks Island, East Hampton, NY	0	0	0		
Gardiners Island-Cartwright Point, NY	0	0	0		
Young's Island, Smithtown, NY	0	0	0		
Warner Island, Southampton, NY	0	0			
Lanes Island, Southampton, NY	0	0	0		
Greater Greenbacks Island, Southampton, NY	0	0	0		
East Inlet Island, Brookhaven, NY	0	0	0		
Pattersquash Island, Brookhaven, NY	0	0	0		
Sexton Island, Islip, NY	0	0	0		
Cedar Beach, Babylon, NY	0	0	0		
Goose Flat, Babylon, NY	0	0	0		
West End Jones Beach, Hempstead, NY	0	0	0		
Breezy Point, Queens City, NY	0	0	0		

Source: U.S. Fish and Wildlife Service (2010) and subsequent data compiled by C. S. Mostello for the Roseate Tern Recovery Team. CT: Connecticut; MA: Massachusetts; MV: Martha's Vineyard; NY: New York (Long Island).

The model equations are defined as follows: If no colonization or decolonization event occurs on site i and year t, then $N_{i,t+1} = round((AS_{i,t} + JS_{i,t} + I_{i,t+1}))$, where *round* is the standard round function for real numbers; i.e., rounding to the nearest integer. The terms in this equation are defined as follows:

- $AS_{i,t}$ (for Adults Staying) represents the number of adult pairs that breed at site i in year t and return to breed at the same site in year $t+1$. $AS_{i,t}$ is calculated as $AS_{i,t} = \omega_{i,t} \times \phi_{i,t} \times N_{i,t}$, where $\omega_{i,t}$ is the proportion of adult birds that survive between consecutive years, and $\phi_{i,t}$ is the site fidelity ratio; that is, the proportion of pairs that breed at site i in year t and return to the same site in year $t+1$, conditional to survival in year t. $\omega_{i,t}$ was estimated using a log-linear regression model $\omega_{i,t} = 1/(1 + \exp(\omega^0 + \omega^1 \times q_i + \omega^2 \times a_{i,t})) + \epsilon^{\omega_{i,t}}$, where $\epsilon^{\omega_{i,t}}$ is the model error for site i and year t. The ground-truth values for $\omega_{i,t}$ are shown in Table 6. The model coefficients are $\omega^0 = 1.53$, $\omega^1 = 9.368 \times 10^{-5}$ and $\omega^2 = -3.161 \times 10^{-1}$. Values for $\phi_{i,t}$ are estimated using the log-linear regression model $\phi_{i,t} = 1/(1 + \exp(\phi^0 + \phi^1 \times q_i + \phi^2 \times a_{i,t})) + \epsilon^{\phi_{i,t}}$. The ground-truth values for $\phi_{i,t}$ were obtained from the frequencies of

same-site transitions shown in Fig. 2 in Spendelow et al. (2016), and the model coefficients are $\phi^0 = 0.931$, $\phi^1 = 3.818$ and $\phi^2 = -0.741$.

- $JS_{i,t}$ (for Juveniles Staying) represents the number of juvenile birds (counted as pairs) raised to fledging at site i in year $t-3$ that survive to enter the breeding population and breed in site i in year $t+1$. We assume that all surviving juveniles enter the breeding population at age 4 (see caption to Table 8). $JS_{i,t}$ is calculated as $JS_{i,t} = col_i \times H_{i,t-3} \times \gamma_{i,t-3} \times \rho_{i,t} \times N_{i,t-3}/2$, where:
  - $H_{i,t-3}$ represents the productivity as the mean number of chicks reared to fledging per pair at site i in year $t-3$. We used the log-linear regression model: $H_{i,t} = maxH/(1 + \exp(H^0 + H^1 \times N_{i,t} + H^2 \times q_i)) + \epsilon^{H_{i,t}}$ to estimate productivity values. The ground-truth values for $H_{i,t}$ were derived from a dataset on average productivity at most sites in years 1998 to 2015 (Table 3). $maxH = 1.82$ is the maximum productivity value from this dataset, and is a scaling factor for the log-linear model. Based on empirical data and using log-linear regression, the model coefficients were estimated to be $H^0 = -0.214$, $H^1 = 0$ and $H^2 = -0.006$.

Table 3

Estimated productivity of roseate terns (*Sterna dougallii*) at each of 32 sites in the Northwest Atlantic metapopulation, 1988–2015. Productivity is the average number of chicks raised to fledging per breeding pair. *xx* means that one or more breeding pairs were present (Table 2) but productivity was not estimated. Empty cells are site-year combinations for which no breeding pairs were reported (Table 2). For site coordinates (latitude and longitude), see Table 1. Productivity data are incomplete for years prior to 1998.

Colony site	1998	1999	2000	2001	2002
Bird Island, Marion, MA	1.40	1.40	1.10	1.00	1.02
Ram Island, Mattapoisett, MA	1.45	1.04	1.11	1.05	0.96
Muskeget sandbars, Nantucket, MA		xx			
Penikese Island, Gosnold, MA					
Nashawena Island, Gosnold, MA					
Haystack Point, MV, MA					
Norton Point, MV, MA					
Falkner Island, CT	0.74	0.70	0.75	0.72	0.18
Great Gull Island, NY	1.50	1.40	1.27	1.13	0.90
Gardiners Point Island (Fort Tyler), NY					
Gardiners Island, NY	xx	1.00			
Gardiners Island-Cartwright Point, NY		xx		0.75	xx
Young's Island, Smithtown, NY					
Warner Island, Southampton, NY	1.05	1.17	0.00		
Lanes Island, Southampton, NY	xx	0.00	0.00	0.00	
Greater Greenbacks Island, Southampton, NY	xx			xx	xx
Pattersquash Island, Brookhaven, NY					
Sexton Island, Islip, NY					
Goose Flat, Babylon, NY	xx	xx	xx	xx	xx
Breezy Point, Queens City, NY	xx				
Colony site	2003	2004	2005	2006	2007
Bird Island, Marion, MA	1.25	1.25	0.95	1.29	1.26
Ram Island, Mattapoisett, MA	1.14	0.92	0.93	1.00	1.16
Muskeget sandbars, Nantucket, MA					
Penikese Island, Gosnold, MA	0.87	0.97	0.79	0.44	1.54
Nashawena Island, Gosnold, MA					
Haystack Point, MV, MA					
Norton Point, MV, MA					
Falkner Island, CT	0.26	0.53	0.67	0.34	0.54
Great Gull Island, NY	1.00	1.17	1.60	1.30	0.90
Gardiners Point Island (Fort Tyler), NY	xx				
Gardiners Island, NY					
Gardiners Island-Cartwright Point, NY	xx	xx	xx	xx	xx
Young's Island, Smithtown, NY	0.00				
Warner Island, Southampton, NY	0.00	xx			
Lanes Island, Southampton, NY	xx	xx	xx		xx
Greater Greenbacks Island, Southampton, NY				xx	xx
Pattersquash Island, Brookhaven, NY			xx		
Sexton Island, Islip, NY	xx	xx	xx		
Goose Flat, Babylon, NY		xx	1.82	xx	xx
Breezy Point, Queens City, NY					
Colony site	2008	2009	2010	2011	2012
Bird Island, Marion, MA	1.12	1.44	1.33	1.23	1.12
Ram Island, Mattapoisett, MA	1.25	1.04	1.30	1.10	1.31
Muskeget sandbars, Nantucket, MA					
Penikese Island, Gosnold, MA	1.42	0.73	xx	xx	0.11
Nashawena Island, Gosnold, MA		0.00			
Haystack Point, MV, MA					
Norton Point, MV, MA		xx	0.20		1.30
Falkner Island, CT	1.06	1.15	0.98	0.91	0.87
Great Gull Island, NY	0.98	1.10	1.40	1.30	0.80
Gardiners Point Island (Fort Tyler), NY					
Gardiners Island, NY					
Gardiners Island-Cartwright Point, NY	xx	xx			
Young's Island, Smithtown, NY					
Warner Island, Southampton, NY					
Lanes Island, Southampton, NY					
Greater Greenbacks Island, Southampton, NY	xx	xx			
Pattersquash Island, Brookhaven, NY					
Sexton Island, Islip, NY					
Goose Flat, Babylon, NY	xx				
Breezy Point, Queens City, NY					
Colony site	2013	2014	2015		
Bird Island, Marion, MA	1.34	0.85	0.86		
Ram Island, Mattapoisett, MA	1.31	0.98	0.87		
Muskeget sandbars, Nantucket, MA					
Penikese Island, Gosnold, MA		1.08	1.12		
Nashawena Island, Gosnold, MA					
Haystack Point, MV, MA			0.00		
Norton Point, MV, MA	1.20		xx		

