

# Relationship among prey availability, habitat, and the foraging behavior, distribution, and abundance of common terns *Sterna hirundo* and roseate terns *S. dougallii*

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**ABSTRACT:** Analyses of the behavior, distribution, and abundance of seabirds tend to identify the importance of habitat variability and prey availability, yet ignore social facilitation. To quantify such influences on the foraging strategies of common terns *Sterna hirundo* and roseate terns *S. dougallii*, I implemented nonlinear density-surface models with distance sampling, using remotely-sensed habitat covariates. I collected tern and prey data aboard trawl surveys off the coast of Massachusetts, USA, selecting the 3 dominant regional prey categories: northern sandlance *Ammodytes dubius*, herring (*Clupea* spp., primarily Atlantic herring *C. harengus*), and anchovies (*Anchoa* spp.). The best models showed significant positive effects of tern flock size and variable sandlance abundance on common and roseate tern spatial patterns; additional predictors included herring abundance, relatively shallow water, high primary productivity, and intermediate sea surface temperatures. Furthermore, foraging roseate terns were associated with high sandlance abundance. By establishing direct, positive relationships among terns, prey, and habitat, this study demonstrates how common and roseate terns act as community, fisheries, and ecological indicators. These 2 species evidently provide interspecific cues to the presence of prey; therefore, the conservation and management of roseate terns depends not only on the availability of sandlance and suitable habitat, but also on the ecology of common terns.

**KEY WORDS:** Social facilitation · Foraging strategy · Community ecology · Prey availability · Sand lance · Distance sampling · Distribution patterns · Spatial habitat models

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## INTRODUCTION

The direct effect of prey availability on the spatial distribution and abundance of top marine predators is difficult to quantify, and although essential for conservation (Safina & Burger 1988, Diamond & Devlin 2003, Dänhardt & Becker 2011a), such information remains sparse in the literature (Heinemann 1992, Shealer & Kress 1994, Einoder 2009, Williams et al. 2009). Behavioral and ecological factors together

impact prey availability, conventionally through bottom-up processes in the marine realm (Hunt & Schneider 1987, Frederiksen et al. 2006, Grémillet et al. 2008): habitat influences resource predictability, and this, in turn, drives interspecific differences in prey utilization (Davoren et al. 2003, Weimerskirch 2007, Elliott et al. 2009, Weimerskirch et al. 2010).

Seabirds are recognized as good ecological and fisheries indicator species, because they tend to be highly sensitive to habitat and prey patterns (Furness

& Camphuysen 1997, Camphuysen & Webb 1999, Furness & Tasker 2000, Diamond & Devlin 2003, Jaquemet et al. 2004, Le Corre & Jaquemet 2005, Jaquemet et al. 2007, Monticelli et al. 2007, Einoder 2009, Dänhardt & Becker 2011a). Still, little is understood about the trophic relationships involved in the spatial patterns of habitat, prey, and top marine predators, which largely reflects the practical difficulties of at-sea sampling. For example, sandlance (*Ammodytes* spp.) are very important prey to many seabird species in the Northwest Atlantic Ocean, particularly roseate terns *Sterna dougallii* and common terns *S. hirundo* (Safina et al. 1990, Heinemann 1992, Gochfeld et al. 1998, Nisbet 2002, Rock et al. 2007), yet these forage fish are notoriously difficult to sample, due to their slender body shape, burrowing habits, and irregular distribution in the water column (Robards et al. 2000, Dänhardt et al. 2011). Also, it is well documented at tern breeding grounds in the state of Massachusetts (MA), USA, that northern sandlance *A. dubius*, herring (*Clupea* spp., primarily Atlantic herring *C. harengus*), and anchovies (*Anchoa* spp.) are the dominant 3 prey items delivered to common and roseate tern chicks (Kirkham 1986, Safina et al. 1990, Tims et al. 2004, author's unpubl. data). Yet, poor coverage of terns at sea has kept biologists from uncovering how the spatial distribution of terns links to the abundance of these prey. Sandlance, sea herring, and anchovies are neritic or epipelagic baitfish that experience short (interannual) and long-term (decadal) fluctuations in their distribution and abundance, resulting from consumptive impacts, fisheries pressure, and climate change (Overholtz et al. 2000, Overholtz & Link 2007, Lucey & Nye 2010, Nye et al. 2013); however, only Atlantic herring is commercially regulated. Common and roseate terns are susceptible to prey limitation (Safina et al. 1988), although roseate terns are potentially more vulnerable to fluctuations in sandlance availability, given that they are feeding specialists (Gochfeld et al. 1998) that exhibit high foraging site fidelity (Heinemann 1992) and have better breeding success during years of high sandlance abundance (author's unpubl. data). Common terns, on the other hand, are opportunistic generalists (Nisbet 2002) that may be more resilient to prey instability, through the use of local enhancement (Erwin 1977, author's unpubl. data). Local enhancement is a type of social facilitation, where individuals are drawn towards the feeding cues issued by neighbors, as a way to exploit unpredictable prey patches (Davoren et al. 2003). Identifying differences in the foraging strategies of common and roseate terns, with respect to prey and habitat selection, is a high conservation priority (Ama-

ral & Saliva 2010), since the U.S. population of roseate terns is federally 'endangered' and continues to decline, whereas common terns have recovered since the end of the 20th century millinery trade, and are listed as 'special concern' pursuant to the Massachusetts Endangered Species Act (Mostello 2012).

