



Spatial ecology of endangered roseate terns and foraging habitat suitability around a colony in the western North Atlantic

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ABSTRACT: Predicting habitat suitability and understanding habitat utilization are important to inform and orient conservation and management decisions for the recovery of endangered species. In North America, the roseate tern *Sterna dougallii* is listed as endangered in both the northeastern USA and Canada, where little is known about the foraging spatial ecology of the species. We equipped breeding roseate terns with miniature GPS tracking devices during incubation at North Brother Island, the main Canadian colony. Our aim was to characterize the spatial foraging ecology of the species, identify marine zones of importance, and develop a habitat suitability model around the colony. Our results provide novel, high resolution information on individual foraging trips, notably showing that individuals restricted their range around the colony (15.4 km) while performing multiple foraging trips: up to 11 daytime trips and a maximum total of 152.9 km travelled per day. Roseate terns concentrated their foraging effort around the colony and further south along the coast to the Cockerwit Passage. Using distance from colony, sea surface temperature, distance from land, bathymetry, and subtidal substrate type as covariates in a habitat suitability model, a high proportion of the deviance was explained (72.4 %); the model also predicted high occurrence of foraging near the colony, in Cockerwit Passage, and at additional sites to which the birds were not tracked. Along with the description of important marine areas for roseate terns nesting on North Brother Island, this habitat suitability model provides a relevant and essential context for understanding roseate tern habitat use in a broad sense, but with a focus on habitat requirements during incubation.

KEY WORDS: *Sterna dougallii* · Individual movement · Habitat use · Incubation · North Brother Island · Nova Scotia

1. INTRODUCTION

Habitat suitability models identify habitat requirements of species by modelling their functional response of occurrence or abundance in relation to habitat characteristics (Guisan & Zimmermann 2000, Aarts et al. 2008, Wakefield et al. 2011, Roberts et al. 2016, Warwick-Evans et al. 2018). Such modelling approaches are useful for filling knowledge gaps regarding habitat use and selection by threatened

and endangered species (Jarnevich et al. 2016, Cañadas et al. 2018, García-Barón et al. 2019) and particularly for endangered seabirds, for which the study of spatial ecology is challenging (e.g. when a small sample of individuals is followed). Moreover, habitat suitability modelling for endangered species can be valuable for making inferences about the spatial ecology of the species in other areas across its range (Warwick-Evans et al. 2018), assessing the suitability of habitats in re-colonized areas (Cianfrani

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et al. 2010), predicting where seabirds, for example, may colonize in the future, or prioritising conservation efforts such as habitat protection and restoration. Understanding habitat utilization and predicting habitat suitability is thus essential to inform and orient conservation and management decisions geared toward the recovery of endangered species.

Seabirds are bound to their colony site for the duration of the breeding season as they court, mate, lay eggs, incubate, and feed their young in 1 location. Thus, for nesting seabirds, the habitat available is basically circumscribed by the maximum range of individuals while foraging at sea (Thaxter et al. 2012). However, within that maximum range, habitat can be used heterogeneously based on the availability of preferred prey, which is driven by ocean characteristics, and on prey accessibility, which, in turn, is determined by foraging tactics. For seabirds, distance from land, bathymetry, ocean fronts, and sea surface temperature (SST) (Louzao et al. 2006, Wakefield et al. 2011, 2017, Soanes et al. 2016) are among those habitat characteristics considered as proxies for prey availability and occurrence, and they thus serve as useful correlates for explaining the distribution and occurrence of foraging seabirds.

The roseate tern *Sterna dougallii* has an almost cosmopolitan breeding distribution, abundant in the tropics and fragmented in the North Atlantic Ocean. In the North Atlantic, adult survival rate and genetic diversity are low compared to other seabird species with comparable life-history characteristics (Nisbet & Ratcliffe 2008). The western North Atlantic population (subspecies *S. d. dougallii*) is listed as endangered in both Canada and the USA (COSEWIC 2009, US Fish and Wildlife Service 2010). The historical population size in northeastern North America was estimated at 8500 pairs (1930s; Nisbet et al. 2014); however, the plume trade for the millinery industry led to the near extirpation of the population in the late 19th century (<2000 individuals). The most current estimate of 4274 pairs (2019; Canada and the USA) represents a slight increase since the late 1970s (2500 pairs; Nisbet et al. 2014). However, this increase has been driven by population growth in the US colonies, whereas low productivity and habitat degradation are thought to be limiting the growth of Canadian colonies (COSEWIC 2009), with peak breeding numbers of 69 pairs in 2019. In the western North Atlantic, roseate terns always nest with common terns *S. hirundo* and occasionally with both common and Arctic terns *S. paradisaea* (Donehower et al. 2007). Little is known about the movements and habitat use of foraging roseate terns during the

breeding season; most information has come from VHF telemetry studies (Rock et al. 2007, Loring et al. 2019) or boat surveys (Perrow et al. 2011, Goyert 2014, Robertson et al. 2014). Those studies corroborated previous observations (Safina 1990, Monticelli et al. 2006) underlining the coastal behaviour of foraging roseate terns and their apparent preference for shallow areas, especially in comparison to co-nesting common and Arctic terns (e.g. Rock et al. 2007, Robertson et al. 2014). Advancements in tracking technologies have led to the development of smaller and lighter devices, enabling the collection of fine-scale movement data to investigate habitat use and spatial ecology of relatively small species such as roseate terns (e.g. Soanes et al. 2015).