Table 3 (*Continued*)

Colony site	1998	1999	2000	2001	2002
Falkner Island, CT	1.00	0.64	1.02		
Great Gull Island, NY	1.16	1.00	1.25		
Gardiners Point Island (Fort Tyler), NY					
Gardiners Island, NY					
Gardiners Island-Cartwright Point, NY					
Young's Island, Smithtown, NY					
Warner Island, Southampton, NY					
Lanes Island, Southampton, NY					
Greater Greenbacks Island, Southampton, NY					
Pattersquash Island, Brookhaven, NY					
Sexton Island, Islip, NY					
Goose Flat, Babylon, NY					
Breezy Point, Queens City, NY					

Source: U.S. Fish and Wildlife Service (2010) and subsequent data compiled by C. S. Mostello for the Roseate Tern Recovery Team. MV: Martha's Vineyard.
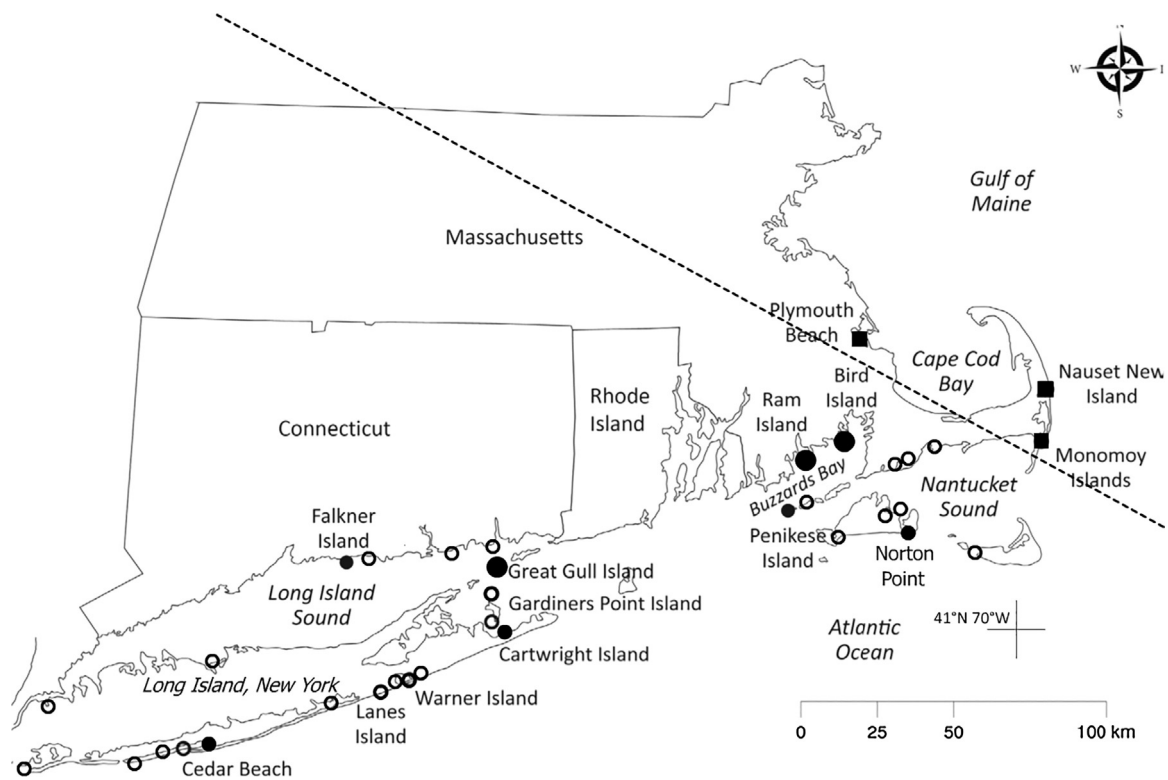
Fig. 1. Map of the colony sites composing the modeled population. Open circles: 'small' colony sites; small closed circles: 'medium' colony sites; large closed circles: 'large' colony sites. The dashed line marks the boundary of the modeled population; the colonies to the right of this line are not included in our model.

- $\gamma_{i,t-3}$ represents the survival rate of juveniles raised at site i in year $t-3$ to year $t+1$. $\gamma_{i,t-3}$ was estimated using a log-linear regression model $\gamma_{i,t-3} = \gamma_w \times \omega_{i,t}^2 / (1 + \exp(\gamma^0 + \gamma^1 \times q_i)) + \epsilon^{\gamma_{i,t}}$. The ground-truth values for $\gamma_{i,t}$ are shown in Table 7, and the model coefficients were adjusted as $\gamma^0 = -0.510$ and $\gamma^1 = 2.56$. This estimated value was multiplied by $\omega_{i,t}^2$ to yield survival to age 4. This value is multiplied by a scaling factor γ_w empirically adjusted to 1.218, that minimizes the difference between the number of pairs in large sites at the end of the model simulation and in the historical data (Table 2).

- $\rho_{i,t}$ represents juvenile philopatry; that is, the proportion of birds that were reared at site i in year $t-3$ and first bred at site i in year $t+1$, conditional on survival to age 4. $\rho_{i,t}$ is calculated as $\rho_{i,t} = \phi_{i,t} \times \eta_i$, where η_i represents the ratio of juvenile fidelity divided by adult fidelity in site i and year t. We estimated these values using the log-linear regression model $\eta_i = 1/(1 + \exp(\eta^0 + \eta^1 \times N_{i,t})) + \epsilon^{\eta_i}$. The ground-truth values for η_i were obtained by dividing the values in the diagonals of

Tables 9 and 10, and the model coefficients were adjusted as $\eta^0 = 0.444$ and $\eta^1 = 0.002$.