The objective of this study was to evaluate potential drivers of the behavior, distribution, and abundance of common and roseate terns at sea, pre- and/or post-breeding, and to assess the extent to which prey availability, habitat variability, and social interactions predict interspecific similarities and differences in their spatial foraging patterns. I hypothesized that common and roseate terns associate with each other and productive habitat in the search for selected prey species, where sandlance largely determines the foraging behavior and ecology of the highly specialized roseate tern. To assess the ecological context of such trophic interactions between terns and their prey, I used shipboard survey data on the distribution and abundance of selected seabirds and fish species, along with standard remotely sensed oceanographic parameters, viz. sea surface temperature (SST) and chlorophyll concentration, an index of primary productivity (Amorim et al. 2009). My analysis involved behavioral statistics and predictive models with distance sampling, to evaluate how tern foraging behavior and ecology respond to habitat, forage fish, and flocks of other common or roseate terns, at sea.

## MATERIALS AND METHODS

### Data collection

The North American breeding population of roseate terns is divided amongst a few islands that support a dominant proportion of the continental subspecies *Sterna dougallii dougallii* (Gochfeld et al. 1998). Three of their largest breeding colonies in the northeastern US are shared with common terns and are located in Buzzards Bay, MA, on Bird, Ram, and Penikese Islands (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m506p291\\_supp.pdf](http://www.int-res.com/articles/suppl/m506p291_supp.pdf)). The breeding season generally runs from June to July, although terns frequent the waters surrounding Cape Cod, MA, from post- to pre-migration, in May to September. Throughout this study region, the Massachusetts Division of Marine Fisheries (MADMF) provides one of the only long-term datasets available on fish abundance by season. Their Resource Assessment Bottom Trawl Surveys use sys-

tematic methods to provide an index of relative prey availability from sampled fish numbers (Garrison et al. 2002, King et al. 2010, Dänhardt & Becker 2011b, Nye et al. 2013). Shipboard surveys are valuable resources in assessing animal movement patterns, because they provide continuous data on real-time interactions among terns, other marine predators, and their prey, as gauged by their offshore behaviors, numbers, locations, and habitats (Camphuysen & Garthe 2004, Camphuysen et al. 2004). I joined the MADMF cruise, aboard the National Oceanic and Atmospheric Administration's (NOAA) RV 'Gloria Michelle,' for a period of 21 sampling days: 13 to 18 May and 17 to 23 September 2010, and 11 to 20 May 2011. Trawls were conducted from dawn to dusk, during which I continuously recorded data on all observed species and behaviors while in transit (stations were located up to 3 h apart). I followed established protocols from offshore surveys (Goyert et al. 2014), using distance sampling along line transects but resorting to 300 m strip transects during occasional bursts of high densities (Tasker et al. 1984, Thomas et al. 2010). I used binoculars and entered data directly into a computer using dLOG3 (R.G. Ford Consulting), recording the bearing and distance of observations using a rangefinder, with distance bands calculated based on the geometry of observer height above the water (Heinemann 1981).

Two outside sources supplemented my seabird observation data: (1) bottom trawl catch results, and (2) online geographic information system (GIS) marine data layers. NOAA and MADMF employees deployed an otter trawl net at stations that were randomly stratified by region and depth in MA state waters: each tow was standardized to 20 min at 2.5 knots (King et al. 2010). I selected a subset of these data to represent the dominant categories of fish species, by composition and size, delivered to tern chicks in MA for those same years (2010–2011, author's unpubl. data). By focusing on the distribution of sand lance, herring, and anchovy numbers, no longer than 15 cm, I evaluated whether the foraging patterns of pre- and post-breeding adults (May or September) overlap spatially with the distribution and abundance of those same prey species that they feed to chicks (in June and July). The 3 fish categories included the following species, in order of decreasing biomass: (1) sand lance: northern sand lance; (2) herring: Atlantic herring, alewife *Alosa pseudoharengus*, blueback herring *A. aestivalis*, American shad *A. sapidissima*, and Atlantic menhaden *Brevoortia tyrannus* (negligible in biomass); (3) anchovy: bay anchovy *Anchoa mitchilli* and

striped anchovy *A. hepsetus*, along with rainbow smelt *Osmerus mordax*, which made up <1% of this category, but was included to account for possible misidentification as anchovy during tern colony-based provisioning studies (author's unpubl. data).

To access marine habitat data, I downloaded raster layers into ArcGIS: (1) 30 m bathymetry for MA and adjacent federal waters from the online Office of Geographic Information (MassGIS), and (2) remotely-sensed data from the National Aeronautics and Space Administration's (NASA) Aqua satellite using Duke's Marine Geospatial Ecology Tools (Roberts et al. 2010): 4 km monthly daytime SST (JPL PO.DAAC MODIS Global Level 3) and chlorophyll *a* (chl *a*; GSFC OceanColor Level 3 Standard Mapped Image). These covariates made up 8 data layers: (1) depth (m); (2) SST (°C); (3) chl *a* concentration ('Chl', mg m<sup>-3</sup>); counts at length of (4) sand lance ('Sl'), (5) herring ('Hg'), and (6) anchovy ('An'); and total number of (7) common and mixed terns ('CMT') or (8) roseate and mixed terns ('RMT'); 'mixed' refers to mixed species flocks of common and roseate terns that were difficult to distinguish at farther distance (e.g. 500 m). CMT and RMT are mutually exclusive as covariates (depending on which species is treated as a response variable); therefore, only 7 covariates could be analyzed at one time.