Roseate terns currently breed at 3 sites in Canada, all 3 of which are in Nova Scotia: North Brother Island, Country Island, and Sable Island (see Fig. 1). A previous study conducted at Country Island using VHF telemetry revealed that most tagged birds foraged close to land in shallow water (<5 m), typically within 7 km of their colony (Rock et al. 2007). Sample size in that study was small and did not allow for detailed characterization of foraging trips, as extensive effort is required to track birds using VHF telemetry.

North Brother Island is located 375 km to the southwest of Country Island in Lobster Bay, and currently supports ~75% of the Canadian roseate tern population. The island is small (0.2 ha) and located within 700 m of the mainland (see Fig. 1). Marine habitat use by roseate terns nesting at this site has never been quantified. With the aim of qualifying and quantifying habitat characteristics and marine areas of primary importance for foraging roseate terns breeding on North Brother Island, we equipped nesting roseate terns with small GPS tracking devices to obtain fine-scale at-sea movement data associated with foraging trips. Currently, new development for aquaculture infrastructure is being assessed in the Lobster Bay area, though the bay is already subject to a range of anthropogenic stressors including, among others, rockweed *Ascophyllum nodosum* harvesting, activities relating to commercial fishing (e.g. vessel traffic, harbours, effluent from fish processing plants), and the associated risk of oil spills. Given this range of coastal development stressors, defining foraging habitat for this endangered and restricted population has important implications for conservation planning in this region

Specifically, we aimed to (1) identify marine zones of relatively high use, (2) assess population-level fidelity to those zones, and (3) assess preferred habitat characteristics to develop a predictive model for

foraging roseate terns. Using this habitat suitability model, we describe important marine areas for roseate terns nesting on North Brother Island located within Lobster Bay. The development of a habitat-based model targeting foraging terns' occurrence in waters near established colonies or newly formed colonies in Atlantic Canada will help guide management and conservation decisions relating to the species' recovery (Environment Canada 2014).

2. MATERIALS AND METHODS

2.1. Study site and capture

Roseate terns *Sterna dougallii* were captured at North Brother Island (43.6364° N, 65.8235° W), Nova Scotia (Fig. 1). North Brother is a managed colony with measures in place to support roseate tern nesting, including the instalment of 50–150 nest shelters on suitable nesting substrate (e.g. cobble) each year. Adult roseate terns were trapped on their nests during the incubation period using modified potter trap/walk-in treadle traps. PathTrack® nanoFix-GEO GPS tags (2.5 g) were attached to the interscapular region using Tesa tape and subcutaneous suture thread (Loring et al. 2017). All trapping and tag attachment methods were undertaken according to Animal Care permit #16JMK02, 17JMK02, BBO #10745 (and associated Canadian Wildlife Service Scientific permit ST2714 in addition to provincial endangered species permits). We deployed tags in both the 2016 (16 and 17 June, $n = 14$) and 2017 (15 June,

$n = 7$) breeding seasons. No tags were retrieved during 2017 due to colony abandonment following high nest depredation (J. McKnight pers. obs.). In 2016, we recaptured 8 birds (7 tags) after 6 d of deployment during which the tags recorded positions every day. We suspected the remaining 6 tags fell off following suture wear, as we saw no birds carrying tags during subsequent tag retrieval trips to the island. Thirteen of the 14 nests incubated by tagged birds hatched (93%); 1 nest was abandoned, although the adult was re-sighted on Country Island that summer and later that year in Cape Cod. Out of 48 control nests with no adults tagged, 75% hatched ($n = 36$), 19% failed ($n = 9$), and the fate was unknown for 6% ($n = 3$). These apparent differences between groups were not significant (chi-squared test; $\chi^2 = 2.23$, $df = 2$, $p = 0.33$). Tags recorded locations when more than 3 satellites were available. Terns plunge-dive from various heights to capture small fish, and are generally thought to forage during daylight hours. Each tag was thus set to record GPS locations at 15 min intervals and was set off-duty between 01:00 and 08:00 h UTC, except for one individual (rt14) that was also tracked at night to explore the possibility that individuals in this population forage nocturnally.

2.2. Data analysis

2.2.1. Identifying foraging trips

To assess foraging behaviour using the residence in space and time method (RST; Torres et al. 2017;