The equations describing $JS_{i,t}$ and $JL_{i,t}$ (see below) include a factor of 1/2 to convert from individual juveniles ($H_{i,t-3}$) to pairs of adults; this was done for calculational convenience.

- $AL_{i,t}$ (for Adults Leaving) represents the number of pairs of adult birds that bred at site i in year t, survived to year $t+1$ but did not breed at site i in year $t+1$. $AL_{i,t}$ is calculated as $AL_{i,t} = (1 - \phi_{i,t}) \times \omega_{i,t} \times N_{i,t}$.

- $JL_{i,t}$ (for Juveniles Leaving) represents the number of pairs of juvenile birds that were raised to fledging at site i in year $t-3$, survived to breed for the first time in year t, but did not breed at site i in year $t+1$. $JL_{i,t}$ is calculated as $JL_{i,t} = H_{i,t-3} \times \gamma_{i,t} \times (1 - \rho_{i,t}) \times N_{i,t-3}/2$.

- $I_{i,t}$ for (Immigrants) represents the pairs that breed at site i in year $t+1$ that did not breed at site i in year t. $I_{i,t}$ is calculated as follows. First, a pool with the total number of pairs leaving their site and available for immigration into all sites is calculated as $pool_t =$

Table 4
Changes in numbers of breeding pairs at colonies within the WWG, 1988–2015.

Pairs in year t	Pairs in year $t+1$						
	0	1	2	3	4	5	6–10
0	541	4	11	1	6	2	2
1	7	1	1			1	
2	12	1	9		3	1	
3	2						
4	6	2	1	2		1	
5	5						
6–10	2	1					
11–20	2	1	1			1	1
21–50	6		2				2
51–100							
101–300						1	1
300–800							
801–1200							
1200–1800							

Pairs in year t	11–20	21–50	51–100	101–300	300–800	801–1200	1200–1800
0	2	3	2	2			
1	1						
2		1					
3							
4	1	1					
5		1					
06–10	3		1				
11–20	3	6					
21–50	3	19	3	1			
51–100		7	7	5			
101–300		1	5	12	2		
300–800				15	7		
801–1200				7	14	2	
1200–1800					3	23	

Source: Table 2.

Table 5
Probability of decolonization in relation to colony size.

Pairs in year t	Number of cases	Probability of decolonization
1	11	64%
2	27	44%
3	2	100%
4	14	43%
5	6	83%
6–10	7	29%
11–20	15	13%
21–50	36	14%
>50	93	0%

Source: Table 2.

$\sum_{j=1}^{M}(AL_{j,t}+JL_{j,t}) - settlers_t + desettlers_t$. The terms $settlers_t$ and $desettlers_t$ refer to the sum of all pairs that colonize and decolonize any site in year t, and they are explained below.

We define a model $RID_{i,t}$ for the relative distribution of this pool across the sites in year t as a weighted sum of a deterministic component $ID_{i,t}$ and a stochastic component $IS_{i,t}$. The deterministic component is a log-linear regression model $ID_{i,t} = 1/(1 + \exp(ID^0 + ID^1 \times q_i + ID^2 \times a_{i,t})) + \epsilon_{i,t}^{ID}$.

The ground-truth values for $ID_{i,t}$ were calculated as $(\sum_{j=1, j \neq i}^{M} p_{j,i,t} \times N_{j,t})/(\sum_{j=1, j \neq i}^{M} \sum_{k=1, k \neq j}^{M} p_{j,k,t} \times N_{j,t})$, where values $p_{j,i,t}$ are the proportion of birds that leave site j in year t and breed in site i in year $t+1$. These values are taken for transitions for adults between large sites from Table 4 in Spendelow et al. (2016) (Table 8) We assume that transition values for adults and juveniles are quantitatively similar. The model coefficients were adjusted as $ID^0 = -0.485$, $ID^1 = -6.025$ and $ID^2 = 2.117$.

The stochastic component $IS_{i,t}$ is drawn from a normal distribution $IS_{i,t} \sim \mathcal{N}(\mu, \sigma^2)$ with mean ($\mu = 0.241$) and standard deviation ($\sigma = 0.176$) derived from the ground-truth values for

Table 6
Site-specific estimates (mean ± standard error) of annual survival of adult roseate terns during three time periods between 1988 and 2008. Survival of the 1991 cohort was severely reduced by a hurricane that passed through the staging area in August 1991.

Site	Study period		
	1988–1990 and 1992–1999	1991	2000–2008
Falkner Island	0.863 ± 0.010	0.667 ± 0.035	0.805 ± 0.019
Great Gull Island	0.788 ± 0.012	0.807 ± 0.067	0.822 ± 0.013
Bird Island	0.851 ± 0.007	0.751 ± 0.027	0.830 ± 0.007
Ram Island	0.822 ± 0.017	–	0.841 ± 0.008
Penikese Island	–	–	0.771 ± 0.028

Source: Spendelow et al. (2008) and Spendelow et al. (2016), Table 10 in Lebreton et al. (2003).

Table 7
Estimates of survival probability of juvenile roseate terns raised at the three major sites in the WWG from fledging to age 2 years over 10 years, 1988–1997. ± denotes standard error. Survival of the 1991 cohort was severely reduced by a hurricane that passed through the staging area in August 1991.

Time period	Site		
	Falkner Island	Bird Island	Great Gull Island
1998–1990	0.310 ± 0.111	0.325 ± 0.087	0.352 ± 0.147
1989–1991	0.320 ± 0.148	0.340 ± 0.090	0.505 ± 0.165
1990–1992	0.336 ± 0.127	0.378 ± 0.088	0.490 ± 0.144
1991–1993	0.063 ± 0.057	0.185 ± 0.095	0.065 ± 0.044
1992–1994	0.593 ± 0.227	0.748 ± 0.204	0.496 ± 0.167
1993–1995	0.547 ± 0.172	0.275 ± 0.109	0.498 ± 0.159
1994–1996	0.354 ± 0.154	0.415 ± 0.150	0.354 ± 0.154
1995–1997	0.407 ± 0.249	0.046 ± 0.066	0.434 ± 0.259

Source: Table 11 in Lebreton et al. (2003).

$ID_{i,t}$. The stochasticity of the model rn is calculated as the average squared standard error of $ID_{i,t}$. We calculate this error as $rn = \sqrt{(\sum_{j=1}^{M'} \sum_{l=k_1}^{k_{T\max}} (epsilon_{j,l}^{ID})^2)/(M' \times T_{\max})}$, where, j, $1 \leq j \leq M'$ and $k_1, \ldots, k_{T\max}$ represent the sites and years for which transition data across sites is available; in our case, large sites from 1988 through 2008.