The most suitable spatial scale for analysis fit the following criteria: large enough to accommodate autocorrelation (due to continuous tern sampling) and to minimize the number of covariate cells with missing data (attributable to discrete prey sampling), yet small enough to prevent diluting predictions with missing data, for example by projecting onto land. The spatial dispersion of bottom trawl stations largely determined the optimal resolution: 15 km × 15 km raster cells (225 km<sup>2</sup>). Therefore, I aggregated covariate values by mean (depth, SST, chlorophyll, number of fish by species), and tern abundance by sum, into this grid resolution. The total study area (6750 km<sup>2</sup>) was made up of 30 cells, but data coverage varied slightly by parameter and survey. I calculated the length of track lines within each cell to determine transect effort. Due to the size of these grid cells, the 3 largest shared MA breeding colonies of common and roseate terns in the study area occupied neighboring grid cells (Fig. S1).

### Data analysis

Distance sampling computes the detection probability of study subjects from their observed range

(perpendicular distance to a line transect), for the purpose of evaluating population abundance (Thomas et al. 2010, Gjerdrum et al. 2012). Density-surface modeling (DSM, Miller et al. 2013a) implements distance sampling to determine the relationship among the spatial distribution of population abundance and covariates. I used the package 'dsm' (Miller et al. 2013b) in R (R Development Core Team 2012), which integrates 2 components (a 2-stage approach) to model the effect of habitat covariates on the distribution and abundance of terns. First, DSM relies on the package 'Distance' (Miller 2012) to perform conventional distance sampling (CDS), or alternatively, with the addition of 1 covariate (visibility), multiple covariate distance sampling (MCDS): these analysis engines fit a detection function (Fig. S2 in the Supplement) onto the observed tern counts. The detection probabilities ( $P$ ) are then used to calculate abundance over the sampled area ( $N$ , Table S1 in the supplement), as well as estimated abundance over the entire study area. The second DSM component runs a generalized additive model (GAM) on the sampled data cells ( $n$ , Table 1), fitting abundance ( $N$ , Table S1) to covariates; next, by projecting the results over modified (mean) covariate values that span the entire study area (at an identical scale), the user may predict population distribution and abundance (of terns, see Fig. 2). The benefit of this approach is that it allows the user to consolidate many surveys into 1 set of spatially-explicit predictions.

Model selection involved testing combinations of a limited number of parameters (depending on the degrees of freedom in each GAM), given the 7 possible covariates. I evaluated 4 model categories defined by the response variable and number of surveys analyzed: (1) common, roseate, and mixed terns ('CRMT') over all 3 surveys (62 possible combinations of a maximum of 5 parameters, given 6 possible covariates), (2) common terns ('CT') over all 3 surveys (126 combinations of 6 parameters given 7 optional covariates; no roseate terns were identified in the fall 2010 survey), (3) common terns in the 2 spring surveys (56 combinations of 4 parameters, given 6 covariates), (4) roseate terns ('RT') in the 2 spring surveys (56 combinations). Additionally, models varied by distribution (Poisson or negative binomial), and distance sampling engine (CDS or MCDS). I used a backwards stepwise approach, starting with the 'beyond optimal' models (most complex, e.g. 7 covariates, 6 parameters), then subsequently dropping 1 parameter. Once all covariates in the models reached significance ( $p < 0.05$ ), I compared nested models with likelihood ratio tests and

selected those with the lowest Akaike's information criterion (AIC) scores (Wood 2006, Zuur et al. 2012). There was no need to account for autocorrelation in the models, since the 15 km grid scale properly accommodated for spatial autocorrelation, rendering it insignificant; Moran's  $I$  values were computed with the midpoint coordinates of each cell using package 'ncf' (Bjornstad 2009).

Density-surface models were developed to estimate the distribution and abundance of all observed common and roseate terns, irrespective of behavior. Therefore, to determine the effect of sampled prey numbers on the comparative behavior of each tern species in the spring, I classified behaviors into 'foraging' (milling or feeding, i.e. plunge-diving) and 'not foraging' (traveling, resting), then used a 2-factor analysis of variance (ANOVA) and Tukey's multiple comparisons.

## RESULTS

The generalized variance inflation factors (GVIFs, Zuur et al. 2010) of all covariates were  $< 2$ , indicating negligible collinearity, to allow that all combinations of explanatory variables be assessed in the models (Fig. S3 in the Supplement). The distribution of the response variables (histograms in Fig. S3) illustrates that the Poisson and negative binomial families were indeed more appropriate for analysis than a Gaussian curve. For the DSM, the study area (and prediction grid) consisted of 30 data cells, but the total number of sampled data cells ( $n$ , Table 1) was  $< 90$  for all 3 surveys, and  $< 60$  for the 2 spring surveys, due to missing data (survey coverage or data availability).

