

Key seabird areas in southern New England identified using a community occupancy model

Nicholas P. Flanders^{1,2,*}, Beth Gardner¹, Kristopher J. Winiarski³, Peter W. C. Paton⁴,
Taber Allison^{5,7}, Allan F. O'Connell⁶

¹Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

²Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA

³Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003, USA

⁴Department of Natural Resources Science, University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881, USA

⁵Mass Audubon, 208 South Great Road, Lincoln, MA 01773, USA

⁶US Geological Survey, Patuxent Wildlife Research Center-Beltsville Lab, Beltsville, MD 20705, USA

⁷Present address: American Wind Wildlife Institute, 1110 Vermont Ave., NW, Washington, DC 20005, USA

ABSTRACT: Seabirds are of conservation concern, and as new potential risks to seabirds are arising, the need to provide unbiased estimates of species' distributions is growing. We applied community occupancy models to detection/non-detection data collected from repeated aerial strip-transect surveys conducted in 2 large study plots off southern New England, USA; one off the coast of Rhode Island and the other in Nantucket Sound. A total of 17 seabird species were observed at least once in each study plot. We found that detection varied by survey date and effort for most species and the average detection probability across species was less than 0.4. We estimated the influence of water depth, sea surface temperature, and sea surface chl *a* concentration on species-specific occupancy. Diving species showed large differences between the 2 study plots in their predicted winter distributions, which were largely explained by water depth acting as a stronger predictor of occupancy in Rhode Island than in Nantucket Sound. Conversely, similarities between the 2 study plots in predicted winter distributions of surface-feeding species were explained by sea surface temperature or chlorophyll *a* concentration acting as predictors of these species' occupancy in both study plots. We predicted the number of species at each site using the observed data in order to detect 'hot-spots' of seabird diversity and use in the 2 study plots. These results provide new information on detection of species, areas of use, and relationships with environmental variables that will be valuable for biologists and planners interested in seabird conservation in the region.

KEY WORDS: Aerial strip-transect survey · Community occupancy model · Imperfect detection · Seabird habitat relationships · Species distribution models

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INTRODUCTION

Determining relationships between seabird distributions and environmental variables is challenging due to the difficulties associated with collecting accurate data on seabird distributions and the dynamic nature of their marine habitats (Camphuysen et al. 2004, Louzao et al. 2006, 2009, Nur et al. 2011, Kinlan et al. 2012a). Numerous analytical techniques have

been used to draw inference on the relationship between seabird distributions and environmental conditions (Tremblay et al. 2009), but historically analyses have failed to account for the imperfect detection (i.e. detectability) of foraging birds at sea. Failure to account for incomplete detection can bias estimates of ecological relationships and can cause comparisons of parameter estimates across time or space to suggest false patterns (MacKenzie et al. 2002, Tyre et

al. 2003, Kéry et al. 2008, Ruiz-Gutiérrez et al. 2010). Apparent ecological differences can be confounded with differences in detection probability caused by variation in species' behavior, human observers, or logistical details.

One approach for collecting and analyzing at-sea seabird survey data that accounts for detection bias is distance sampling (Camphuysen et al. 2004, Petersen et al. 2011, Winiarski et al. 2013, 2014). Line-transect survey protocols require the collection of auxiliary distance and angle information (Camphuysen et al. 2004, Winiarski et al. 2013, 2014) that allows researchers to account for detection probabilities of individual animals that typically decline as distance from the transect increases (Buckland et al. 2001). Estimates from distance sampling analyses can then be incorporated into density surface models (Hedley & Buckland 2004) to explore environmental covariate relationships and make spatially explicit predictions (Winiarski et al. 2013, 2014). However, other approaches for addressing detection are necessary for species with too few observations to fit a detection function in distance sampling (Winiarski et al. 2014), or if data are collected utilizing strip-transect survey protocols, in which case distance information is not recorded (Briggs et al. 1985, Camphuysen et al. 2004).

