



BREEDING DISPERSAL AND SURVIVAL OF ARCTIC TERNS (*STERNA PARADISAEA*) NESTING IN THE GULF OF MAINE

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ABSTRACT.—We used capture–mark–recapture (or re-encounter) analysis of a metapopulation to estimate the probability of survival, re-encounter, and dispersal of Arctic Terns (*Sterna paradisaea*) nesting in the Gulf of Maine and the Bay of Fundy. Before our study, there were only a few anecdotal accounts of breeding dispersal, and the only estimates of survival for this species were calculated in the 1950s and 1960s in the United Kingdom, using return rates unadjusted for recapture probability. Approximately 45% of the North American breeding population nests in the Gulf of Maine region; 95% of these nest on the four islands studied. Re-encounter observations of 2,295 adult Arctic Terns banded on these four key islands were collected from 1999 to 2005. An information-theoretic approach was used to determine the model best describing survival and movement patterns. Models using the program M-SURGE suggested that the apparent survival of adult Arctic Terns was colony- and year-specific, ranging from 0.704 to 0.960 when transient individuals were accounted for. Re-encounter probabilities were generally low, ranging from 0.12 to 0.74, depending on colony and year. Fidelity to previous breeding colonies was high; estimated probability of movement among colonies ranged from 0.000 to 0.015. Breeding dispersal was negatively correlated with distances among islands, but not with colony size. There was no difference between male and female Arctic Terns in survival, re-encounter, or breeding dispersal. Received 14 April 2007, accepted 6 March 2008.

Key words: Arctic Tern, breeding dispersal, Gulf of Maine islands, intercolony movement, seabird, *Sterna paradisaea*, survival.

Dispersion de reproduction et survie de *Sterna paradisaea* nichant dans le golfe du Maine

RÉSUMÉ.—Nous avons utilisé la méthode de capture-marquage-recapture d'une métapopulation afin d'estimer la probabilité de survie, de recapture et de dispersion de *Sterna paradisaea* nichant dans le golfe du Maine et la baie de Fundy. Avant notre étude, il n'y avait que quelques mentions anecdotiques de dispersion de reproduction et les seules estimations de la survie pour cette espèce ont été calculées dans les années 1950 et 1960 au Royaume-Uni, en utilisant les taux de retour non ajustés en fonction de la probabilité de recapture. Environnementalement 45% de la population reproductrice nord-américaine niche dans la région du golfe du Maine; 95% d'entre eux nichent sur les quatre îles étudiées. Les observations de recapture de 2 295 *S. paradisaea* adultes bagués sur ces quatre îles ont été récoltées entre 1999 et 2005. L'information théorique a été utilisée afin de déterminer le meilleur modèle pour décrire la survie et les patrons de déplacements. Les modèles réalisés à partir du programme M-SURGE suggéraient que la survie apparente des adultes était spécifique à la colonie et à l'année, variant de 0,704 à 0,960 lorsque les individus en transit étaient pris en compte. Les probabilités de recapture étaient généralement faibles, variant de 0,12 à 0,74 en fonction de la colonie et de l'année. La fidélité aux colonies utilisées précédemment pour la reproduction était élevée; la probabilité estimée du déplacement entre les colonies variait de 0,000 à 0,015. La dispersion de reproduction était négativement corrélée à la distance entre les îles et non à la taille de la colonie. Il n'y avait pas de différence entre les mâles et les femelles en ce qui a trait à la survie, la recapture ou la dispersion de reproduction.

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SEABIRD NESTING COLONIES offer a unique opportunity to examine metapopulation dynamics in habitat that is relatively predator- and disturbance-free (Buckley and Downer 1992). Many long-term studies have examined dispersal of seabirds such as the Wandering Albatross (*Diomedea exulans chionoptera*; Inchausti and Weimerskirch 2004a), Atlantic Puffin (*Fratercula arctica*; Harris and Wanless 1991; Breton et al. 2005, 2006), Marbled Murrelet (*Brachyramphus marmoratus*; Cam et al. 2003), gulls (*Larus* spp.; Cam et al. 2004a, Oro et al. 2004), and Roseate Tern (*Sterna dougallii*; Spindel et al. 1995, Lebreton et al. 2003). However, there is still a need for empirical data regarding the patterns and processes that drive dispersal or movement among populations of various types of organisms (Clobert and Lebreton 1991, Wooller et al. 1992, Walters 2000, Weimerskirch 2002, Lebreton et al. 2003).

Natal dispersal occurs with a greater probability than breeding dispersal and has been found often in seabirds (Lebreton et al. 2003). However, we focus here on the survival and breeding dispersal of adult Arctic Terns (*S. paradisaea*) in the Gulf of Maine and Bay of Fundy region (*sensu* Greenwood and Harvey 1982). The life history and historical population dynamics of Arctic Terns nesting in this region are described in detail in Hatch (2002) and Devlin (2006). Our simultaneous measures of dispersal and survival are the first for this species in North America.