The 4 selected density-surface models (Table 1) differed from the other candidate models chiefly in habitat covariate influences (SST versus chlorophyll or depth); only in the case of roseate terns did prey covariates have a distinct effect on model selection (the only difference between the best and second-best model was the influence of herring). Model 10 had an AIC value that did not differ significantly from its nested model (Table 1); given that model 10 was more complex (with the addition of 1 prey parameter, herring, to accompany sandlance), the likelihood ratio test evaluated it as significantly better (Johnson & Omland 2004). The combination of a negative binomial distribution with MCDS produced best-fit models only for roseate terns—although there were few 3- or 4-parameter candidate models that showed significance in all covariates, they had

Table 1. Density-surface model selection. The best models selected from the candidate set are shown in **bold** (with significant predictors shaded in gray) and indicate: the response variable; number of surveys analyzed; number of data cells sampled (n); distribution family (negative binomial: 'Neg Bin'); type of distance sampling used in the detection (Detect.) function – either conventional (CDS) or multiple covariate distance sampling (MCDS); number of model parameters (Param.); significance of each covariate (\*\*p < 0.001, \*p < 0.01, \*p < 0.05); the explained deviance (Dev.); and Akaike's information criterion (AIC) value. Covariates for habitat (columns at left) are sea surface temperature (SST), chlorophyll concentration (Chl), and depth. Prey covariates (middle columns) are anchovy (An), herring (Hg), and sand lance (Sl). Other tern covariates (columns at right) are common tern *Sterna hirundo* and mixed terns (CMT) or roseate tern *S. dougallii* and mixed (RMT) terns. The 'x' indicates parameters that were not tested (i.e. not included in the data), '-' indicates covariates that were not considered as predictors in the models shown (i.e. they were not significant in more complex models), spr: spring

Model	Res- ponse	Sur- veys	n	Family	Detect.	Param.	Habitat			Prey			Other tern		Dev. (%)	AIC
							SST	Chl	Depth	An	Hg	Sl	CMT	RMT		
1	CRMT	3	55	Poisson	CDS	5	***	–	***	**	***	***	x	x	94.2	360
2			<b>52</b>	<b>Poisson</b>	<b>CDS</b>	<b>4</b>	–	***	***	–	***	***	<b>x</b>	<b>x</b>	<b>95.4</b>	<b>333</b>
3			52	Poisson	CDS	3	***	***	***	–	–	–	x	x	83.9	520
4	CT	3	52	Poisson	CDS	5	***	***	–	***	–	***	x	***	96.5	297
5			52	Neg Bin	CDS	5	–	*	***	–	*	**	x	*	48.3	373
6			<b>52</b>	<b>Poisson</b>	<b>CDS</b>	<b>4</b>	–	***	***	–	–	***	<b>x</b>	***	<b>98.5</b>	<b>266</b>
7			52	Neg Bin	MCDS	4	–	***	***	–	–	***	x	***	88.5	674
8		2 - spr	<b>39</b>	<b>Poisson</b>	<b>CDS</b>	<b>4</b>	***	–	–	<b>x</b>	*	***	<b>x</b>	***	<b>99.8</b>	<b>223</b>
9			37	Poisson	CDS	3	–	***	***	x	–	***	x	–	92.6	274
10	RT	2 - spr	<b>40</b>	<b>Neg Bin</b>	<b>MCDS</b>	<b>4</b>	–	–	*	<b>x</b>	**	*	***	<b>x</b>	<b>95.3</b>	<b>209</b>
11			40	Neg Bin	MCDS	3	–	–	***	x	–	***	***	x	92.5	208

especially low AIC values; these unique properties reflect the low incidence of roseate tern observations relative to common terns at sea. Overall, distance sampling resulted in well-fit density-surface models (high explained deviance, Table 1), and reasonable estimations of common tern abundance over the survey area, yet it over-inflated roseate tern abundance estimates, compared to the censused MA breeding population size (Table S1).

Sand lance was the only covariate that influenced all 4 selected models (Table 1, Fig. 1), demonstrating its strong effect on common and roseate tern distribution and abundance. While model 10 suggests that roseate tern abundance had an inverse relationship with sand lance, model 2 suggests otherwise: common, roseate, and mixed terns were likely to be observed at high and low values of sand lance (Fig. 1). The grid cell between the island of Martha's Vineyard and Buzzards Bay (Fig. S1b) gives an example of where persistent sand lance abundance and roseate tern observations contributed to predictions of relatively high roseate tern abundance in spring 2010 and 2011 (Fig. 2d). There were clear differences between seasons, notably that no roseate terns were observed in the fall of 2010, which was characterized by higher SST and more anchovies (Fig. S1); this seasonal increase in anchovy availability is supported by the positive correlation between this prey category and SST (Fig. S3). In the spring, common terns (model 8, Table 1) were likely to be found in higher

numbers where intermediate SST, 8–10°C, characterized the habitat (Fig. 1). Of the selected 4 models, only in model 8 did SST emerge as a significant predictor, stronger than depth or chlorophyll (note that I assigned depth a negative value, and it was positively correlated with SST and chlorophyll, such that shallow water embodied higher values). Additionally, this model singly excluded bathymetry, suggesting that SST may sufficiently account for variation in depth, given their co-dependence. Overall, higher counts of common and roseate terns were likely to occur where waters were shallow, less than 40 m deep, with variable sand lance abundance, and sampled herring numbers that reached 200 cell<sup>-1</sup> (Fig. 1). The distribution of sand lance and herring (Fig. S1) appeared to follow colder water than anchovies, as supported by a negative correlation with SST (Fig. S3). Models 2 and 6 indicate that, across the 3 surveys, common terns, and apparently roseate terns, associated positively with chlorophyll concentration above 4 mg m<sup>-3</sup> (with a peak at 6 mg m<sup>-3</sup>); since both seasons were analyzed in these 2 models, this effect of primary productivity is attributable to the fall. Unmistakably, the presence of neighboring conspecific and heterospecific tern flocks shows co-dependency: common terns aggregate with any number of roseate and mixed terns (RMT > 100, model 6; RMT < 100, model 8); roseate terns assemble with intermediate counts of common and mixed terns (CMT 50–300, model 10).