Occupancy models (MacKenzie et al. 2002, 2006, Dorazio & Royle 2005) offer an alternative approach for the analysis of aerial seabird survey data, provided there is temporal replication of strip-transect surveys within a period during which the occupancy state is assumed not to change. Occupancy models do not estimate abundance, but instead the probability of site-occupancy by a species. At the same time, occupancy models also estimate the probability of a species being detected, which provides unbiased estimates of the true occupancy state (Tyre et al. 2003, MacKenzie 2005, MacKenzie et al. 2006, Kéry & Schaub 2012). To address issues of limited data for rare and elusive species, community occupancy models were developed to allow information to be shared across species in a hierarchical formulation (Dorazio & Royle 2005) while estimating species-specific detection, occupancy, and habitat relationships (Russell et al. 2009, Ruiz-Gutiérrez et al. 2010). In addition to this, community-level metrics such as species richness can also be estimated in community occupancy models (Dorazio et al. 2006, Royle et al. 2007, Zipkin et al. 2009, 2010b).

Improving our understanding of seabird distributions is particularly timely as offshore wind resources in the northeastern United States have been shown to provide a viable option for generating renewable energy (Kempton et al. 2007). Seabirds that use near-

shore (<5 km) and offshore waters in the northwestern Atlantic Ocean are potentially vulnerable to negative effects of proposed offshore wind energy development projects (OWEDs; Drewitt & Langston 2006, Langston 2013). This is compounded by the fact that seabirds in general are of great conservation concern (Sydeman et al. 2012). As OWEDs are now being proposed along the eastern coast of the USA, including one in Nantucket Sound and two in the waters off Rhode Island, there is an imminent need to acquire baseline information on seabird distributions in order to start to evaluate the potential risk OWEDs pose to seabird populations.

Here, we applied community occupancy models to estimate relationships between seabird occupancy and a suite of environmental covariates to predict areas of high seabird occupancy across 2 study plots in the northwestern Atlantic Ocean. We used *a priori* knowledge about seabird ecology to evaluate estimated relationships and distributions. We expected foraging sea ducks and other avian benthivores to be associated with shallow depths (Guillemette et al. 1993, Nehls & Ketzenberg 2002, Zipkin et al. 2010a). Important foraging habitat for many other seabird species often occurs in areas of high primary productivity, usually related to levels of nutrient enrichment (Kinlan et al. 2012b), where seabird prey are concentrated (Hyrenbach et al. 2000, Spear et al. 2001, Ballance et al. 2006, Louzao et al. 2006, 2009, Bost et al. 2009). Sea surface temperature and chl *a* concentration can be used as indices for primary productivity and prey density near the surface of the ocean; thus we expected these covariates to be significant predictors of the distributions of many species restricted to feeding at or near the ocean surface. Diving piscivores present in the study region are able to forage at a variety of depths in the water column, and a number of surface water characteristics were expected to predict foraging habitat for these species as well (Harrison 1983, Winiarski et al. 2013).

Our aim was to account for imperfect detection, which we expected to vary by species due to differences in behavior, size, coloration, and similarity to other species, as well as by date due to within season changes in abundance. By using aerial survey data on all species observed in our 2 study plots, the community modeling approach allowed us to include species that were rarely detected and would not have been able to be analyzed separately due to limited data. Our results provide insight into the spatial variation of areas important to foraging seabirds, as well as valuable information on habitat relationships for 17 seabird species in both of our study plots. This ap-

proach has been used to study many other species, including forest birds (Russell et al. 2009, Ruiz-Gutiérrez et al. 2010), and we believe it has potential to be applied more generally in a number of marine studies.

MATERIALS AND METHODS

Study area

Our study area encompassed 2 study plots in the northwestern North Atlantic off southern New England. One 3800 km² study plot was located south of Rhode Island, USA, and included Block Island Sound, Rhode Island Sound and portions of the Continental Shelf (Fig. 1, hereafter Rhode Island study plot, Winiarski et al. 2014). The Rhode Island study plot encompassed the boundaries of the Rhode Island Ocean Special Area Management Plan (RIOSAMP; Winiarski et al. 2011). The other study plot was located in Massachusetts, USA, and included much of Nantucket Sound (Fig. 1, hereafter Nantucket Sound study plot). Both study plots provide important habitat for a diversity of seabird species (Huettmann & Diamond 2000) including species of conservation concern such as the common loon *Gavia immer* and red-throated loon *Gavia stellata* (Kinlan et al. 2012a, Winiarski et al. 2013). The study area is also globally important for wintering sea ducks *Tringa mergini* (Caithamer et al. 2000, Zipkin et al. 2010a, Silverman et al. 2013).