The models we examine were geared toward identifying the model(s) that best describe the life-history patterns observed in banded adult Arctic Terns. The modeling methods we used are widely applicable to other studies of marked individuals. Recent work exploring the population dynamics of endangered Roseate Terns (Spindel et al. 1995, Nisbet and Spindel 1999, Lebreton et al. 2003) has been a model for the present study.

Annual survival of adult seabirds is often $\geq 90\%$, and life span can reach 20–30 years or more (Hudson 1985, Schreiber and Burger 2002). The only previous estimates of adult survival in Arctic Terns were 82–87% (from Great Britain in the 1950s and 1960s; Cullen 1957, Coulson and Horobin 1976) and 90% (Schreiber and Burger 2002). There have been no estimates using modern capture–mark–recapture techniques. Survivorship of congeneric Roseate Terns in the northeastern United States can vary from 74% to 84%, depending on the colony (Spindel et al. 1995). We had no reason to believe that individual colonies of nesting Arctic Terns in the Gulf of Maine might have different survival rates. We expected that survival of adult Arctic Terns would be within the 83–95% range reported for other terns (Schreiber and Burger 2002, Feare and Doherty 2004, Gaston 2004, Collins and Doherty 2006).

Seabirds generally display high fidelity to breeding colonies (Bried and Jouventin 2002, Coulson 2002, Weimerskirch 2002); however, this may not be the case for all colonies or species (Danchin and Monnat 1992, Danchin et al. 1998, Cam et al. 2004b, Oro et al. 2004). Arctic Terns in the United Kingdom have been documented as moving among available breeding sites in response to predation events and other disturbances (Brindley et al. 1999). Other species of terns have also displayed movement among colonies (Spindel et al. 1995, Tims et al. 2004).

Within the Gulf of Maine, there has been a history of management since the mid-1980s. Before this, Arctic Terns in the Gulf of Maine regularly moved from island to island (Drury 1973, Kress et al. 1983). Since management began, there has been a concentration of Arctic Terns and other seabirds on a select number of

islands (Kress and Hall 2004). Although some breeding dispersal was recorded informally, records were sporadic. We predicted that there would be high fidelity to colonies by Arctic Terns that were banded as breeding adults, because estimates of nesting populations had remained relatively stable for several years (Devlin 2006). We also predicted that there would be some movement among colonies by breeding Arctic Terns, because such movements have been reported both in this region and in others (Drury 1973; Kress et al. 1983; Anderson and Devlin 1996, 1999). In places where colonies are numerous and unmanaged, as in Europe, the species frequently changes colony location (Brindley et al. 1999, Mitchell et al. 2004).

Nesting in colonies can lead to competition for nesting sites and food resources. Larger colonies may experience increased competition. However, social attraction to conspecifics may induce individuals to change colonies (Kress 1983, Bried and Jouventin 2002, Coulson 2002). We predicted that conspecific social attraction influences intercolony movement and that larger colonies attract more immigrants than smaller ones. We also predicted that colonies closer together would show higher rates of exchange than colonies farther apart.

Many female seabirds (e.g., kittiwakes [*Rissa* spp.]) and females of most other bird species except waterfowl have higher rates of dispersal than males (Coulson 2002). Sex-related dispersal in terns has not been examined. Although female Roseate Terns have higher apparent survival rates than males, there is no evident difference in survival by sex in Common Terns (*S. hirundo*; Nisbet and Cam 2002, Nichols et al. 2004). We had no reason to suspect that either sex of Arctic Tern would have a higher rate of survival than the other, but, given the sex-related dispersal in most other birds, we predicted that females would have higher rates of breeding dispersal than males.

METHODS

Study area and data collection.—The present study is focused on Arctic Terns breeding in the Gulf of Maine and the Bay of Fundy. More than 95% of the Arctic Terns in this region nest on four colonies: Machias Seal Island (MSI; 44°30'N, 67°06'W), Petit Manan Island (PMI; 44°22'N, 67°52'W), Seal Island (SI; 43°54'N, 68°48'W), and Matinicus Rock (MR; 43°47'N, 68°51'W) (Gulf of Maine Seabird Working Group unpubl. data). Detailed descriptions of these four main colonies can be found in Anderson and Devlin (1999), Diamond and Devlin (2003), and Devlin (2006). There are three other colonies in the region where field crews were stationed during the present study and before 1999, at which only small numbers (<95 pairs) of Arctic Terns nested: Stratton Island (43°30'N, 70°19'W), Metinic Island (43°50'N, 69°05'W), and Eastern Egg Rock (43°52'N, 69°23'W) (Gulf of Maine Seabird Working Group unpubl. data). The Brothers (43°36'N, 65°50'W) in Nova Scotia also supports a few hundred breeding Arctic Terns and is visited sporadically by an observer. Figure 1 illustrates locations and distances among the four study colonies. These islands support a diverse group of nesting seabirds, including Arctic Terns, Common Terns, Roseate Terns, Atlantic Puffins, Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), Common Murres (*Uria aalge*), Laughing Gulls (*Larus atricilla*), Common Eiders (*Somateria mollissima*), and Leach's Storm-Petrels (*Oceanodroma*