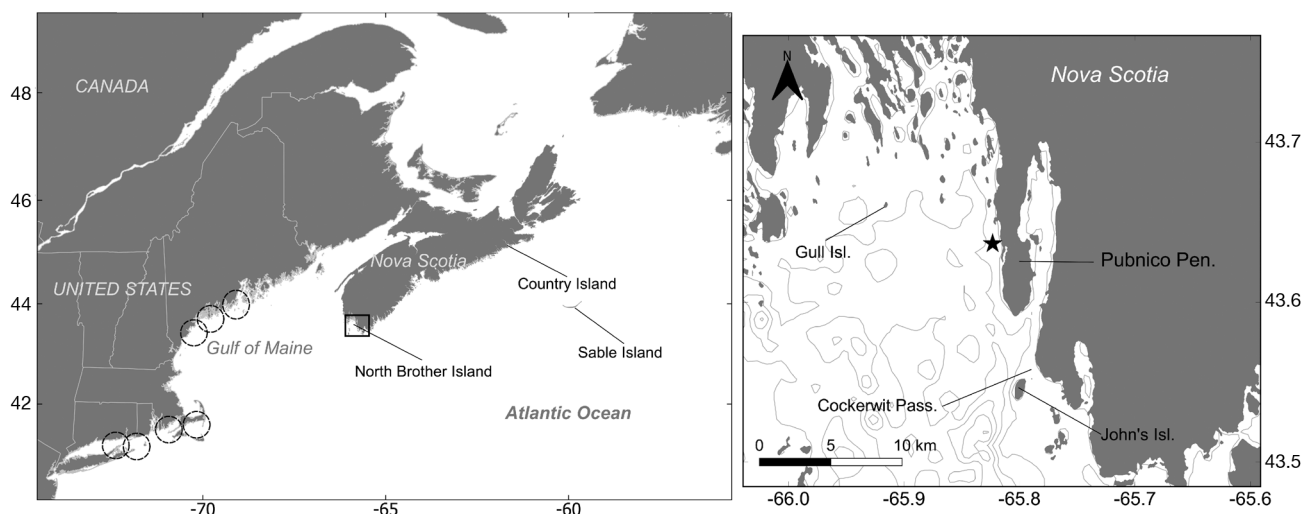


Fig. 1. The 3 major roseate tern colonies in Canada: North Brother Island, Country Island, and Sable Island, as well as general areas where roseate terns nest in the USA (circles). Right panel: close-up view of the area around North Brother Island (black star) with bathymetry contour lines at 10 m depth intervals. Projection: WGS84 Pseudo-Mercator

see also next section), we first regularized positions for each individual track at 5 min intervals (Benhamou & Riotte-Lambert 2012) using the package 'adehabitatLT' (Calenge 2006) in program R (R Core Team 2020). Next, each individual track was split into foraging trips according to the distance travelled from the colony and the time spent away from the colony (Lascelles et al. 2015). Only travelling movement away from the colony beyond a 100 m buffer and lasting more than 15 min was considered a foraging trip. An individual was considered to have returned when the distance from the colony in an identified trip passed a threshold of 150 m toward the colony. For example, if a bird departed the colony (and passed the 100 m buffer for more than 15 min) and one of the subsequent locations when considered sequentially fell within the return threshold of 150 m, then its travelling movement was considered a finite foraging trip. We chose these thresholds through visual examination of the data to ensure buffers allowed the identification of travelling movement away from the colony while also correctly identifying unique trips. By doing so, we excluded from this study foraging activity known to happen very close to the colony (a few meters from shore and lasting less than 15 min; S. R. Craik pers. obs.). Such activity would have been hard to characterize given the temporal resolution of the GPS devices. Regardless, the exclusion of this data likely did not influence the conclusions of the study, given that foraging trips within 100 m of the colony are not common (S. R. Craik pers. obs.)

2.2.2. RST

We used the RST method (Torres et al. 2017) to discriminate 3 behaviours: (1) travelling, (2) area restricted search (ARS) associated with foraging activity, and (3) resting. The RST method enabled us to associate each at-sea location as regularized (above) with one of the 3 behavioural states based on the distance travelled within a radius and the time spent in that radius. For a location to be considered as resting, time spent in a radius around the location must be sufficiently long and the distance travelled short (time intensive). For ARS, both time spent and distance travelled in the radius must be relatively long (time and distance intensive). For travelling, time spent and distance travelled would be minimal in order to cross a given radius. We selected the radius for each individual based on the diagnostic tool provided by Torres et al. (2017), which identifies best

radius, i.e. the one where all points have at least one other point inside its circle. In our case, we tested for radii 50–500 m at 10 m intervals, and radii 1–15 km at 500 m intervals; see Torres et al. (2017) for a detailed description of the RST method. The RST method enabled us to exclude locations categorized as resting and travelling from the remaining analysis of habitat use and habitat modelling. We further used foraging locations (i.e. ARS) to assess habitat use and to develop our habitat suitability model for roseate terns.

2.2.3. Habitat use

We used the marine Important Bird and Biodiversity Areas (mIBA) protocol developed by Lascelles et al. (2015) to identify important areas of utilization for roseate terns. Namely, we used kernel density estimator to identify the core utilization areas (50% utilization distribution, UD) for each individual foraging trip using the 'kernelUD' function from the R package 'adehabitatHR' (Calenge 2006). We followed the method by Lascelles et al. (2015) to estimate the smoothing term h used in the kernel density calculation. This method uses first passage time (FPT) analysis at different scales on each trip for each individual tracked, and identifies the scale at which each trip interacts with the environment based on the maximum variance in FPT value found across the tested scales. We tested scales of different radius from 500–5000 m at 100 m intervals, between 6 and 10 km at 1 km intervals, and between 11 and 15 km (the maximum distance for a trip) at 2.5 km intervals. This method returns the median scale for each individual, and we used the average of that median across individuals as the value of h in the kernel density calculation ($h = 0.85$ km). We estimated core areas of each individual trip by using the average h found across individuals to facilitate the population estimate of spatial aggregation and area of concentrated use obtained as follows. We assessed the 'spatial aggregation' of each individual foraging trip core area (50% UD overlap) using Bhattacharyya's affinity index (BA). The spatial aggregation corresponded to the median of all the pairwise BA overlap across all trip core areas for all individuals. In other words, 'spatial aggregation' is an index of repeated use of an area across all birds. We also calculated the area of concentrated use for all birds, which corresponded to areas where more than 12.5% of the core areas occurred (Lascelles et al. 2015, Oppel et al. 2018), i.e. grid cells that intersected with at least

12.5% of the core areas (Lascelles et al. 2015). Grid cell size corresponded to h divided by 100. For each individual, we further calculated the recursion of foraging trip within the area of concentrated use defined within the Cockerwit Passage (Fig. 1).