Aerial strip-transect surveys

Aerial surveys were conducted in both study plots using similar survey protocols. Aerial surveys of 24 transect lines within the Rhode Island study plot were conducted every 1 to 2 wk during the winter season from December 2009 to February 2010 (Winiarski et al. 2011). Aerial surveys of 15 transect lines within Nantucket Sound were conducted from December 2003 to February 2004 (though more surveys were conducted through March 2006). The transect lines in the Rhode Island study plot were positioned perpendicular to the coast, were separated by 3 km, and had a mean length of 46.3 km (SD = 12.3) (Fig. 1). Transect lines within Nantucket Sound were separated by approximately 2.3 km and had a mean length of 26.7 km (SD = 3.82) (Fig. 1).

Surveys of the Rhode Island study plot consisted of fixed-width strip transects flown at an altitude of 152 m. Two observers recorded the locations of all avian detections within a 107 m wide strip on each side of the plane; each record had a count attribute to reflect whether the observer had detected a single individual or a flock. If glare on the ocean's surface was problematic on one side of the plane, the respective observer stopped surveying and recorded this reduction in effort. Nantucket Sound surveys used strips that were 91 m wide on each side of the plane and no ancillary information on glare was recorded.

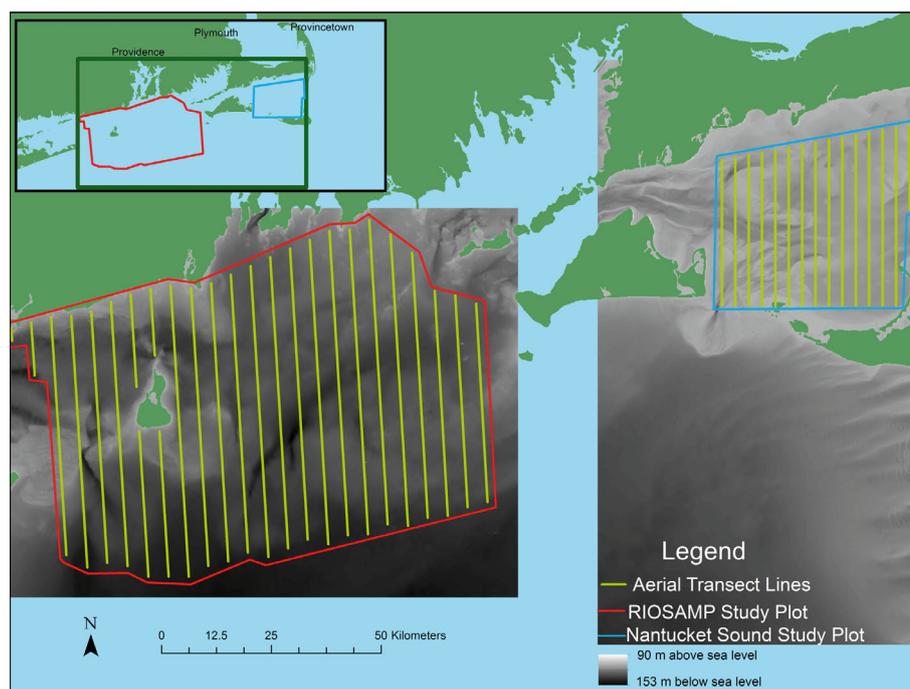


Fig. 1. Location of aerial transects (green lines) where seabirds were surveyed in Rhode Island (red boundary) and Nantucket Sound (blue boundary) study plots during the winter of 2009–2010 and 2003–2004, respectively

For both study plots, transect lines were divided into 2.27 km-long sections to form unique segments. This segment size was chosen to minimize variation in site-level covariates and to better meet assumptions of independence and species co-occurrence (see 'Discussion'). The length of the southernmost segment of most transects in the Nantucket Sound study plot was variable due to different transect lengths; these variable segments had a mean length of 1.065 km (SD = 640). All avian observations used in this analysis were identified to species level and given the appropriate segment identification as an attribute. Data were separated by species and survey-specific counts were reduced to binary data to represent the detection or non-detection of a species during a survey within each segment.