The relative immigration distribution $RID_{i,t}$ is defined as: $RID_{i,t} = ((1 - rn) \times ID_{i,t} + rn \times IS_{i,t}) \times (\sum_{j=1}^{M} d_{i,j} \times N_{i,t})$, where $d_{i,j}$, $1 \leq i, j \leq M$ is the distance in kilometers between sites i and j. The component $\sum_{j=1}^{M} d_{i,j} \times N_{i,t}$ introduces a penalizing factor for sites with neighboring attractive breeding sites. This distribution is normalized, i.e., $RID_{i,t}^{Norm} = RID_{i,t}/(\sum_{j=1}^{M} RID_{j,t})$. Finally, $I_{i,t}$ is calculated as $I_{i,t} = col_{i,t} \times RID_{i,t}^{Norm} \times (pool_t - AL_{i,t} - JL_{i,t})$.

Non-large sites are subjected to colonization and decolonization events. The probabilities for colonization $P(col_i = 1)$ and decolonization $P(decol_i = 1)$ are site-specific, and are modeled as the probability for each site i to transit from having 0 pairs in year t ($N_{i,t} = 0$) to 1 or more pairs in year $t+1$ ($N_{i,t+1} > 0$), and the probability to transit from $N_{i,t} > 0$ to $N_{i,t} = 0$, respectively. These are estimated as sample probabilities from Table 2:

$$P(col_i = 1) = \sum_{l=k_1}^{k_{T\max}} Pred(N_{i,l} = 0) \times Pred(N_{i,l+1} > 0) / \left(\sum_{l=k_1}^{k_{T\max}} Pred(N_{i,l} = 0) \right) \quad (1)$$

and

$$P(decol_i = 1) = \sum_{l=k_1}^{k_{T\max}} Pred(N_{i,l} > 0) \times Pred(N_{i,l+1} = 0) / \left(\sum_{l=k_1}^{k_{T\max}} Pred(N_{i,l} > 0) \right) \quad (2)$$

where $k_1 = 1988$ and $k_{T\max} = 2015$ and $Pred(N_{i,l} = 0)$ and $Pred(N_{i,l} > 0)|1 \leq i \leq M$, $l = k_1 \leq l \leq k_{T\max}$ are predicates that evaluate to 1 if $N_{i,l} = 0$ and $N_{i,l} > 0$, respectively, and evaluate to 0 otherwise.

Table 8
Ages at first breeding of roseate terns at the three major colony sites in the WWG, 1988–1997.

Breeding site	Age (years)			
	2	3	4	5
Falkner Island	0.010 ± 0.012	0.515 ± 0.085	0.620 ± 0.145	0.912 ± 0.244
Bird Island	0.046 ± 0.036	0.674 ± 0.180	1.000	1.000
Great Gull Island	0.019 ± 0.023	0.448 ± 0.159	0.668 ± 0.411	1.000

Source: Lebreton et al. (2003). Each entry is the estimate (± standard error) of the probability that a bird that survived to ages 2, 3, 4, 5 years would have entered the breeding population at that age. Estimates are averaged over all years. For the model developed in this paper, we simplify this table by assuming that all roseate terns breed for the first time at age 4, because birds that bred at ages 2 and 3 would not have been included in the 'peak of season' nest counts that are the source of population numbers (see text of Supplementary Material).

Table 9
Probabilities of breeding dispersal, conditional on survival, for adult roseate terns among 5 'large' and 'medium' colonies in 5 time periods between 1988 and 2008. Standard errors are in parentheses. – indicates that one or both sites were not occupied in the specified time periods.

	Time period				
	1988–1992	1993	1994–2001	2002	2003–2008
Bird Island → Falkner Island	0.004 (0.001)	0.000	0.002 (0.001)	0.003 (0.002)	0.000
Bird Island → Great Gull Island	0.021 (0.005)	0.000	0.011 (0.002)	0.004 (0.007)	0.011 (0.003)
Bird Island → Penikese Island	–	–	–	0.101 (0.013)	0.035 (0.004)
Bird Island → Ram Island	–	0.009 (0.004)	0.211 (0.014)	0.114 (0.021)	0.145 (0.008)
Falkner Island → Bird Island	0.015 (0.004)	0.078 (0.018)	0.010 (0.003)	0.000	0.012 (0.007)
Falkner Island → Great Gull Island	0.077 (0.012)	0.047 (0.017)	0.080 (0.010)	0.097 (0.040)	0.062 (0.021)
Falkner Island → Penikese Island	–	–	–	0.017 (0.012)	0.000
Falkner Island → Ram Island	–	0.004 (0.004)	0.009 (0.003)	0.000	0.007 (0.006)
Great Gull Island → Bird Island	0.037 (0.005)	0.064 (0.013)	0.014 (0.002)	0.011 (0.006)	0.007 (0.002)
Great Gull Island → Falkner Island	0.022 (0.004)	0.026 (0.007)	0.016 (0.002)	0.004 (0.004)	0.006 (0.002)
Great Gull Island → Penikese Island	–	–	–	0.016 (0.006)	0.008 (0.002)
Great Gull Island → Ram Island	–	0.012 (0.005)	0.014 (0.003)	0.012 (0.008)	0.015 (0.003)
Penikese Island → Bird Island	–	–	–	–	0.315 (0.027)
Penikese Island → Falkner Island	–	–	–	–	0.007 (0.005)
Penikese Island → Great Gull Island	–	–	–	–	0.026 (0.011)
Penikese Island → Ram Island	–	–	–	–	0.384 (0.030)
Ram Island → Bird Island	–	–	0.234 (0.014)	0.228 (0.030)	0.197 (0.010)
Ram Island → Falkner Island	–	–	0.001 (0.001)	0.000	0.001 (0.001)
Ram Island → Great Gull Island	–	–	0.018 (0.004)	0.004 (0.004)	0.013 (0.003)
Ram Island → Penikese Island	–	–	–	0.100 (0.015)	0.029 (0.004)

Source: Spendelow et al. (2010), Table 8 in Lebreton et al. (2003).

Table 10
Juvenile dispersal rates of Roseate Terns among the three major sites in the WWG, 1988–1997.

First breeding site	Second breeding site		
	Falkner Island	Bird Island	Great Gull Island
Falkner Island	0.582*	0.004 ± 0.004	0.020 ± 0.009
Bird Island	0.047 ± 0.060	0.913*	0.082 ± 0.038
Great Gull Island	0.378 ± 0.130	0.082 ± 0.042	0.898*

Source: Table 7 in Lebreton et al. (2003). Each entry is the estimate (± standard error) of the probability that a bird raised as a chick at one site would breed for the first time at another site, conditional on survival to first breeding. Values on the diagonal (*) are fidelity rates (1 − sum of emigration rates); standard errors were not estimated for fidelity rates. Estimates are averaged over all years.

For each year t and site i, a random number is drawn from a uniform distribution $u_{i,t} \sim U(0, 1)$. If $N_{i,t} = 0$, $decol_{i,t} = 0$ and $u_{i,t} < P(col_i = 1)$, small or medium-sized site i enters colonization mode in year $t+1$ ($col_{i,t+1} = 1$). Likewise, if $N_{i,t} > 0$, $col_{i,t} = 0$ and $u_{i,t} < P(decol_i = 1)$, small or medium-sized site i enters decolonization mode in year $t+1$ ($decol_{i,t+1} = 1$).