2.2.4. Habitat modelling

Within the maximum foraging range observed from North Brother Island (15.4 km), we randomly resampled background points (pseudo-absence), excluding land and excluding a 100 m buffer around each observed foraging location, in order to compare characteristics of the locations used by the terns (true presence) from the randomly sampled background points. For each observed foraging location, we randomly sampled 3 background points (total of 4635 pseudo-absence points). Five characteristics were measured at each location: distance to the colony (dist2col), distance to the nearest land including islands (dist2land), daily SST ($^{\circ}\text{C}$) averaged over the 6 d of the tracking study, water depth (ETOPO1, spatial resolution of 0.03° , approximately 3 km; vertical resolution of approximately 10 m), and subtidal substrate type (Greenlaw et al. 2013). SST data were Multi-scale Ultra-high Resolution (MUR) downloaded from <https://coastwatch.pfeg.noaa.gov/erddap> (spatial resolution of 0.01°). The subtidal substrate types included boulders, mixed sediments, mud, sand, sand/gravel, and sand/mud.

To obtain a habitat suitability index (HSI), we used a generalized additive model (GAM; package 'mgcv' in R) with a binomial distribution; a value of 1 was given to observed locations and 0 to randomly sampled background points. We created single variable models for each of the 4 continuous covariates as smooth terms, with the number of knots (k) initially set to 3, and using cubic regression spline to reduce model overfitting (Wood 2006). We further adjusted the number of k for each smooth term to obtain a better fit according to the percentage of deviance explained and reduction of Akaike's information criterion (AIC) scores of single variable models. We limited k to 7 to limit overfitting models and ease model interpretation (Wood 2006). The final model included all 4 continuous covariates in addition to substrate type. Given that our goal was to obtain the best predictive model rather than finding which environmental variables were more important for roseate tern foraging occurrence, all variables were included in the final model with disregard for potential correlation between them. The addition of each

variable improved the area under the receiver operating curve (AUC) score, helped reduce the AIC score, and increased the percentage of explained deviance. We used the AUC score as a diagnostic measure of our final model over 10-fold cross validation (with AUC = 0.5 meaning no better than random, and AUC = 1 meaning model with perfect fit).

We used our final model to predict the probability of occurrence of foraging roseate terns around North Brother Island for the study period within an area corresponding to the maximum foraging range around the colony. We divided the maximum foraging range into a grid of 850×850 m squares, and at each grid square centroid, covariates were extracted and used as the predictor data frame; average daily SST over the study period was calculated as indicated above. HSI ranged from 0–1 and represents the predicted probability of occurrence of foraging roseate terns.

3. RESULTS

Seven roseate terns *Sterna dougallii* nesting on North Brother Island were tracked during the incubation period, resulting in 42 bird-tracking days and 4435 GPS points. We identified 270 trips at sea (Table 1). Roseate terns from North Brother Island travelled up to 152.9 km in a single day, which represents 11 daytime foraging trips. The maximum range among individuals for a trip varied between 100 m and 12.6 km (Table 1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n044p339_supp.pdf). The total distance travelled during a trip was as short as 230 m and as long as 32.3 km (Fig. S2). The longest trip lasted 170 min (excluding night trips [$n = 3$] of rt14; Table 1). Considering the 267 daytime foraging trips across all individuals, the average (\pm SE) maximum range was 4.6 ± 0.2 km trip $^{-1}$, with the average trip lasting 49 ± 2 min and totalling 10.9 ± 0.5 km. As has been shown elsewhere, we did not identify daytime resting on the sea (red dots in Fig. S1). Roosting behaviour was limited to the vicinity of the colony (Fig. S1). In general, terns appeared active throughout the day, with slightly lower numbers of departing trips at mid-day and relatively higher activity near sunrise (Fig. S3). We identified 3 nocturnal trips from rt14 occurring during 3 different nights (Text S1) with maximum distances of 300 m, 13.7 km, and 15.4 km and respective durations of 20 min, 4.5 h, and 6.8 h. RST analyses suggest that the purpose of the night travel was different from that observed during daylight hours and in-

Table 1. Foraging trips of 7 roseate terns tracked from 16–23 June 2016 during the incubation period at North Brother Island, Nova Scotia, Canada. All data are from daytime trips except rt14, which includes tracking for 24 h. The right-hand column presents the number of each individual's foraging trip revisits (and associated proportion over all foraging trips) to the area of concentrated use defined in Fig. 2 in the Cockerwit Passage

Bird ID	Maximum range (km)		Total distance (km)		—Duration— (min)		No. of trips	Tracking duration	No. of revisits to Cockerwit Pass. area
	Mean	Range	Mean	Range	Mean	Range			
rt14	5.2	0.3–15.4	12.7	0.5–31.5	61.0	20–405	46	17–23 June	8 (0.19)
rt15	5.9	0.4–9.4	13.4	0.8–25.0	50.4	20–145	26	17–23 June	8 (0.31)
rt17	5.5	0.6–9.9	12.9	1.2–32.3	49.5	20–105	33	17–23 June	19 (0.58)
rt19	5.0	0.2–12.6	11.2	0.5–31.9	42.6	20–90	38	17–23 June	9 (0.23)
rt21	3.9	0.2–9.9	8.9	0.4–21.3	39.7	20–85	35	17–23 June	7 (0.20)
rt22	3.9	0.1–9.0	8.8	0.2–19.3	43.1	20–85	37	16–22 June	6 (0.16)
rt30	3.7	0.3–9.3	9.4	0.6–28.7	53.7	20–170	55	16–22 June	4 (0.07)

cluded resting periods while at sea and travel interspaced with foraging bouts (Text S1).

The spatial aggregation (BA index) at the population level was 64%, indicating moderately high similarity in space use among individuals. The size of the area of concentrated use reached 7.1 km² when considering a minimum overlap of 12.5% in the core areas across trips by all individuals. This area was located mostly around and to the south of the colony and included the Cockerwit Passage (Fig. 2), a shallow zone of sand and gravel with a rocky bar joining John's Island. All individuals revisited this area, some more frequently than others: 58% of foraging trips made by rt17 were to Cockerwit Passage, compared to only 7% for rt30 (Table 1).