Environmental covariates

We collected remotely sensed data on sea surface temperature (SST), water depth, and chl *a* surface concentration throughout the study area. These abiotic and biotic variables were chosen as they were available at biologically relevant spatial and temporal scales and are important predictors of seabird distributions (Ballance et al. 2006, Nur et al. 2011, Kinlan et al. 2012a). Monthly composites of SST and chl *a* concentration (mg m⁻³) collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite were retrieved at a 16 km² (4 × 4 km) grid cell resolution using Marine Geospatial Ecology Tools (Roberts et al. 2010) and averaged across the survey-specific winter seasons (December 2009 to February 2010 for the Rhode Island study plot, December 2003 to February 2004 for the Nantucket Sound study plot). A fine-scale resolution bathymetry grid of the Rhode Island study plot was retrieved from the Design-a-Grid tool of the National Oceanic and Atmospheric Administration (NOAA) Geophysical Data System (GEODAS) Grid Translator (www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html) and we acquired a 1/3 arc-second resolution bathymetry digital elevation model (DEM) of Nantucket Sound from NOAA (Eakins et al. 2009). These grids were overlaid with the transect segments and a spatially weighted average of the seasonal covariate was calculated for each segment (Zipkin et al. 2010a). This raster processing was accomplished using Spatial Analyst Tools in ArcMap10 (ESRI 2011).

Based on the data collected for the survey locations, the distribution of water depth values in the Rhode Island study plot covered a larger range of values

and the overall mean depth was greater than in the Nantucket Sound study plot (Fig. 1). Ranges of SST and chl *a* concentration values were similar between the 2 study plots (for details, see Section 1 of the Supplement at www.int-res.com/articles/suppl/m533p277_supp.pdf). The mean of the SST values was slightly greater in the Rhode Island study plot, whereas the chl *a* concentration values from the Nantucket Sound study plot had a greater mean than the Rhode Island study plot.

Single-species occupancy model description

For each single-season model, we assumed that a survey segment was either occupied or not by a given species over the course of the sampling season (December to February). The latent state z_{ik} represents this process, as $z_{ik} = 0$ if segment i is occupied by species k and $z_{ik} = 1$ if segment i is not occupied by species k (MacKenzie et al. 2002, 2006). These binary latent states were modeled as Bernoulli random variables with success probability ψ , which represents the occupancy probability.

The segment-level covariate values were standardized by subtracting from the mean and dividing by the standard deviation. We then used a logit link to model ψ_{ik} at segment i for species k as a function of water depth and seasonal averages of both SST and chl *a* concentration ($chlA_i$) such that

$$\text{logit}(\psi_{ik}) = \text{occint}_k + \beta_{1,k} \text{depth}_i + \beta_{2,k} \text{SST}_i + \beta_{3,k} \text{chlA}_i \quad (1)$$

where occint_k is the species-specific intercept and the β_k parameters are species-specific coefficients for the covariates of water depth, SST, and chl *a* (Kéry & Royle 2008a,b, Russell et al. 2009).

We assumed that the season-specific data came from an imperfect observation process, with $y_{ijk} = 1$ if species k is observed at site i during survey occasion j and $y_{ijk} = 0$ if species k is not observed at site i during survey occasion j (MacKenzie et al. 2002, 2006). We also assumed that there were no false positives (or misidentification errors), thus a positive detection means that the site was occupied by the species during the survey season. However, the outcome $y_{ijk} = 0$ could arise from 2 scenarios: either site i is not occupied by species k during the survey season or site i is occupied but the observer failed to detect species k during survey occasion j . The temporal replication of surveys at segments closed to changes in occupancy by a species enabled us to estimate the detection probability. Detection probability, p , is defined as the

success probability of a random Bernoulli process that generates y_{ijk} , given that site i is occupied by species k during the survey season. Specifically, $y_{ijk}|z_{ik} \sim \text{Bern}(p_{ijk} \cdot z_{ik})$; thus, when $z_{ik} = 0$ the probability of a detection is 0 and when $z_{ik} = 1$ the probability of a detection is p_{ij} .