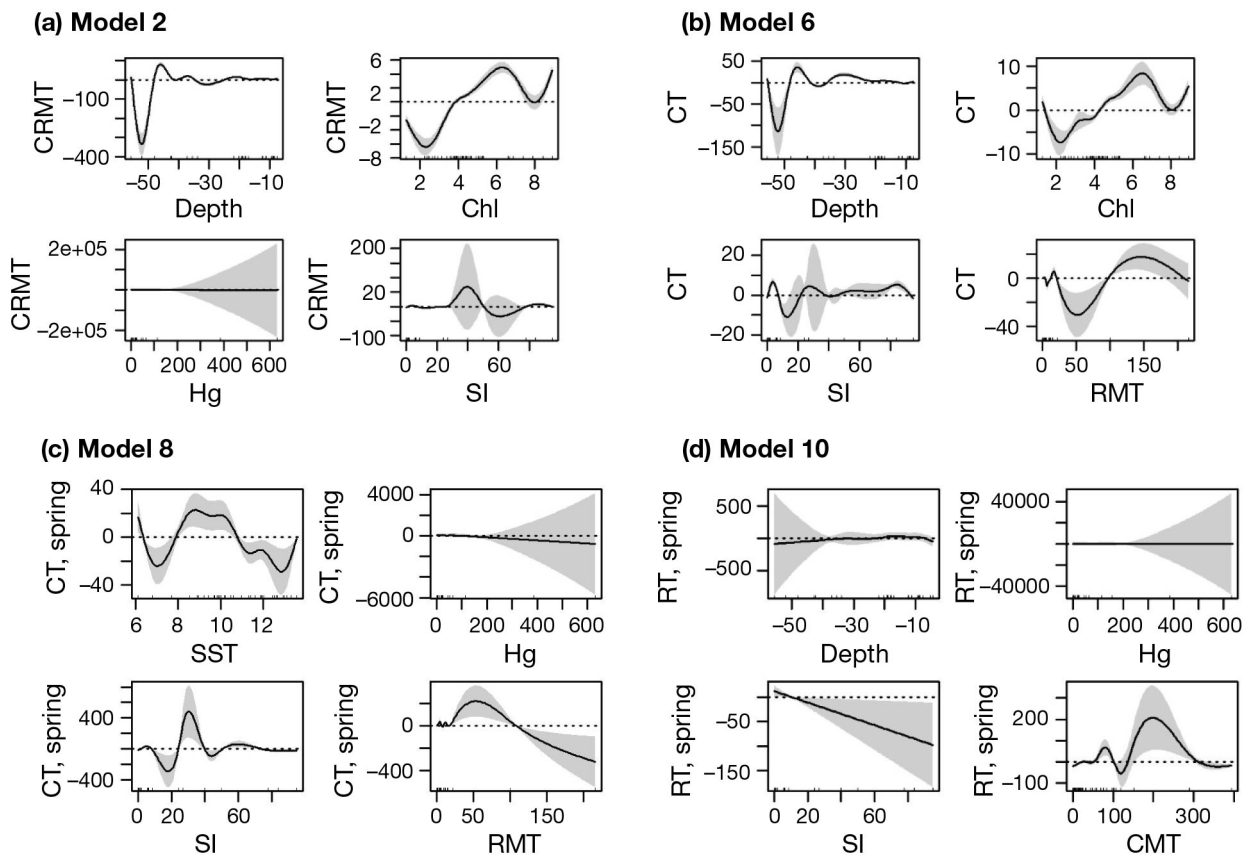


Fig. 1. Generalized additive model plots of the 4 selected models. The y-axes show the effects of the covariates (x-axes) on the response variables (fitted tern abundance), for all 3 surveys: (a) common tern *Sterna hirundo*, roseate tern *S. dougallii*, and mixed terns (CRMT; model 2), (b) common terns (CT; model 6); and the 2 spring surveys: (c) common terns (model 8), and (d) roseate terns (RT; model 10). Shaded areas demarcate the standard error bounds of uncertainty (confidence bands), and dotted lines delineate where  $y = 0$ . Habitat covariates are sea surface temperature (SST), chlorophyll concentration (Chl), and depth; prey covariates are anchovy (An), herring (Hg), and sand lance (SI); other tern covariates are common and mixed terns (CMT) or roseate and mixed (RMT) terns

In the 2 spring surveys, common tern numbers (mean  $\pm$  SE:  $19.1 \pm 0.9$ ;  $n = 1766$ ) were observed over areas with significantly higher numbers of sampled herring than roseate terns ( $8.7 \pm 2.6$ ;  $n = 97$ ):  $t_{121,0} = 3.7$ ,  $p < 0.001$  ( $n = 1863$ ); however, comparisons between behavioral groups, within or between tern species, were not significant for sampled herring numbers (Fig. 3b). As for sand lance, the interaction between tern species and behavior was significant ( $F_{1, 1863} = 47.1$ ,  $p < 0.001$ ), where individual foraging roseate terns were observed over areas with significantly higher numbers of sampled sand lance ( $59.6 \pm 10.0$ ,  $p < 0.001$ ) than were foraging common terns ( $19.0 \pm 1.2$ ), and non-foraging common ( $22.1 \pm 1.0$ ) or roseate terns ( $5.9 \pm 1.9$ ); individual foraging and non-foraging common terns were found over significantly more sand lance than non-foraging roseate terns ( $p < 0.01$ , Fig. 3a). All other behavioral group comparisons of sand lance and herring were insignificant (Fig. 3).