Our final GAM AUC score was 0.98, with the model explaining 72.4% of the deviance, indicating good model fit. Relative habitat suitability over the tracking study was mostly influenced by distance from the colony. Roseate terns' occurrence decreased with distance from the colony and distance to nearest land as they showed a preference for areas relatively close to shore (<1 km) and to their colony (about <5km), although the effect was less pronounced for the latter (Fig. 3, Table 2). Roseate terns foraged in areas with relatively warm SST (Fig. 3). The inclusion of bathymetry in the final model also helped in improving model fit (Table 2) despite larger confi-

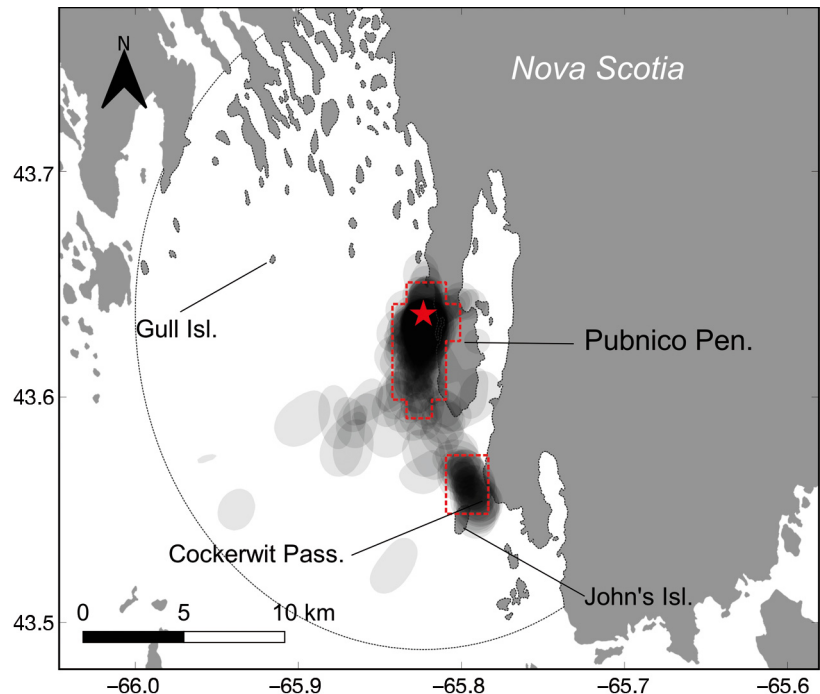


Fig. 2. Core foraging areas (50% utilization distribution [UD]; transparent polygons) calculated based on the foraging locations (residence in space and time method >0; blue dots in Fig. S1) of each roseate tern foraging trip tracked during incubation (16–23 June 2016) at the North Brother Island colony. The smoothing term h (0.85 km) corresponds to the average of each individual h calculated previously to facilitate and enable comparison of all individuals' UD. Red dashed boxes (grid size = $h / 100$): 'areas of concentrated use' estimated following the marine Important Bird and Biodiversity Areas approach (Lascelles et al. 2015) for all individuals (i.e. where at least 12.5% of all core areas overlapped); black dotted line: maximum range reached for a foraging trip (15.36 km). Projection: WGS84 Pseudo-Mercator

dence intervals at deeper areas and shallower depths (Fig. 3), and the relatively lower spatial resolution of that layer. Foraging roseate terns were more likely to occur in areas characterized by boulders, sand/gravel, and sand/mud substrate. Boulders repre-