When a small or medium-sized site enters colonization mode, a number of pairs breed for the first time into the site. This number of pairs is drawn from a Poisson distribution ($N_{i,t+1} \sim \mathcal{P}(\lambda = ExpSettlers)$), where $ExpSettlers$ is the expected number of pairs that colonize a previously abandoned site. This value has been estimated to 4 as the median from historical data (Table 4).

When a small or medium-sized site enters decolonization mode, a number of pairs leave the site. This number is drawn from a binomial distribution ($N_{i,t+1} \sim \mathcal{B}(MaxDec, Pdec)$), where $MaxDec$ is the maximum number of pairs that have ever been observed in the historical data (U.S. Fish and Wildlife Service, 2010) to leave any site the year before that site was abandoned $N_{i,t+1} = 0$, and $Pdec$ is the probability that each pair leaves its current site in these events. $Pdec$ is calculated as:

$$Pdec = \frac{\sum_{j=1}^{M} \sum_{l=k_1}^{k_{T\max}} Pred(N_{j,l} > 0) \times Pred(N_{j,l+1} = 0) \times N_{j,l})}{MaxDec \times \sum_{j=1}^{M} \sum_{l=k_1}^{k_{T\max}} Pred(N_{j,l} > 0) \times Pred(N_{j,l+1} = 0)} \quad (3)$$

These parameters are estimated from historical data (Table 5) as $MaxDec = 37$ and $Pdec = 0.026$. Once a small or medium-sized site has entered decolonization mode, it will remain in this mode until $N_{i,t} = 0$, when $decol_{i,t} = 0$. The model was implemented in R language (Core Team, 2016). Log-linear models were calculated using function *glm* from package *stats*, and the truncated normal distribution was simulated using package *truncnorm* (Trautmann et al., 2014).

Colonization and decolonization events override the dynamics defined by equation $N_{i,t+1} = round((AS_{i,t} + JS_{i,t} + I_{i,t+1}))$ in the sites in colonization and decolonization mode. Moreover, the pairs that colonize any site the same year that it enters colonization mode (i.e., the settlers) are subtracted from the immigration pool in year t ($pool_t$) as the term $settlers_t$. Likewise, the pairs that decolonize any site the same year that it enters decolonization mode (i.e., the desettlers) are added to the immigration pool in year t ($pool_t$) as the term $desettlers_t$. These terms are calculated as $settlers_t = \sum_i N_{i,t+1}$ and $desettlers_t = \sum_j N_{j,t}$, for each site i and j that enters colonization and decolonization mode, respectively, in year t.
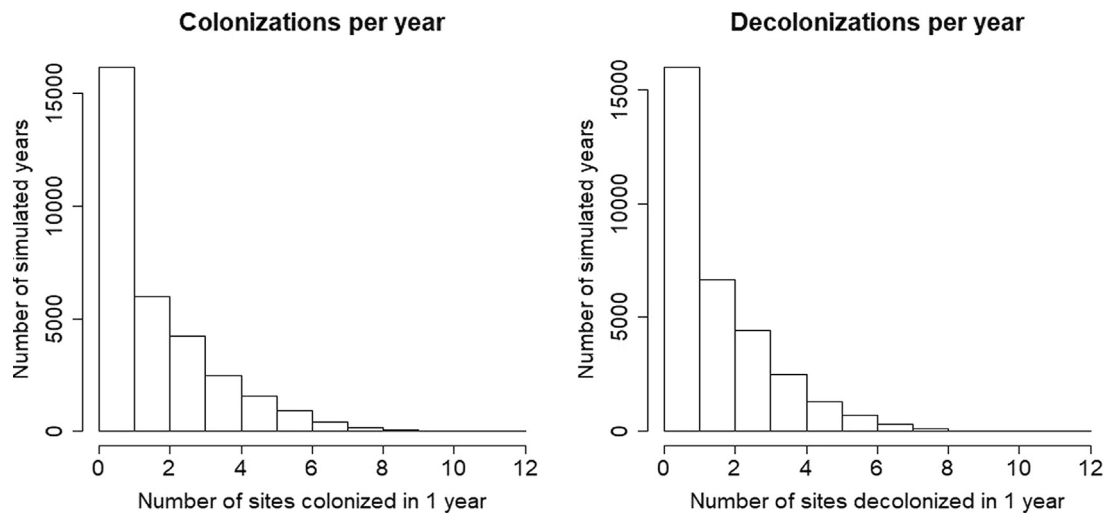
Colonizations per year

Decolonizations per year

Fig. 2. Frequency distributions of colonizations (left) and decolonizations (right) among the 50,000 years simulated.

Number of pairs after colonization
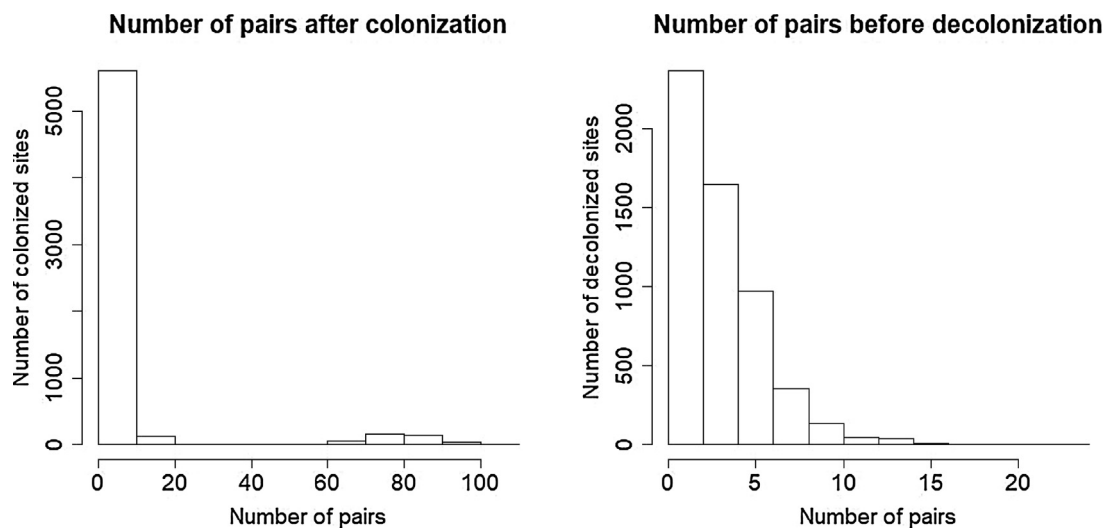

Number of pairs before decolonization

Fig. 3. Number of pairs that settle in a site in the year of its colonization (left) and number of pairs that abandon a site in the year of its decolonization (right).

3. Results

We ran 1000 simulations of our model; each run was simulated for 50 years. We analyzed the following metrics from the simulations' output: (a) the number of colonizations and decolonizations per year; (b) the number of pairs that colonize each site, i.e., breed at a site the year that it enters colonization mode; (c) the number of pairs that decolonize each site, i.e., abandon a site the year that it enters decolonization mode; (d) the proportion of birds that breed at 'large' sites at the end of each simulation; (e) the minimum and maximum number of pairs that breed in 'large' sites in each simulation across all simulated years; (f) the length of occupation, i.e., the number of years that 'small' and 'medium' colonies remain colonized (i.e., with at least 1 pair) until their abandonment; and (g) the number of initially 'small' colonies that become 'large' or 'medium' during the simulated years and maintain this size until the end of the simulation. We also simulated one type of disaster by eliminating the breeders in a large colony.