## DISCUSSION

This research demonstrates a clear relationship among prey availability, habitat, and the social foraging behavior, distribution, and abundance of common and roseate terns. The distribution and abundance of principal prey items were associated positively with the spatial patterns of common and roseate terns, which supports the importance of herring and sand lance to adults, and not just chicks (as established in colony-based provisioning studies, Kirkham 1986, Safina et al. 1990, Tims et al. 2004, author's unpubl. data). The relative spatial availability of sand lance was a key determinant of roseate tern foraging behavior and ecology, in Massachusetts and, likely, the NW Atlantic Ocean. High abundance of common terns predicted high abundance of roseate terns, and the reverse also occurred, suggesting that terns may be able to use each other as cues

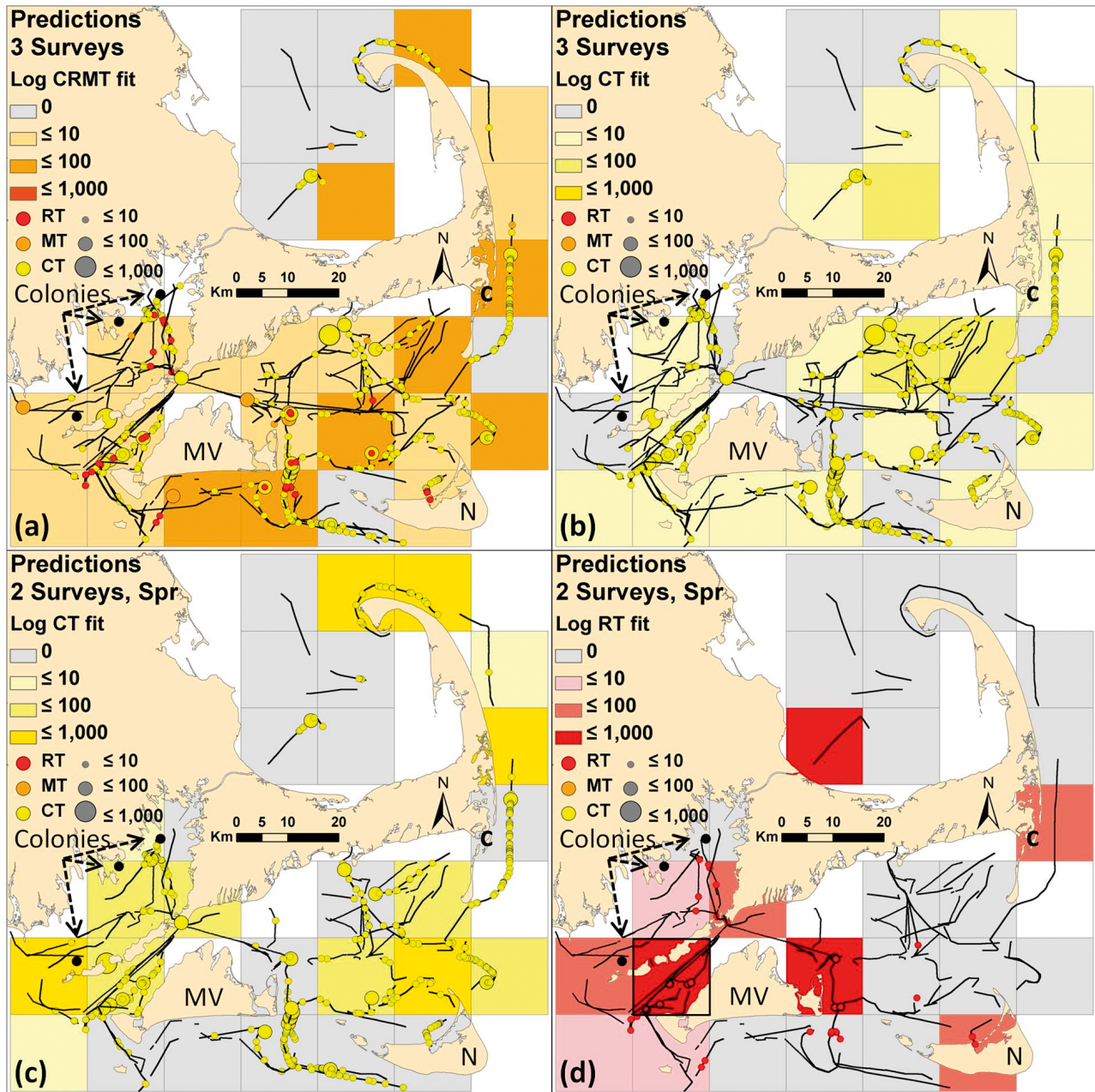


Fig. 2. Predicted tern distribution and abundance in Massachusetts, USA, waters. The study region includes Cape Cod, the islands of Martha's Vineyard (MV) and Nantucket (N), and Buzzards Bay, which contains the 3 largest shared breeding colonies of common tern *Sterna hirundo* and roseate tern *S. dougallii* on Bird, Ram, and Penikese Islands (● and dashed arrows); the 'c' on the 'elbow' of Cape Cod marks the location of a major common tern colony. Transect effort (black lines) is overlapped by counts of observed common, roseate, and mixed terns (circles). Thirty sampled grid cells (each 15 km × 15 km) were used in the density-surface modeling; white cells indicate missing covariate data (resulting in  $n = 28$  for all 4 predictive grids). Fitted common, roseate, and/or mixed terns (log abundance per 225 km<sup>2</sup> shaded grid cell) are based on predictions from the covariates corresponding to each of the 4 selected models, averaged across either all 3 surveys: (a) common, roseate, and mixed terns (CRMT; model 2), (b) common terns (CT; model 6); or the 2 spring surveys: (c) common terns (model 8), and (d) roseate terns (RT; model 10). The grid cell between MV and Buzzards Bay is outlined in (d) to give an example of where persistent sandlance abundance (see Fig. S1b in the Supplement) and roseate tern observations contributed to predictions of relatively high roseate tern abundance in spring 2010 and 2011.

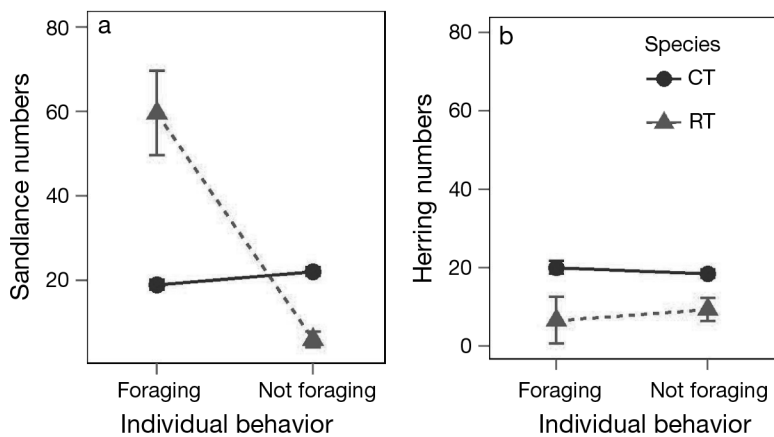


Fig. 3. Mean prey numbers by tern species and behavior across the 2 spring inshore surveys. (a) Interaction between tern species and behavior was significant for sampled sandlance numbers ( $F_{1,1863} = 47.1$ ,  $p < 0.001$ ), where individual foraging roseate terns *Sterna dougallii* (RT) were observed over areas with significantly higher numbers of sampled sandlance ( $59.6 \pm 10.0$ ,  $p < 0.001$ ) than were foraging common terns *S. hirundo* (CT,  $19.0 \pm 1.2$ ), and non-foraging common ( $22.1 \pm 1.0$ ) or roseate terns ( $5.9 \pm 1.9$ ), with mean  $\pm$  SE; individual foraging and non-foraging common terns were found over significantly more sandlance than non-foraging roseate terns ( $p < 0.01$ ); all other behavioral group comparisons of (a) sandlance and (b) herring were non-significant