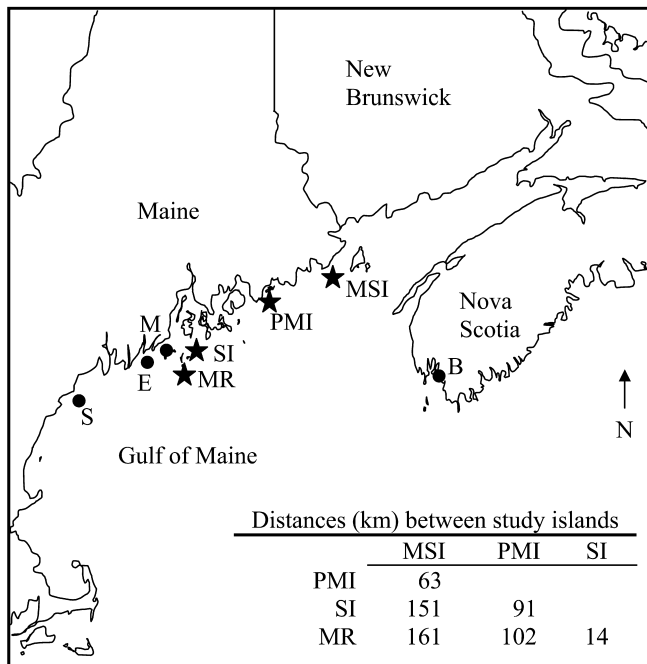


FIG. 1. Map of the locations of the four study islands (stars) and other islands in the Gulf of Maine where Arctic Terns were observed from 1999 to 2005 (circles): Stratton Island (S), Eastern Egg Rock (E), Metinic Island (M), Matinicus Rock (MR), Seal Island (SI), Petit Manan Island (PMI), Machias Seal Island (MSI), and The Brothers (B).

leucorhoa). All four sites are managed to reduce nesting populations of Herring Gulls (*L. argentatus*) and Great Black-backed Gulls (*L. marinus*) (Kress and Hall 2004).

Trapping and banding.—Arctic Terns were trapped using modified treadle traps or bow traps beginning in the second week of incubation (Bub 1991, Devlin 2006). Most trapping was done early in the nesting season (mid-June through early-July), ceasing once peak hatching occurred. On MSI and PMI, Arctic Terns were trapped on all parts of the islands in all years of the study. This method ensured that the sample would not be biased toward birds nesting near research blinds or in other specific areas of the islands. In the early years of the study, different groups of Arctic Terns on SI and MR were targeted for trapping. In this case, sampling of individuals that were banded early in the study may have been biased toward those that were easy to resight. In 2002 and subsequent years, trapping on these islands was expanded to include all parts of the islands. Birds were banded with standard Bird Banding Laboratory bands and, in addition, were banded (on the opposite leg) with an incoloy field-readable band with two letters printed above two numbers repeated twice (bands manufactured by Porzana, Icklesham, United Kingdom). Researchers living on each island monitored the Arctic Terns, conducted a census of nesting Arctic Terns, and determined the species composition of each colony (annually on all islands except MSI, where censuses were biannual).

Re-encounters.—Most Arctic Terns resighted were observed between late May and mid-June. Methods used to enhance resighting probability included providing artificial perches or small platforms

for the birds to land on and portable or stationary blinds to hide researchers. The bands were often read from distances of 10–40 m using high-powered spotting scopes (e.g., Kowa TSN-824).

Encounter histories, parameter definitions, and models.—The encounter histories of banded Arctic Terns were summarized and imported into the program M-SURGE for analysis (Choquet et al. 2004, 2005b). There were seven encounter opportunities from 1999 to 2005 for individuals banded in 1999, and progressively fewer opportunities to encounter individuals banded later. In the multisite Arnason-Schwarz model, the survival parameter is modeled for each site separately (S_i^r), and movement among sites is also modeled (ψ_i^{rs}). The survival parameter, S_i^r , is the probability that a bird at colony r in the breeding season of year i is alive and at one of the four other colonies in the breeding season of year $i + 1$. The movement parameter, ψ_i^{rs} , is the probability that a bird at colony r in the breeding season of year i is at colony s in the breeding season of year $i + 1$, given that the bird is alive and at one of the colonies in year i (Hestbeck et al. 1991). The re-encounter parameter, p_i^r , depends on time (period i) and the colony (r) where an individual is originally banded (Brownie et al. 1993).