The simulation results suggest that the percentage of years in which a single site was colonized is about 32% (around 16,000 from the total of $1000 \times 50 = 50,000$ years simulated). Years where 2 colonizations occur are more infrequent, and this tendency continues

as the number of colonizations grows. This trend is mirrored by the distribution of decolonizations that occur in each year (Fig. 2).

The results also show that the majority of the colonizations and decolonizations involve a small number of pairs (1–10; Fig. 3). Nevertheless, a small proportion of colonizations involve a larger number of pairs, in the range 50–100 pairs. These rare colonizations involving large numbers of pairs have been observed in historical data (Table 4). However, a few decolonizations involving 27–37 pairs (Table 5) were not captured by our model.

The model also predicts that the duration of occupation for 'small' and 'medium' size colonies is short in the majority of cases (the median and mode are 10 and 4 years respectively; Fig. 4). This result is consistent with the observed fact that most 'small' and 'medium' sites are intermittently occupied, i.e., they become colonized and then are abandoned a few years later (Table 2).

The simulations also predict that the proportion of pairs that breed in 'large' colonies in the last year of the simulation falls in the range 0.65–1.00 (Fig. 5). This is a broader range than the proportion observed in the period 1988–2015 (0.85–0.99: Table 2), but proportions as low as 0.7 were recorded in historical data prior to 1988 (Nisbet, 1980).

The model predicts that the total number of pairs that breed in 'large' colonies is usually in the range 2700–4000 (Fig. 6). Due to
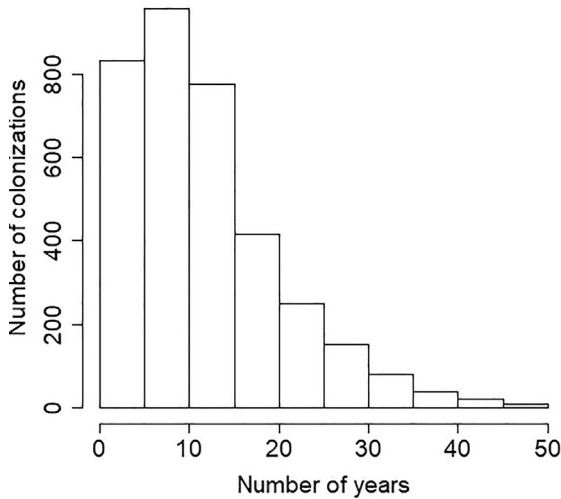
Occupation of small and medium colonies

Fig. 4. Duration (years between colonization and decolonization) of occupation of 'small' and 'medium' colonies.

Proportion of pairs in large colonies

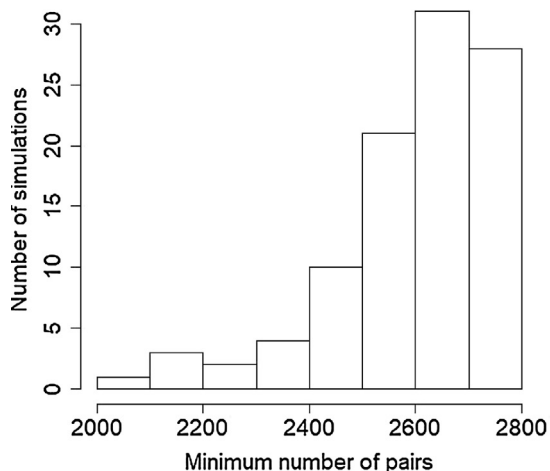**Fig. 5.** Proportion of pairs that breed in 'large' colonies in the last year of each simulation.

the unstable occupation dynamics of 'small' and 'medium' size sites, we decided to use this metric instead of using the total number of pairs across all sites. This metric is also consistent with historical data (Table 2).

The number of initially 'small' colonies that become 'medium' or 'large' and maintain this size until the last year of the 50-year simulation is about 1.2 and 1, respectively. This conforms to the historical data, which indicate that the frequencies of formation of persistently 'large' and persistently 'medium' colonies are both on the order of $0.03\,\mathrm{y}^{-1}$ (see Supplementary Material).

We also simulated an alternative scenario where one large colony (Bird Island) is not present in the system. This could emulate the effect of a sudden catastrophe in the population. With the exception of the pairs that were provided by this colony and are now absent, the metrics analyzed do not differ substantially from those from the original scenario. This could be an indicator of the high resilience of the studied system. In order to assess the sensitivity of our model to changes in parameters, we simulated different variations of it. Particularly, we analyzed the effect of changes in juvenile and adult fidelity on the proportion of birds that breed in
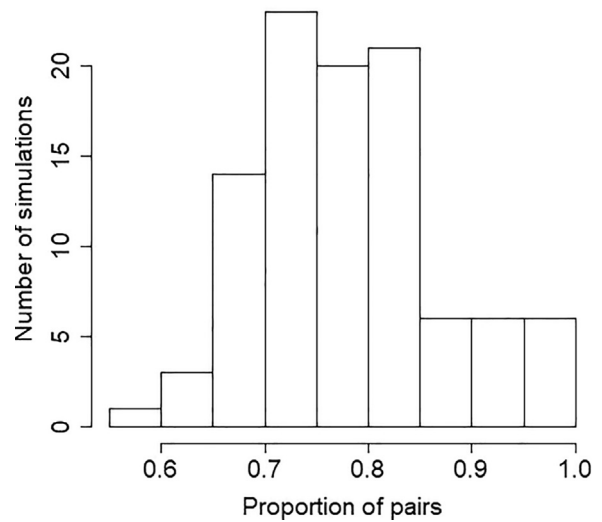
'large' colonies in the last simulated year (Fig. 7). In these variations, a common (adult or juvenile) fidelity value was set for all colonies, overriding the derived values from the regression models for $\phi_{i,t}$ and $\rho_{i,t}$ defined in Section 2. The results show small fluctuations in the proportion of pairs breeding in 'large' colonies at the end of the simulation. However, we did not observe any clear tendency linking juvenile and adult fidelity with this proportion.

We also analyzed the effect of varying productivity, juvenile and adult survival on the maximum number of pairs in 'large' colonies across all simulated years (Fig. 8). The results show that the system collapses for values lower than a threshold. For instance, for adult survival this threshold is found around 0.8. After this threshold is reached, the results show an exponential relationship between each one of these parameters and this number of pairs. The steepness of this relationship depends on the altered parameter.