to the presence of prey, in line with the hypothesis that positive interspecies interactions may result from facilitation (e.g. local enhancement). Therefore, the conservation and management of roseate terns depends not only on the availability of sandlance, but also on the ecology of common terns. These findings highlight the need to assess the health of forage fish populations through proper management of commercial fisheries stocks (e.g. herring), or to designate Marine Protected Areas (i.e. sandlance habitat) for the protection of endangered species (roseate terns).

Sandlance distribution and abundance was the primary predictor of the abundance and foraging behavior of terns, among all covariates; flocks of other terns were secondary. The inconsistencies in the positive relationship between sandlance and common or roseate tern counts likely had more to do with unreliability in sandlance behavior and sampling regime than in actual occurrence. The distribution and abundance of sandlance, caught at bottom depths, provided a limited 2-dimensional index of availability (Dänhardt & Becker 2011b) and, certainly, sandlance may have been accessible elsewhere in the water column (Dänhardt et al. 2011). The prevalence of sandlance and herring in the spring (Fig. S1) fits their profile as colder-water species, as compared to anchovies (Garrison et al. 2002, Lucey & Nye 2010). I suspect that this places a temporal constraint on

roseate tern phenology, explaining, in part, the timing of chick-rearing and migration: why it might be important for chick-provisioning to occur while sandlance persist, and why roseate terns stage earlier than common terns (Nisbet et al. 2013). Nest provisioning studies have been widely used to assess chick diets (Barrett et al. 2007), and my study suggests that they can also reflect adult foraging in the weeks prior to peak hatch, since the spatial patterns of common and roseate terns in May overlapped with the distribution and abundance of those prey representative of the dominant species later fed to chicks (in June and July 2010 and 2011, author's unpubl. data), i.e. herring and sandlance. With respect to the post-breeding season, my speculation is that during their pre-migratory dispersal, when roseate terns have been observed >100 km east of Cape Cod (Goyert et al. 2014), they pursue adult sandlance that move offshore (Robards et al. 2000),