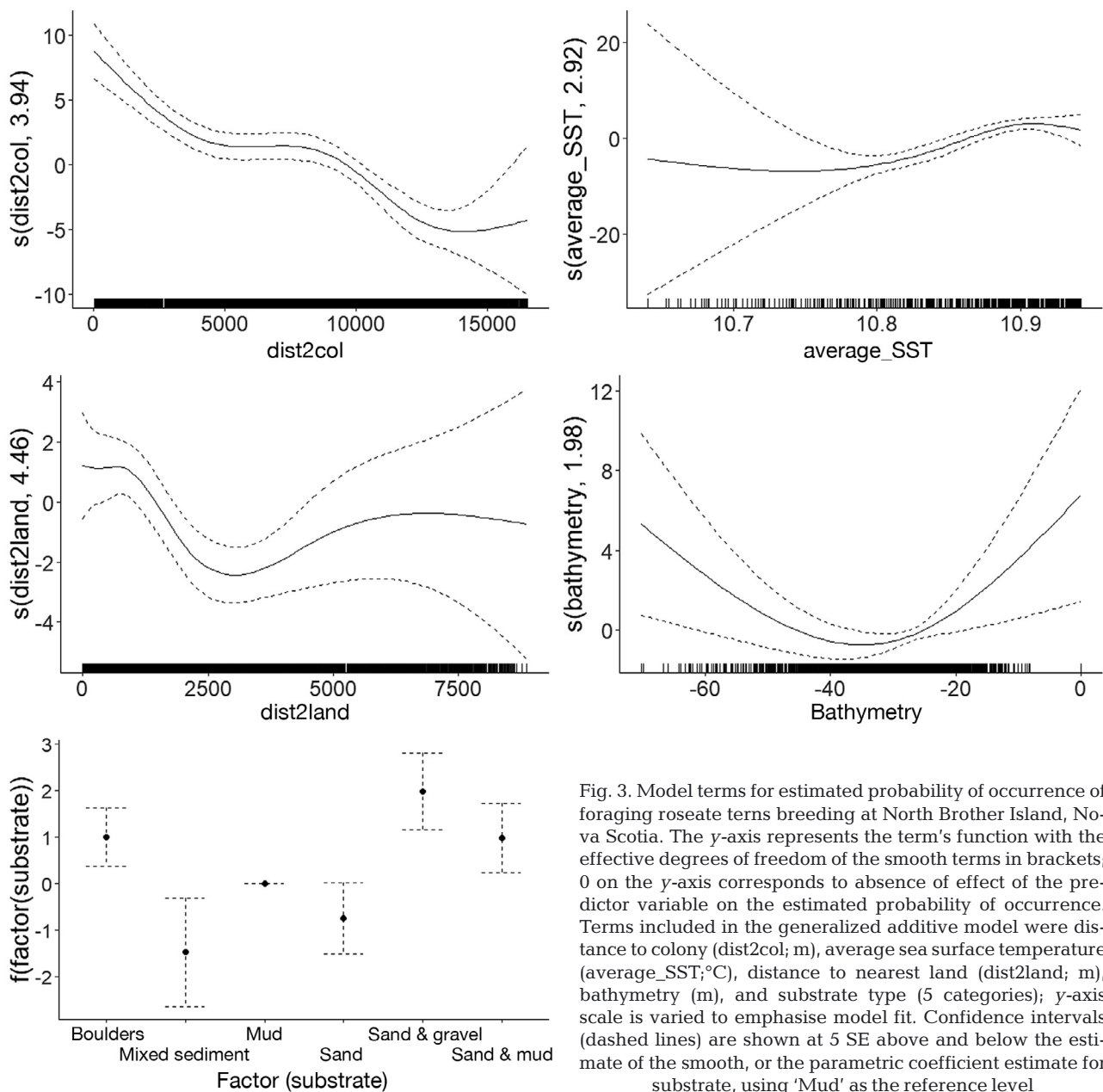


Fig. 3. Model terms for estimated probability of occurrence of foraging roseate terns breeding at North Brother Island, Nova Scotia. The y-axis represents the term's function with the effective degrees of freedom of the smooth terms in brackets; 0 on the y-axis corresponds to absence of effect of the predictor variable on the estimated probability of occurrence. Terms included in the generalized additive model were distance to colony (dist2col; m), average sea surface temperature (average_SST; °C), distance to nearest land (dist2land; m), bathymetry (m), and substrate type (5 categories); y-axis scale is varied to emphasise model fit. Confidence intervals (dashed lines) are shown at 5 SE above and below the estimate of the smooth, or the parametric coefficient estimate for substrate, using 'Mud' as the reference level

sented 40% of the study area at 318 km², while sand/gravel and sand/mud together totalled 23% of the study area at 184 km² (Fig. S4). Areas with bottom substrate consisting of only sand did not appear suitable for foraging terns (Fig. 3), despite this type of substrate covering 27% of the study area (216 km²; Fig. S4). Habitat suitability modelling revealed that a relatively high occurrence of foraging terns was predicted for areas around the colony and farther south along the Pubnico Peninsula to the Cockerwit Passage and west towards nearshore areas of Gull Island, the island which roseate terns colonized in

2017 following abandonment of North Brother Island (see Section 2.1) (Fig. 4).

4. DISCUSSION

Understanding endangered seabird spatial ecology and habitat use can be challenging because researchers are often limited by small sample sizes. The roseate tern *Sterna dougallii* is listed as endangered in Canada, where the small breeding population (69 pairs in 2019) is generally restricted to 3

Table 2. Generalized additive models built with single covariates (upper section of table) and forward step-wise model selection procedure to assess multiple covariate models (lower section of table). Number of knots used in the smooth function (k), percentage of model deviance explained, and area under the curve (AUC) are presented. The model in **bold** is the final model selected based on increase in AUC score and percentage of deviance explained, and a decrease in Akaike's information criterion (AIC) score following the successive addition of each covariate. Dist2col: distance to colony; SST: sea surface temperature; dist2land: distance to nearest land

Covariate	k	% dev.	AUC
Dist2col	5	55.4	0.92
SST	4	34.8	0.87
Dist2land	6	18.7	0.78
Bathymetry	3	8.0	0.69
Substrate	na	16.1	0.46
Model	AIC	% dev.	AUC
Presence ~ s(dist2col) + s(SST)	2437	63.8	0.95
Presence ~ s(dist2col) + s(SST) + s(dist2land)	2008	70.4	0.97
Presence ~ s(dist2col) + s(SST) + s(dist2land) + s(bathymetry)	1952	71.3	0.97
Presence ~ s(dist2col) + s(SST) + s(dist2land) + s(bathymetry) + substrate	1819	72.4	0.98