4. Discussion and conclusions

Seabird populations are often considered to function as metapopulations (e.g., Breton et al., 2014; Ponchon et al., 2015;

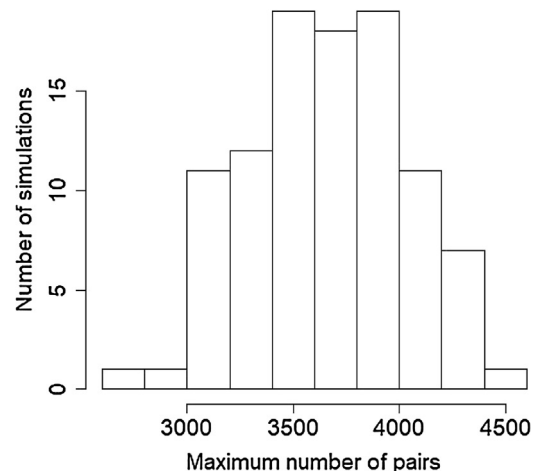## Minimum pairs in large colonies

Maximum pairs in large colonies

Fig. 6. Minimum (left) and maximum (right) number of pairs that breed in 'large' colonies in each simulation across all simulated years.

Proportion of pairs in large colonies versus adult fidelity

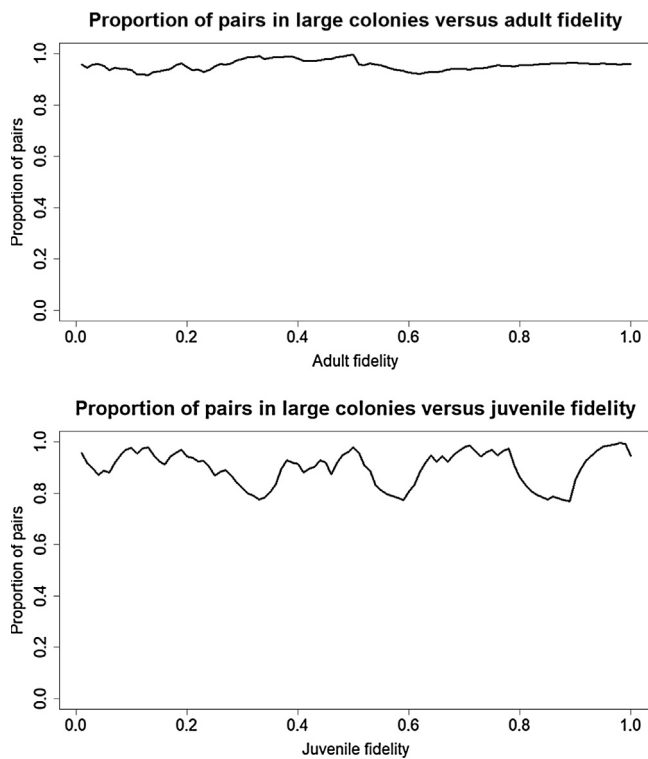**Proportion of pairs in large colonies versus juvenile fidelity**

Fig. 7. Effect of changes in adult and juvenile fidelity on the proportion of pairs that breed in 'large' colonies in the last simulated year. The results show small oscillations in this proportion, but not a definite relationship.

Sanz-Aguilar et al., 2016). This tendency is driven, in part, by the naturally fragmented nature of the populations. This is insufficient, however, for concluding a metapopulation exists rather than a suite of isolated populations or a single large population (Smith and Green, 2005). One needs evidence of somewhat isolated local dynamics, as well as extinction-recolonization dynamics. Colonial seabirds can exhibit a type of metapopulation dynamics referred to as mainland-island metapopulation dynamics, whereby one or a few very large colonies exhibit long-term persistence, with ephemeral smaller patches that are colonized by birds emigrating from the larger patches (Dolman, 2012). Looking at the map (Fig. 1), three large colonies lie on an axis of about 140 km running from WSW to ENE, and almost all of the 'small' and 'medium' colonies lie either to the west or east of them. This is probably a quirk of geomorphology; there are very few suitable islands along this axis except for the three occupied by large colonies (historically, Penikese Island was also very large, but that conforms to the same pattern). Thus, the mainland-island configuration of our metapopulation is also a central-peripheral pattern.

The biggest difficulty in understanding metapopulation dynamics for seabirds can be documenting, quantifying, and modeling colonization and decolonization events (Payo-Payo et al., 2017; Sherley et al., 2017; Southwell et al., 2017). This can be problematic when colonization events are rare (Munilla et al., 2016), which can occur when most colonies are large and in species where social dynamics affect colonization (Ponchon et al., 2015; Reed and Levine, 2005; Schippers et al., 2011). The difficulty of understanding colonization–decolonization dynamics is exacerbated in species with delayed breeding, by the difficulty of tracking juvenile and long-distance movements (Bicknell et al., 2014; Yannic et al., 2016). We used data from a long-term study to quantify the long-term dynamics of site occupancy of roseate terns in the north Atlantic (Spendelow et al., 2016), and we used the model to make inferences about the dynamics governing the system.
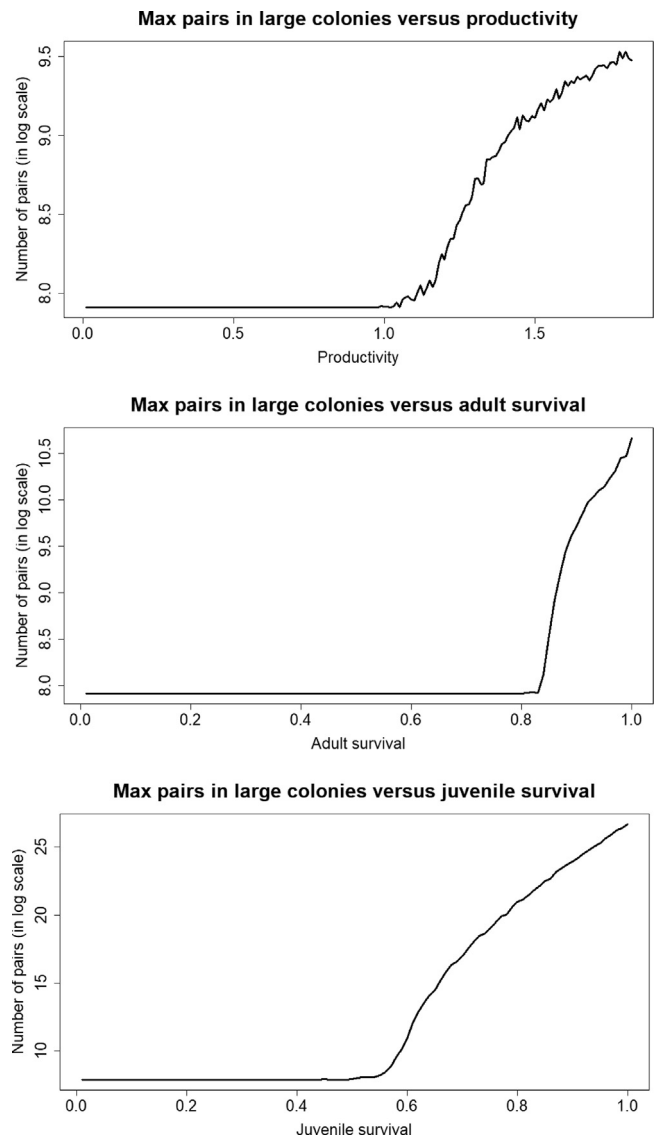
Max pairs in large colonies versus productivity

Max pairs in large colonies versus adult survival

Max pairs in large colonies versus juvenile survival

Fig. 8. Effect of changes in different parameters on the maximum number of pairs in 'large' colonies across all simulated years. These numbers of pairs are shown in logarithmic scale.