When applied to the specifications of our study of Arctic Terns, the Arnason-Schwarz model, S_i^r , p_i^r , ψ_i^{rs} , has 144 parameters. Survival accounts for 24 parameters. There are separate survival parameter estimates for each colony (four colonies) and each transition period between years of the study (six transition periods: 1999–2000, 2000–2001, 2001–2002, 2002–2003, 2003–2004, and 2004–2005). Re-encounters also account for 24 parameters, one for each colony and year of the study. The estimates of movement account for the remaining 96 parameters. There are 16 possible combinations of movement (or nonmovement) among pairs of colonies, and a parameter is calculated for each possibility and each transition period between years of the study (six periods).

Knowing that only a small amount of breeding dispersal occurred during the six years of the study, we used as our starting model one that eliminated the time variable from the movement parameter. This reduced the number of parameters generated and the number of models that we examined. This model was defined as S_i^r , p_i^r , ψ^{rs} , where $r \neq s$ (Model A1), and had 64 parameters (24 survival parameters, 24 re-encounter parameters, and 16 movement parameters).

Goodness-of-fit and overdispersion.—It is challenging to examine goodness-of-fit and to estimate overdispersion (\hat{c}) in multisite models (Williams et al. 2002, Lebreton et al. 2003, Pradel et al. 2003). Before analyzing the mark-recapture data in detail, we used the program U-CARE to apply the “peeling and pooling” goodness-of-fit method (Pradel et al. 2003, Choquet et al. 2005a). This program also includes tests for transients and a test for trap-dependence. Test 3G assumes “behavioral equivalence” of marked individuals released within the same year, regardless of their past capture history. If there are transients in a sample of marked individuals, this assumption will not be met. Test M assumes “equivalence” among those marked individuals that are eventually re-encountered. If there is evidence of trap-dependence (either “trap-happiness” or “trap-shyness”), this assumption will not be met.

The goodness-of-fit analysis using the “pooling and peeling” method described by Pradel et al. (2003) indicated that the fully parameterized model did not fit the data ($\chi^2 = 296.62$, $df = 1$ and

139, $P < 0.001$). Additionally, the results of test 3G indicated a lack of behavioral equivalence among birds that were banded (test statistic = 221.54, $df = 79$, $P < 0.001$), but there was equivalence among birds that were subsequently re-encountered (test $M = 75.08$, $df = 60$, $P = 0.091$). To account for this, we included the parameter of “time since banding” to control for transients (Pradel et al. 1997, Cam et al. 2004b). This involves the calculation of different estimates of survival for the first time an individual is encountered and for subsequent encounters and is defined in the models as τ .

The overdispersion parameter (\hat{c}), a measure of variance inflation, was calculated by dividing the sum of chi-square values of the U-CARE goodness-of-fit tests by degrees of freedom (Lebreton et al. 1992, Choquet et al. 2005a). When $\hat{c} = 1.0$, the model fits the data; if $\hat{c} \geq 1$, a lack of fit is indicated (White et al. 2001). This is generally acceptable if the overdispersion parameter is $1 \leq \hat{c} \leq 4$ (though some use a more conservative cut-off of 2.5); otherwise, there is some structural lack of fit in the model and a different model should be examined (Burnham and Anderson 1998).

Our approach to the modeling was exploratory, and we tested all variations and combinations of apparent survival ($S_{i\tau}^r$), re-encounter (p_i^r), and movement (ψ^{rs}) parameters (Table 1). To examine covariates to movement, we included models that

TABLE 1. Parameters of models used to explore factors affecting the probability of survival, re-encounter, and breeding dispersal of adult Arctic Terns. Survival (S) varied by colony of origin (r), time (i), or time since banding (τ). The re-encounter parameter varied among colonies or by time (p_i^r), and the movement parameter (ψ^{rs} $r \neq s$) varied by pairwise combination—where $r =$ the colony where an individual was originally captured and $s =$ the colony where an individual was re-encountered—and was correlated with distance between colonies and colony size (mean number of nesting pairs).