which would explain the lack of roseate terns observed inshore during September. The association of terns with shallow water likely related to improved prey accessibility, since terns have been known to exploit tidal patterns across coastal shoals (Heinemann 1992, Becker et al. 1993). Habitat strongly affected common terns seasonally, where SST had a greater impact in the spring, and chlorophyll in the fall. Primary productivity (chlorophyll) showed greater importance in this study than in offshore surveys (Goyert et al. 2014), likely due to an inshore coastal effect, and the use of a larger scale to account for spatiotemporal lag in bottom-up trophic interactions that attract fish to plankton (e.g. a large scale allots more room for trophic mismatch, as opposed to a fine scale, Hunt & Schneider 1987, Grémillet et al. 2008). The behavioral relationship between foraging roseate terns and sandlance illustrates that terns may signal the presence of prey, which supports the notion that terns rely on each other to find food. The aggregation of common and roseate terns with flocks of conspecifics and heterospecifics provides evidence for local enhancement: high-density mixed-species flocks had a positive effect on the distribution and abundance of both roseate and common terns, suggesting that facilitation may be at play, as opposed to competition. Facilitation and competition can occur together, yet vary in intensity by scale and resource



availability (Fauchald et al. 2011): at coarse spatial scales (as in this study), terns may attract each other to feeding flocks (local enhancement; Erwin 1977, author's unpubl. data), facilitating prey detection as long as prey remain abundant (Lack 1946, Langham 1968, Dunn 1972, Poysa 1992, Buckley 1997, Ramos 2000); once those resources become limited, however, then spatial partitioning may occur as a result of tern competition (Duffy 1986, Safina 1990).

The advantage of using density-surface modeling was its performance at predicting the distribution of terns (Fig. 2); the disadvantage was its inflated abundance predictions. The intrinsic nature of seabird distributions likely explains why the GAM and distance sampling contribute to over-inflation in abundance estimation. First, seabird aggregation patterns produce large counts at few covariate values, resulting in high fitted values, as predicted by the GAM (D. Miller pers. comm.). Second, the problem may be inherent to using distance sampling with a biological population such as seabirds (e.g. as opposed to whales, which presumably have a lower detection probability since they are below the surface). For example, a mean detection probability of 25 % (as in model 2), is low for an experienced seabird observer scanning the 300–500 m range, and 2 % detection of roseate terns (model 10) is artificially low. MCDS seemed to over-compensate for attributing lack of visibility to sparse observations of roseate terns, by estimating high abundance from low detection probability; low detection should have matched more closely to low abundance. However, MCDS did allow for exceptional fit in roseate terns (provided the appropriate distribution family), resulting in a suitably complex model that retained biologically meaningful variation instead of favoring parsimony-induced fit (Johnson & Omland 2004). Given its strengths and weaknesses, DSM was an effective method of estimating seabird distribution and relative abundance, but users need to exercise caution in making over-estimated predictions of absolute abundance, especially with respect to the management of roseate terns.

This study highlights the importance of sandlance to the distribution and abundance of roseate terns, which raises concerns regarding the adaptability of such a specialized endangered species, in response to global climate change and fisheries pressure. On one hand, a potential top-down effect of global warming, in the reduction of top marine predators, could reduce consumptive impacts on pelagic forage fish, and perhaps increase their availability to terns (Nye et al. 2013). A more likely outcome is the bottom-up cascade of climatological shifts in SST and

primary productivity, resulting in habitat degradation or a northerly redistribution of prey, such as sandlance (Lucey & Nye 2010). A flexible foraging response to such fluctuations would be required for common and roseate terns to search for food, given that they associate with SST and primary productivity (models 2, 6, and 8). As opportunistic generalists, common terns are more likely than roseate terns to withstand drastic change over the long term (Montevicchi et al. 2009). However, model 10 suggests that roseate terns may pursue prey in 3 ways: directly, via association with shallow water (independently of SST and primary productivity), or by remaining in the vicinity of other mixed species terns flocks. If roseate terns opportunistically rely on social facilitation like other seabirds (e.g. via local enhancement), then their chances of encountering prey are improved (Grünbaum & Veit 2003). Alternatively, rapid, unpredictable changes in sandlance distribution could result in prey limitation and allow tern competition to overpower the benefits and incidence of facilitative interactions (Safina & Burger 1988). Redistribution of sandlance is a serious concern for roseate terns, because these highly philopatric species would either expend too much energy traveling between the colony and distant foraging areas, causing chicks to starve, or they would have to endure nesting displacement, as they often have in the past (Gochfeld et al. 1998, Nisbet 2002). Prey depletion has compromised the breeding success of common and roseate terns in the past (Safina et al. 1988) and has contributed to population declines (Szostek & Becker 2012). Since the 1990s, herring stocks in the NW Atlantic Ocean have generally followed a slowly increasing trend, in contrast to sandlance abundance, which has been on the decline since the late 1980s (Overholtz et al. 2000). Roseate terns were federally listed as endangered in 1987, and their populations currently show no improvement; therefore, further research should assess whether their productivity mirrors long-term historical trends in sandlance, to address the extent to which prey sensitivity may limit their potential for population recovery (Nisbet & Spendelov 1999) — especially given that common terns have largely rebounded over the past few decades (Mostello 2012). It is important that we better understand not only where common and roseate terns consistently forage across years, but how they will respond to changes in prey availability. The miniaturization of enhanced tracking devices (Burger & Shaffer 2008) should be able to provide a means for future studies to better quantify tern utilization of foraging habitat; such information is

essential to advancing the conservation and management of these protected species. The sensitivity of spatial patterns in common, and especially roseate terns, to habitat, prey availability, and one another, classifies them as conspicuous indicators of ecosystem, fisheries, and community processes (Einoder 2009). Quantifying the spatial relationships among seabirds and their prey, in an ecosystem context, is essential to predicting long-term shifts in the distribution and abundance of marine communities, for the purpose of marine spatial planning.

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