In our system, productivity increases strongly with site quality (q_i) which is destabilizing in the sense that it would increase the concentration of the population into a few large colonies with high q_i. Any additional dependence on $N_{i,t}$ would be additionally destabilizing in the sense that it could lead to a runaway increase in the total population. Feeding into this cycle might be conspecific attraction of dispersers, which is often exhibited by colonial species (Reed and Dobson, 1993). Counteracting this destabilizing tendency, we included an inverse relationship between juvenile survival and site quality (where quality was defined as average population size). So, at our larger sites, we modeled, and find field evidence, of density dependence acting in the large colonies. There is some evidence of density dependent colonization dynamics reported in other seabird metapopulations (Lisnizer et al., 2015; Matthiopoulos et al., 2005; Pozzi et al., 2015), as well as source-sink dynamics (Lisnizer et al., 2015; Ponchon et al., 2015; Sanz-Aguilar et al., 2016). As might be expected in a mainland-island metapopulation, we found different local dynamics in 'small' and 'medium' colonies in our system. These exhibited dynamics that were more stochastic and density independent than those of the 'large' colonies, resulting in local decolonizations and recolonizations. We found that we had to

model colonization and decolonization events separately from our general model of emigration from sites and allocation of the pool of immigrants. When we did not model colonization and decolonization as special cases, our model predicted that these events usually involve large numbers of pairs spearheading the colonization and abandonment of sites. Although colonizations and decolonizations involving large numbers of pairs exist in the historical data, they are rare, and the vast majority of colonizations and decolonizations involve small numbers of pairs. Therefore, we had to adapt the model so that it reflects this property of the system. The difference in local dynamics between 'small' and 'medium' sites and 'large' sites reinforces our view that 'small' and 'medium' sites were qualitatively different from large sites - consequently, the processes governing their dynamics were modeled differently.

In our model, productivity, adult survival and juvenile survival appear to be the fundamental aspects that make the model consistent with the observations. In other words, minor changes in these aspects have profound effects on the dynamics of the model, and slight deviations in the parameter values obtained from our data rapidly lead the model dynamics either to population collapse or to uncontrolled growth in the numbers of pairs, resulting in levels of population significantly larger than in the observed data. We also found that expected population size of large colonies exhibits a threshold sensitivity to adult survival. That is, over a very small range of values, populations went from large to non-existent. This type of threshold vulnerability to changes in adult survival has been reported before (Mortensen and Reed, 2016), but it is not often investigated. Traditional vital rate sensitivity analyses sometimes report adult survival rate to be the most sensitive vital rate for population growth rate in species with low reproductive rates (Breininger et al., 1999), but there is little consistency in this result across analytical methods (Fefferman and Reed, 2006; Mortensen and Reed, 2016; Wisdom et al., 2000).

Conversely, variations in fidelity do not seem to have a significant impact on the dynamics of the model. The model simulations reflect a strong dichotomic distribution with 'large' colonies on one side and 'small' and 'medium' colonies on the other. The vast majority of the pairs (about 80–90%) breed in 'large' colonies during the last year of each simulation. Changes in the parameters associated with fidelity cause minor oscillations on these percentages, but do not reflect a clear monotonic trend linking fidelity and proportion of pairs that breed in 'large' colonies. Interestingly, we found a small but unexpected oscillatory relationship between juvenile and adult fidelity and the proportion of pairs in 'large' colonies in the last year of each simulation. This relationship is especially clear for juvenile fidelity. We were unable to give an explanation for this phenomenon, and we appreciate any hypotheses from readers that would shed light on it.

The inverse correlation between juvenile survival and site quality acts as a stabilizing factor of the population and counterbalances the destabilizing effect of the positive correlation between productivity and site quality. This latter positive correlation tends to destabilize the system because it creates a positive feedback between site quality and productivity that causes the population to grow unrestrained.

Our model treats dispersal as a two-step process. Emigration from colony site i is treated as an intrinsic property of site i, and is independent of the destination colonies of the emigrating pairs. Pairs that emigrate from all sites enter a common pool, and are redistributed with the condition that they do not breed in the same colony from which they emigrated in the same year. The proportion of pairs that immigrate into colony site $j \neq i$ is modeled as a function of q_j, and is independent of the colonies of origin of the immigrating pairs. We found it unnecessary to explicitly consider pairwise co-dependences to model migration between each pair of sites.

We also found that colonization and decolonization needed to be modeled as separate events from the rest of the migration dynamics. This was because the colonization and decolonization dynamics of 'small' and 'medium' colonies and 'large' colonies are different. In fact, colonization and decolonization dynamics of 'small' and 'medium' colonies are stochastic events that frequently involve large numbers of pairs and apparently do not occur in 'large' colonies.

Our model successfully reproduces several distinctive features of the Northwest Atlantic metapopulation of roseate terns:

- The metapopulation includes 2–4 'large' colonies which hold 85–95% of the total numbers and remain similarly 'large' for long periods. In our model, this results from our assumptions that each colony site is characterized by a single constant (intrinsic 'quality'), that adult and juvenile fidelity rates are directly correlated with quality, and that birds that leave their origin sites are allocated among possible destination sites in proportion to the relative quality of these destination sites, generating a source-sink dynamics. We estimated the quality of each site from the average number of pairs over the 28-year observation period.
- The metapopulation also includes about 30 sites with low or medium values of intrinsic quality, most of which are occupied intermittently; colonizations and decolonizations are fairly frequent and sometimes involve much larger numbers of birds than what the intrinsic quality of the site would indicate. In our model, we found it necessary to model colonizations and decolonizations as stochastic events separately from our model of dispersal among sites already occupied, which predicted only small numbers of birds entering or leaving low-quality sites.
- The numbers of breeding pairs in each of the 'large' colonies and the total number of pairs in the metapopulation remain within moderately narrow bounds over periods of decades, in spite of positive correlations between colony size and breeding productivity, adult fidelity and juvenile fidelity, all of which would be expected to be destabilizing. In our model, both colony and total numbers are stabilized by introducing an inverse relationship between juvenile survival and colony size. We did not find it necessary to include other negatively density-dependent factors, either at the level of the colony or the metapopulation.
- In addition to colonizations and decolonizations, numbers of pairs at the 'large' and 'medium' colonies fluctuate from year to year, and several of the demographic parameters that have been measured (juvenile survival, adult and juvenile dispersal rates) also vary among years. Our model was able to reproduce the observed fluctuations in numbers by incorporating stochastic variation in the same demographic parameters, being the amplitude of this variation adjusted to approximate the observed range.
- In the variations of the model where common values for adult survival, juvenile survival and productivity rates were used for all years and sites, there exists a tipping point for the value of adult survival rate around 0.835 over which the population in the system becomes unstable in the long term (Fig. 8). This is consistent with the data from field observations (Table 6). The tipping point for productivity in our model (approximately 1.1) is also consistent with field data (Table 3). The sensitivity of our model to changes in the value of these parameters may help explain the observed oscillations in our population.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2017.12.007.

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