Model notation	Description
S_i^r	Starting model; survival varied by colony and year
S^{r+i}	Survival varied by colony and year (no interaction)
S^r	Survival varied by colony
S_i	Survival varied by time
S	Survival was constant
$S_{i\tau}^r$	Survival varied by colony, time, and time since banding
$S_{i+\tau}^r$	Survival varied by colony, time, and time since banding (no interaction)
$S_{i\tau}$	Survival varied by time and time since banding
$S_{i+\tau}$	Survival varied by time and time since banding (no interaction)
S_τ^r	Survival varied by colony and time since banding
$S^{r+\tau}$	Survival varied by colony and time since banding (no interaction)
S_τ	Survival varied by time since banding
p_i^r	Re-encounter varied by colony and year
p^{r+i}	Re-encounter varied by colony and year (no interaction)
p^r	Re-encounter varied by colony
p^i	Re-encounter varied by year
p	Re-encounter was constant
ψ^{rs}	Movement varied among islands
$\psi_{\text{distance}}^{rs}$	Movement among islands was correlated with distance
ψ_{size}^{rs}	Movement among islands was correlated with mean number of nesting pairs

correlated intercolony distances ($\psi_{\text{distance}}^{rs}$) and mean number of nesting pairs of Arctic Terns on each island from 1999 to 2005 (ψ_{size}^{rs}).

In dividing the birds by sex, all adults that were not sexed genetically were classified as either female or male using the discriminant function developed for the measurement from the back of the head to the tip of the bill (discriminant score = head-bill [0.47] – 33.56; Devlin et al. 2004). Discriminant-score cut-off points were calculated on the basis of the 50% and 95% *a-posteriori* probability of correctly sexing individuals (Devlin et al. 2004). A discriminant score of 0.039 was the cut-off point where the *a-posteriori* probability of correctly sexing males and females was 50% ($n = 1,010$ females, $n = 1,191$ males). The 95% cut-off points were discriminant scores ≤ 2.164 classified females and ≥ 2.164 classified males ($n = 219$ females, $n = 214$ males). We then included sex as a parameter in the demographic analysis.

Model selection.—We used an information-theoretic approach to model selection and based support for models on the ΔQAIC_c values (quasi-likelihood Akaike’s information criterion corrected for overdispersion and small sample size) and Akaike weights of the estimated models (Hurvich and Tsai 1989, Burnham and Anderson 1998, Anderson and Burnham 1999, Johnson and Omland 2004). Estimates of QAIC_c are based on the Kullback-Leibler distance between two models and are an estimate of the relative distance between the fitted model and the actual “true” model or mechanism that generated the data (Burnham and Anderson 1998). The QAIC_c values of the models were calculated within M-SURGE (Choquet et al. 2004, 2005b). The model with the lowest QAIC_c value was considered the model that best described or best fit the data.

RESULTS

Field results.—There are currently >5,000 pairs of Arctic Terns nesting in the Gulf of Maine and Bay of Fundy region. The mean number of pairs (\pm SE) of Arctic Terns nesting on the four study colonies from 1999 to 2005 were as follows: MSI = $2,050 \pm 65$, PMI = 665 ± 55 , SI = $1,027 \pm 42$, and MR = 975 ± 26 . Within the study period, 2,295 individuals were captured and banded on the four islands. By 2005, ~20% of the estimated breeding population in the region was banded. Details regarding the specific annual numbers are illustrated in Devlin (2006).

Of the 2,165 Arctic Terns banded from 1999 to 2004, 54% were re-encountered at least once. More than 2,100 re-encounters of individuals after their initial trapping were documented from 1999 to 2005; 62% of the re-encounters also included observations of breeding behavior (courtship, copulation, nest building, incubation). On the basis of Spendelov et al.’s (1995) observations of the behavior of Roseate Terns, we assumed that if an Arctic Tern was observed on an island early in the breeding season, it was there to breed. In only one case was a banded individual observed on more than one island during the same year; this bird was treated as breeding on the island where it was seen most often that year.

Fifty-four Arctic Terns were recorded breeding on islands outside the colony where they were originally banded as breeding adults. Five of these eventually returned to the colony where they were originally encountered, and one moved to yet another. Movements were recorded among all islands, except for movements from SI to MSI. Two individuals sighted on islands in the region

TABLE 2. Models according to estimated QAIC_c (Akaike's information criterion corrected for overdispersion and small sample size; $\hat{c}=2.13$), Δ QAIC_c < 10, Akaike model weight (w_i), model likelihood, number of estimable population parameters (K), and model deviance. Models are listed according to Δ QAIC_c. The model with the lowest QAIC_c was the best-fit model.