We modeled variation in p as a function of date and observer effort (Kéry & Royle 2008a,b, Russell et al. 2009). Differences in the 2 sampling protocols for the study areas led to the construction of 2 different observation sub-models. Both sub-models estimated both linear and quadratic effects of date on p , as we expected a temporal trend in detection probability across a survey period due to intra-seasonal changes in abundance (Kendall 1999, MacKenzie et al. 2003, Royle & Nichols 2003, Zipkin et al. 2009, O'Connell 2009). For the Rhode Island data, we accounted for reduced observer effort at survey locations with significant glare by including the indicator variable $glare_{ij} = 0$ when only one observer was recording data and $glare_{ij} = 1$ at normal double observer survey occasions, such that:

$$\text{logit}(p_{ijk}) = \text{pint}_{1,k} + \text{pint}_{2,k} glare_{ij} + \alpha_{1,k} date_{ij} + \alpha_{2,k} date_{ij}^2 \quad (2)$$

where $\text{pint}_{1,k}$ is the intercept for species k with glare (only 1 observer on survey) and $\text{pint}_{2,k}$ is the intercept for species k when there is no glare effect (both observers on survey). The α_k parameters are species-specific coefficients for the detection covariates.

Nantucket Sound survey flights through a given segment showed significant variation in length. Therefore, we modeled p as a function of survey length when analyzing these data such that:

$$\text{logit}(p_{ijk}) = \text{pint}_k + \alpha_{1,k} date_{ij} + \alpha_{2,k} date_{ij}^2 + \alpha_{3,k} length_{ij} \quad (3)$$

where pint_k is the species-specific intercept.

Community occupancy model description

To broaden the scope of our inference about the seabird ecology of the study areas, we adopted the community occupancy modeling approach of Dorazio & Royle (2005). This approach has been used to increase the precision of estimates for rare species and for testing hypotheses about habitat relationships at the community level (Russell et al. 2009, Zipkin et al. 2009, 2010b, Ruiz-Gutiérrez et al. 2010). Kéry & Royle (2008b) showed the flexibility of this approach when incorporating covariates on the species-specific sub-models of the hierarchical framework.

Our community occupancy models assumed that each of the species-specific parameters in Eqs. (1) to (3) was a random effect arising from a Normal prior distribution (Sauer & Link 2002, Dorazio & Royle 2005, Royle & Dorazio 2006):

$$\gamma_{n,k} \sim \text{Normal}(\mu_n, \sigma_n^2) \quad (4)$$

where $\gamma_{n,k}$ is a species-specific parameter, e.g. $\beta_{1,k}$ in Eq. (1) or $\alpha_{1,k}$ in Eqs. (2) or (3). The mean and variance, μ_n and σ_n^2 , respectively, of the Normal prior distribution are termed hyperparameters (Kéry & Royle 2008b) and estimates can be used to learn about the collective response of multiple species' occupancy and detection probabilities to covariates (Russell et al. 2009, Zipkin et al. 2009, 2010b, Ruiz-Gutiérrez et al. 2010). While this approach allows the estimation of parameters for all detected species, estimates for species with sparse data will be drawn from the common distribution with estimated hyperparameters and the resulting precision will likely be low (Sauer & Link 2002, Russell et al. 2009).