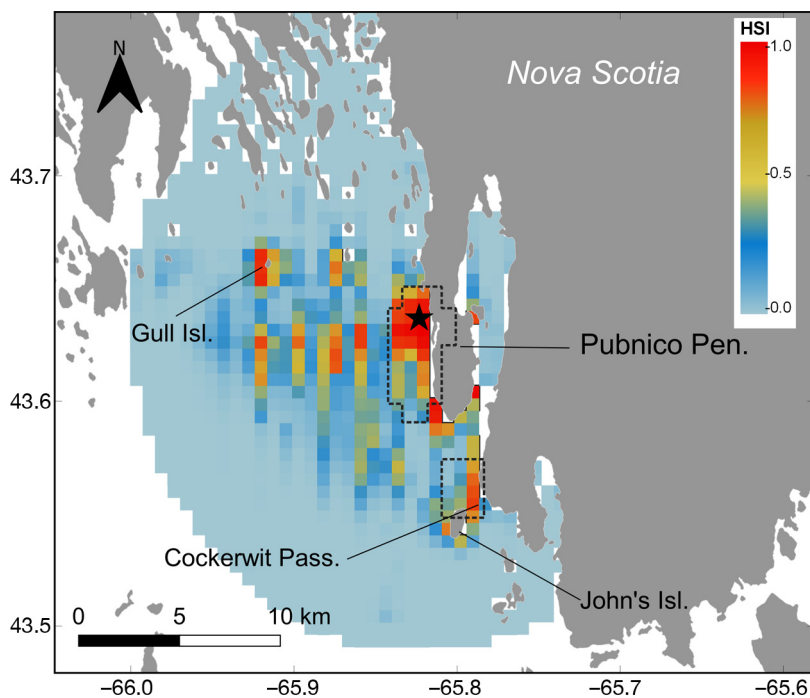


Fig. 4. Spatial predictions of habitat suitability index (HSI; probability of occurrence) over the period of the tracking study per 850×850 m grid square, where 1 is the greatest suitability and 0 is not suitable. Model is based on foraging locations and randomized background points within the maximum foraging range observed for roseate terns tracked from North Brother Island (black star). Black dashed boxes: 'areas of concentrated use' described in Sections 2.2.3 and 3 (Fig. 2). Projection: WGS84 Pseudo-Mercator

islands. In 2016, we tracked 7 adult roseate terns over 1 wk during the incubation period. Birds originated from a colony at which ~75% of the Canadian population currently breed. The level of response to

the covariates included in our habitat suitability model was high, thus providing a useful context for understanding patterns of resource use and predicting suitable foraging habitat for endangered roseate terns around their colony.

4.1. Spatial ecology

Roseate terns breeding on North Brother Island made foraging trips throughout the day; the high number of trips per day corroborates the frequent shifts in incubation bouts observed for the species (Nisbet et al. 2014). Similar to previous studies on roseate terns (mostly using VHF or at-sea observations; Rock et al. 2007, Robertson et al. 2014), we found that individuals from North Brother Island restricted their foraging range to around their breeding colony (Rock et al. 2007), travelling an average of 4.6 km from the island and never exceeding 16 km. These findings support the idea that such a restricted range might be characteristic of the

North Atlantic roseate tern population (Rock et al. 2007), as has been found in some European colonies (Robertson et al. 2014). In contrast, the species has been observed to venture as far as 60 km from the

colony in the tropics (Surman & Wooller 2003). In their North Atlantic range, roseate terns are generally much more specialized in their diet than common *S. hirundo* and Arctic *S. paradisaea* terns, which rely on fewer prey species and specialize mostly on sand lance *Ammodytes* spp. (Safina 1990, Rock et al. 2007, Nisbet et al. 2014). The distance travelled by roseate terns should reflect where important prey species are available, and central-place foraging theory predicts that these birds should select areas of sufficient food that are closest to the colony (Elliott et al. 2009).

The only individual tracked at night (rt14) displayed intriguing nocturnal activity during 3 out of the 6 nights it was tracked. The bird travelled about 15 km west of the colony and rested for several hours (likely on shoal or exposed rock), although some foraging activity was also identified by the RST method. We suggest here that roseate terns can also engage in foraging activity at night. Though nocturnal activity was observed in this particular bird, such nighttime travel was not deemed the norm, as it did not happen every night rt14 was tracked, nor was it frequent during those nights (1 trip night⁻¹). Nonetheless, nocturnal trips may be relatively common; thus, future tracking efforts should include the full 24 h cycle. Spatial aggregation among individuals was high, reaching 64 % overlap, indicating high degree of similarity in space use among individuals. Such aggregation levels likely correspond to predictable forage linked to environmental characteristics such as sandbars, shallow reefs and shoals that, with the concomitance of tidal currents, can help concentrate fish prey and render them more accessible to terns. Roseate terns associate with such features, notably where they breed in the western North Atlantic (e.g. Long Island, NY; Safina 1990). The birds from North Brother Island exhibited concentrated use in the Cockerwit Passage, located to the south east of the colony and characterized by shallow waters with strong tidal currents, a narrow passage corresponding to typical roseate tern foraging habitat (Safina 1990, Nisbet et al. 2014). The bottom substrate on the eastern shore of John's Island in the Cockerwit Passage includes a mix of sand and gravel, which is typical sand lance habitat (Haynes et al. 2007, Staudinger et al. 2020). Indeed, observations undertaken from a boat during the study period confirmed that groups of up to 2–3 roseate terns fed on sand lances at this site during breeding (S. R. Craik unpubl. data), and in some years, sand lances are routinely brought back to North Brother Island during courtship and chick-feeding activities. However, we lack quantitative

data on prey deliveries at this colony. Sand lances are the main food source brought to chicks at the other Canadian colony, Country Island (Rock et al. 2007), and presumably roseate terns from North Brother have a similar diet. Cockerwit Passage could thus represent the closest site from the colony with likely abundance of sand lances, and the availability of these fish could help explain the recurrent use of this site by all tracked birds, although some individuals visited more consistently than others. Similarity in habitat use among individuals can be expected in a specialist species, but exploiting a narrow ecological niche can come at the cost of flexibility (Bolnick et al. 2003). For example, specialist species are predicted to be more vulnerable to habitat and climate changes (Davies et al. 2004, Durner et al. 2009, Clavel et al. 2011, Trivelpiece et al. 2011). Nonetheless, this study presents tracking data from only 1 wk during the incubation phase; thus, similarity in habitat use and how this may relate to specialization should be considered with caution as prey availability and energetic demands of terns may vary among breeding phases (Safina & Burger 1985) and years.