Model	QAIC _c	Δ QAIC _c	w_i	Likelihood	K	Deviance
$S_{i+\tau}^r, p_{i'}^r, \Psi_{\text{distance}}^{rs}$	4,454.06	0.00	0.7203	1.0000	88	9,291.19
$S_{i+\tau}^r, p_{i'}^r, \Psi^{rs}$	4,456.62	2.56	0.2005	0.2783	88	9,296.64
$S^{r+\tau}, p_{i'}^r, \Psi^{rs}$	4,461.12	7.05	0.0212	0.0294	48	9,327.52
$S^{r+\tau}, p_{i'}^r, \Psi_{\text{distance}}^{rs}$	4,461.12	7.05	0.0212	0.0294	48	9,327.52
$S_{\tau}^r, p_{i'}^r, \Psi^{rs}$	4,463.11	9.05	0.0078	0.0108	48	9,318.99
$S_{\tau}^r, p_{i'}^r, \Psi_{\text{distance}}^{rs}$	4,463.11	9.05	0.0078	0.0108	48	9,318.99

that were not included in the study (Fig. 1) were excluded from the analysis. No individuals banded during the study were detected outside the Gulf of Maine region.

Modeling results.—In the model that best fit the data, $S_{i+\tau}^r, p_{i'}^r, \Psi_{\text{distance}}^{rs}$ ($r \neq s$), survival varied by colony, time, and “time since banding” (no interaction), re-encounter varied by colony and year, and movement among islands was negatively correlated with distance between islands (Table 2). The Akaike model weight of the best-fit model was 0.72. The second-ranked model, $S_{i+\tau}^r, p_{i'}^r, \Psi^{rs}$ ($r \neq s$), was virtually the same, except that distance between islands was not included in the model and was separated by Δ QAIC_c = 2.56 (Akaike model weight = 0.20). Model averaging was not considered

in estimating the model parameters, because of the similarities among the models and because the combined Akaike model weight of the top models was 0.92 (Table 2).

The estimate of survival for the first year after banding ranged from 0.38 to 0.914; for subsequent years, the probability of survival ranged from 0.704 to 0.960 (Table 3). Parameter estimates for the probability of re-encounter ranged from 0.12 to 0.74, and probability of movement ranged from 0 to 0.015, depending on the pairing of colonies and the direction of movement (Tables 3 and 4). Colonies that are closer together (<100 km) had more exchange of banded adults ($n = 39$) than islands >100 km apart ($n = 21$). Additionally, twice as many individuals ($n = 38$) moved,

TABLE 3. Probability of survival of adult Arctic Terns, controlling for transient individuals ($\hat{S}_{i+\tau}^r$) and standard errors (\hat{SE}). The time since banding is symbolized by τ and was divided between 1 and >1 year after banding. Colony-specific (r) and time-specific (i) estimates of Arctic Tern re-encounter probabilities (\hat{p}_i^r) and their standard errors (\hat{SE}). Colonies are Machias Seal Island (MSI), Petit Manan Island (PMI), Seal Island (SI), and Matinicus Rock (MR).

Colony	Year	Survival ($\tau = 1$ year)		Survival ($\tau > 1$ year)		Re-encounter	
		\hat{S}_{τ}^r	\hat{SE}	\hat{S}_{τ}^r	\hat{SE}	\hat{p}_i^r	\hat{SE}
MSI	2000	0.745	0.0525			0.33	0.055
	2001	0.630	0.0597	0.861	0.0344	0.37	0.047
	2002	0.616	0.0650	0.815	0.0457	0.35	0.042
	2003	0.531	0.0767	0.704	0.0777	0.54	0.054
	2004	0.380	0.0803	0.812	0.0476	0.40	0.073
	Mean ^a	0.580	0.0668	0.798	0.0514	0.40	0.054
PMI	2000	0.910	0.0430			0.12	0.095
	2001	0.854	0.0585	0.958	0.0192	0.21	0.055
	2002	0.846	0.0645	0.955	0.0211	0.43	0.069
	2003	0.796	0.0856	0.938	0.0299	0.22	0.051
	2004	0.678	0.1085	0.891	0.0495	0.38	0.072
	Mean ^a	0.817	0.0720	0.935	0.0299	0.27	0.068
SI	2000	0.914	0.0274			0.71	0.069
	2001	0.861	0.0380	0.960	0.0133	0.43	0.054
	2002	0.853	0.0454	0.958	0.0153	0.32	0.044
	2003	0.805	0.0575	0.941	0.0203	0.49	0.047
	2004	0.690	0.0759	0.896	0.0362	0.40	0.047
	Mean ^a	0.825	0.0488	0.939	0.0212	0.47	0.052
MR	2000	0.858	0.0372			0.71	0.073
	2001	0.779	0.0531	0.932	0.0225	0.74	0.067
	2002	0.768	0.0536	0.928	0.0224	0.73	0.057
	2003	0.701	0.0715	0.901	0.0319	0.32	0.050
	2004	0.559	0.0792	0.831	0.0526	0.50	0.065
	Mean ^a	0.733	0.0589	0.898	0.0323	0.60	0.063

^aArithmetic mean for 2000–2004.

