



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. Jönsson 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; Spendlow 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 transiently, 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 $k_1, \dots, k_{T_{\max}}$, $k_1 \leq k_{T_{\max}}$ 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.

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