4.2. Habitat modelling

Distance from the colony, SST, distance from nearest land, bathymetry, and subtidal substrate type predicted the occurrence of foraging roseate terns during incubation. The level of response of tern occurrence to the 5 predictors was high, with an explained model deviance of 72.4 %, though some variables had more predictive power than others. The order to which the variables entered the model (based on AUC score) revealed that roseate terns, like other central place foraging seabirds, are strongly bound to their breeding colony. Although roseate terns are known coastal foragers, specializing in the use of shallow-water submerging sandbars, tide rips, and shallow reefs (Safina 1990, Rock et al. 2007, Robertson et al. 2014), bathymetry did not explain a large amount of the deviance of our data, and only slightly improved the overall fit of the model. Roseate terns often occurred at shallow locations (<20 m depth), but sometimes used sites with greater depth (>50 m depth). The species has been observed to forage along exposed coastlines and inshore shallow areas while also making use of deep waters, especially in its more tropical breeding locations (Shealer 1998, Ramos 2000, Surman & Wooller 2003, Monticelli et al. 2006). However, the lesser importance of bathymetry in this study could be

related to the resolution of that data layer (which was coarse considering the local scale at which terns are foraging) and/or to the scarcity of sample points at greater depth and at shallower depth.

Foraging roseate terns occurred at relatively warm SST, which could be linked to shallower and more coastal waters. However, this functional response is less clear to interpretation given the small range of temperatures observed at the time of the study, which spanned between 10.6 and 11.0°C. Given that North Brother Island is located within a bay, preference for warmer SST could be the result of the localised foraging behaviour of the terns within this more enclosed system close to the coast. Despite the narrow range of temperatures observed, SST contributed greatly in improving model fit. Similar to bathymetry, response to distance to nearest land was present but not as important as distance from colony and SST. Nonetheless, the response trajectory was consistent with the known coastal foraging behaviour of roseate terns (Rock et al. 2007, Robertson et al. 2014); terns chose areas closer to land and were unlikely to venture very far offshore.

The probability of occurrence for the roseate tern was highest over substrate types consisting of boulders, sand/mud, and sand/gravel. Sand/gravel substrate has been shown to be a favourable habitat for sand lances (Staudinger et al. 2020). Rock boulders are essential substrate for rockweed *Ascophyllum nodosum*, which creates nursery habitat for many fish species such as Atlantic herring *Clupea harengus*. Sand lances have also been found in abundance in rockweed habitat on the South shore of Nova Scotia (Vercaemer et al. 2018). We lack feeding observations to quantitatively validate the presence of first age class herring in the terns' diet at this colony, but roseate terns have been observed carrying this prey item in this area (S. R. Craik pers. obs.). The rich biogenic habitats growing over rock boulders combined with the restricted coastal range of the roseate tern might explain the higher predicted foraging occurrence over such habitats, as these were predominant around the colony (Fig. S4). Given that rockweed is a resource harvested in the area, our results suggest that the potential impacts of such an industry on roseate tern foraging habitat should not be overlooked. Further study is required to understand the mechanistic link between terns, their prey, and the habitats that provide foraging opportunities.

At North Brother Island, predictions of relative habitat suitability revealed high probabilities of occurrence around the breeding colony, and to the south around the Pubnico Peninsula and the Cocker-

wit Passage. This mirrors the area of concentrated use identified above (Fig. 4). Suitable habitat was also identified at a few smaller sites west of the colony, in particular around Gull Island, which is of interest given that the terns colonised this site in 2017 following abandonment of North Brother Island. Such concomitance suggests that predicting suitable foraging habitat for the roseate tern, in the context of the establishment of additional managed colonies, could be useful in determining other potential breeding sites within their actual at-sea domain. However, manual tracking of this species by boat in recent years (S. R. Craik unpub. data) suggests that the shorelines of this island are not important for feeding terns during the breeding season. Presumably, some features, key in the distribution of preferred prey, may not be present at all sites deemed suitable by the model (e.g. currents). Thus, care should be taken when interpreting some of the model results. Subsequent telemetry studies and/or boat-based work may validate these predictive results, but also enhance our understanding of habitat association at this colony. Roseate tern abundance at sea has been observed to correlate with prey availability (Safina 1990) and also with the abundance of common terns at sea (Goyert 2014), 2 variables that we could not directly quantify in our tracking study but that could greatly refine our understanding of habitat associations for the species at this colony.

Given the species' small, restricted population and the logistical difficulties in studying movement of sensitive and endangered species, we provide novel information concerning their spatial ecology and the first applicable tool to model response to habitat characteristics of foraging roseate terns during the breeding season in the western North Atlantic. This new information could be used to better guide conservation and management decisions at local and regional scales (e.g. Lieske et al. 2020), especially given the gaps in knowledge of at-sea habitat use that currently exist for this species, especially in Canada. Modelling terns' habitat suitability at sea can help researchers provide advice for environmental assessments concerning project developments in marine and coastal ecosystems. Moreover, understanding marine habitat requirements for breeding roseate terns can help identify other candidate sites, which is important since the establishment of new breeding colonies is a stated goal of the recovery strategy for this species in Canada (Environment Canada 2014). Lastly, our model should be interpreted in light of the known local distribution of the species, given that assessing the temporal variation in habitat choice and in foraging

functional response that exists within and across breeding seasons is still necessary to help evaluate the vulnerability of this endangered seabird to anthropogenic or climate-induced changes.

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