TABLE 4. Colony-specific estimates (\pm SE) of Arctic Tern movement probabilities ($\hat{\psi}^{rs}$), where r = colony of origin and s = destination colony. Colonies are Machias Seal Island (MSI), Petit Manan Island (PMI), Seal Island (SI), and Matinicus Rock (MR). Overall dispersal is the percentage of adults dispersing that were banded between 1999 and 2004.

Source colony	Destination colony				Overall dispersal
	MSI	PMI	SI	MR	
MSI	0.982 \pm 0.0059	0.008 \pm 0.0044	0.008 \pm 0.0038	0.002 \pm 0.0016	2.6%
PMI	0.009 \pm 0.0059	0.968 \pm 0.0108	0.015 \pm 0.0071	0.008 \pm 0.0052	5.1%
SI	0	0.003 \pm 0.0026	0.993 \pm 0.0040	0.004 \pm 0.0030	0.9%
MR	0.002 \pm 0.0023	0.004 \pm 0.0038	0.012 \pm 0.0056	0.983 \pm 0.0072	2.2%

between years, from a more northern colony to a southern colony than moved in the opposite direction ($n = 19$).

DISCUSSION

The estimates of apparent survival and breeding dispersal generated in the present study are the first estimates of survival for Arctic Terns breeding in North America and the first that have been modeled for this species using modern capture–mark–recapture techniques. With >40% of the estimated population of this species in North America nesting within the study area, these results are crucial for understanding the population dynamics of this long-distance migrant. In the Arctic and in other parts of the world where this species nests, wide dispersal of nesting colonies and changing of colony locations because of predation or habitat loss make estimation of population levels and dynamics difficult (Mitchell et al. 2004). The high apparent survival observed in the present study indicates the strength of past management decisions in focusing efforts on specific islands for Arctic Terns within the Gulf of Maine region.

Survival.—We corrected our analysis to account for transient birds in our sample. By doing this, we separated the survival estimate of birds for their first encounter from that for re-encounters. It is not possible to determine whether a potential difference in survival between the first encounter and later encounters is attributable to a trapping effect (i.e., trap avoidance in the present study), to movement outside the study region, or to individuals present on a colony but not seen, or whether there is indeed a difference in survival. Our generally low probabilities of re-encounter increase the likelihood that some individuals were missed when observers were resighting or trapping. Not accounting for transients can lead to underestimation of survival (Pradel et al. 1997); however, in accounting for transients, we may have overestimated the “true” survival. It is probable that the “true” survival lies between the two estimates.

The estimates of survival in the present study (0.81–0.96; Table 3) are higher than those reported from the 1950s and 1960s in the United Kingdom (0.82–0.87; Cullen 1957, Coulson and Horobin 1976) or that reported by Schreiber and Burger (2002; 0.90) and, indeed, are among the highest reported for any species of tern or any charadriiform. Survival estimates of other members of this order range from 0.75 for Cassin’s Auklet (*Ptychoramphus aleuticus*) and Black Noddy (*Anous minutus*) to ≥ 0.90 for Common Murre, Atlantic Puffin, South Polar Skua (*Catharacta macormicki*), Razorbill, and Black-Legged Kittiwake (*Rissa trydactyla*;

Hudson 1985; Croxall and Rothery 1991; Harris and Wanless 1991; Schreiber and Burger 2002; Breton et al. 2005, 2006). Large terns, including Caspian, Sandwich, and Royal terns (*Hydroprogne caspia*, *Thalasseus sandvicensis*, and *T. maximus*, respectively), have survival estimates ranging from 0.75 to 0.95 (Schreiber and Burger 2002, Collins and Doherty 2006). Other species of terns, including Least and Sooty terns (*Sternula antillarum* and *Onychoprion fuscatus*) and Common Terns have survival estimates of 0.88 to 0.92 (Nisbet and Cam 2002, Schreiber and Burger 2002). Spendelov et al. (1995) estimated mean annual survival of Roseate Terns between 0.74 and 0.84, depending on the breeding colony; survival rates also varied among colonies in our study. Spendelov et al. (1995) did not account for transients, which may partially explain why they found colony-specific survival and why their estimates for survival of Roseate Terns are so much lower than ours for Arctic Terns.

We did not expect the survival rates to vary among colonies, because Arctic Terns spend only a short part of their lives at the breeding colonies and the colonies are not far enough apart to experience very different environmental fluctuations. Arctic Terns spend most of their lives at sea and in migration. Like Spendelov et al. (1995), we do not know of a specific biological reason for the colony-specific survival; however, the large numbers of transients in the data may be enough to explain a possible underestimation of true survival on MSI. Given that MSI is the northernmost colony in our study area, it may be losing significant numbers of birds to colonies farther north, where they would not be detected.

Nisbet and Cam (2002) found age-related differences in survival but no differences between the two colonies of Common Terns they examined. We assume that Arctic Terns nesting in the Gulf of Maine migrate to the same wintering grounds and are subject to the same mortality pressures, but very little is known about the migration routes and wintering areas of individuals from specific colonies (Salmonsén 1967, Cramp 1985, Bourne and Casement 1996, Hatch 2002, Monaghan 2002).

Re-encounter probability.—In addition to examining the return rates of banded individuals in the mark–recapture analysis, we also incorporated the probability of each banded individual being re-encountered as a factor in generating an estimate of survival. The results of our analysis indicate that the probability of re-encounter was time- and colony-dependent (Table 3). This parameter can help explain some of the differences observed in survival estimations; if re-encounters were higher on MSI, it is possible that the apparent survival would also be higher. However, it is important to note that the goodness-of-fit tests we

conducted indicated some heterogeneity in the estimate of survival (which led us to control for transient individuals) but none in the other parameters.

Breeding dispersal.—Historical data indicated some breeding dispersal of Arctic Terns among the Gulf of Maine colonies. We predicted that the amount of movement among colonies would be low, given that most seabirds display strong fidelity to breeding colonies when disturbance is minimal, as is the case in the study region (Bried and Jouventin 2002; Coulson 2002; Inchausti and Weimerskirch 2004a, b). We observed high rates of breeding-colony fidelity, ranging from 0.968 to 0.993, depending on the colony. Although results of other studies of Arctic Terns have documented breeding dispersal (Brindley et al. 1999), conditions in the Gulf of Maine—owing, in part, to management of colonies—are such that there are only low levels of breeding dispersal among colonies (Table 4).

There was more empirical support for including distance between colonies than for colony size as a covariate to movement (Table 2). This supports the hypothesis that Arctic Terns nesting on islands that are closer together experience higher rates of movement, as Spendelov et al. (1995) observed in Roseate Terns.

We predicted that the social attraction of large colonies would attract more immigrants. Although MSI is the largest colony of Arctic Terns in the region, it did not attract the most immigrants. The most recently occupied tern colony, SI, attracted more immigrants and had the highest breeding-colony fidelity (Table 4). The colony on SI is growing in size (nesting initiated in 1989; Gulf of Maine Seabird Working Group unpubl. data); since 2002, it has been the second largest colony in the region (Kress and Hall 2004, Gulf of Maine Seabird Working Group unpubl. data). Tims et al. (2004) found that Common Terns breeding at a newly formed colony were significantly younger, laid later, and had higher productivity than those nesting at an older colony nearby. It may be that the Arctic Terns attracted to nesting on SI are younger individuals, but the ages of individuals are unknown, so we cannot determine this.

McPeck and Holt (1992) predicted an inverse relationship between colony size and the proportion dispersing from the colony. We did not find support for this trend. Spendelov et al. (1995:2425), failing to find support for this prediction, indicated two possible explanations, that the tern “metapopulation was not at evolutionary and demographic equilibrium, or that fitness is not density dependent in this system.” These explanations may also apply to Arctic Terns in the Gulf of Maine.

In most birds (except waterfowl), females are more likely to disperse than males, but this has not been found in terns. In our mark-recapture analysis, we found no evidence that either sex of Arctic Tern has higher breeding dispersal. However, the number of adults actually dispersing was low ($n = 54$, including 21 females and 33 males; Table 4), and any sex-related tendency may have been masked.

Our main goal in the present study was to clarify the demographic parameters of Arctic Terns nesting in the Gulf of Maine. We determined the apparent adult survival, re-encounter probability, and breeding dispersal of Arctic Terns nesting in the Gulf of Maine from 1999 to 2005. These are the first estimates for this species in North America and the first using capture-mark-recapture analysis. Our estimates of adult survival are among the

highest recorded for terns, and higher than that observed for many other species. The low estimate of re-encounter suggests that this is an area where more observational effort is needed. Movement of breeding adults indicates that the nesting population in the region is dynamic, with breeders moving between islands to find suitable nesting places. Considering that the Gulf of Maine is a key nesting area for the North American population of Arctic Terns, this study supports the importance of managing multiple nesting islands for the benefit of nesting terns (Hatch 2002, Gulf of Maine Seabird Working Group unpubl. data). It is also important to note that modeling of populations relies on rapidly developing tools of analysis and should be re-evaluated regularly (Lebreton and Clobert 1991). The apparent survival estimated in the present study may be an underestimation for MSI and an overestimation for the other colonies, because of the high number of transients detected in our analysis. However, as our research continues, estimates and the influences on those estimates will be clarified. This represents an important lesson for other studies of marked organisms that are long-lived and that may escape detection for many years.

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