Due to the nature of this study, we adopted a different interpretation of the occupancy parameter to allow for more flexibility in meeting the closure assumption of occupancy models. Typically, effective detection probability is defined as the probability of detecting a species given that the site is occupied by the species and the species is available for detection at the site (Kendall 1999, Tyre et al. 2003, MacKenzie 2005, MacKenzie et al. 2006, Kéry & Schaub 2012, Johnson et al. 2014). This interpretation of p assumes that a species' detection probability is confounded with the species' probability of availability (Gray et al. 2013, Johnson et al. 2014). This effective detection probability is reduced compared to the traditional detection probability where a probability of availability equal to 1 is assumed (Kendall 1999, Russell et al. 2009, Gray et al. 2013). Instead of the probability of permanent site occupancy by a species, we interpreted Ψ as the probability of site usage by the species during the study period (MacKenzie 2005, MacKenzie et al. 2006, Kéry & Schaub 2012). If we assume that the process driving the availability of the species, movement on and off of the site, is temporary and random (Burnham 1993, Kendall et al. 1997), we can avoid bias in our estimates despite the lack of strict closure (Kendall 1999, MacKenzie 2005, MacKenzie et al. 2006, Kéry & Schaub 2012). As this effective detection probability is reduced relative to traditional detection probability, the precision of estimates can be expected to decrease accordingly (Kendall 1999).

Implementation

Analysis of hierarchical models is intuitive within a Bayesian framework (Sauer & Link 2002) and we implemented a Bayesian analysis in R (R Development Core Team 2011) using the software JAGS (Plummer 2011). We specified uninformative prior distributions for all hyperparameters in the models. For an example of model specification code see Section 2 of the Supplement. Posterior distributions of parameters were approximated using Markov chain Monte Carlo (MCMC) iteration values from 3 chains run for 500 000 iterations with a burn-in of 139 000 and thinning by 10. We considered coefficient estimates to be significant if their 95% credible intervals did not overlap zero. Convergence of all parameters was reached as determined by R-hat values (Gelman & Hill 2007) and visual inspection of trace plots. To assess model performance, we calculated the area under the curve (AUC) receiver operating characteristic curve using the R package 'ROCR' (Sing et al. 2005). We followed the methods in Zipkin et al. (2012) for determining the AUC of the models; however, we note that this implementation is based on the unobserved occupancy states, the effect of which may influence the estimates.

Making predictions and comparisons

Grids with 4 km² (2 × 2 km) cells were used for spatial predictions of occupancy probability across the 2 study plots. Spatial Analyst Tools in ArcMap10 (ESRI 2011) were used to obtain weighted average seasonal covariate values for each grid cell; these grid-cell-level values were normalized using the same covariate mean and standard deviation values used in the modeling. To estimate the number of observed species predicted to occupy each grid cell we included new z_{ik} parameters for each grid cell i and for each species k observed in the respective study plot. These z_{ik} parameters were modeled as Bernoulli random variables with success probability equal to the occupancy probability predicted at the respective grid cell for the respective species. At each iteration, the binary z_{ik} 's were summed across species to approximate the posterior distribution of the grid-cell-specific predictions.

We compared seabird covariate relationships between the Nantucket Sound and Rhode Island study plots by calculating the probability that the season and species-specific coefficient estimates for a given relationship differed between the 2 study plots for a

given species. These probabilities were calculated following Ruiz-Gutiérrez et al. (2010). We considered there to be a significant difference between species-specific estimates from the 2 study plots if the probability of this difference was ≥ 0.95 .

To generalize observed similarities or differences in species-specific habitat relationships between the 2 study plots, we placed all species included in the models into one of 2 *a priori* foraging guilds (Schneider 1997, Spear et al. 2001, Bost et al. 2009, Kinlan et al. 2012a). Diving species feed primarily by diving to appreciable depths below the ocean surface, whereas surface-feeding species feed primarily at or near the ocean surface (see Section 3 of the Supplement). These foraging guilds were not used during the modeling process but rather for qualifying consistent relationships across species with similar natural histories.

RESULTS

Surveys of the Rhode Island study plot conducted during the 2009–2010 winter season detected 17 species (see Table S2 in Section 4 of the Supplement at www.int-res.com/articles/suppl/m533p277_supp.pdf), 13 of which were diving species and 4 of which were surface-feeding species. The predictive accuracy of the model was very good as indicated by the mean AUC value of 0.95. Water depth was the strongest predictor of occupancy in the Rhode Island study plot, with 8 species having a significant effect, all of which were diving species (Table 1). The great black-backed gull *Larus marinus*, a surface-feeding species, and dovekie *Alle alle*, a diving species, were the only species with significant relationships between SST and occupancy. Common eider *Somateria mollissima*, a diving species, was the only species with a significant relationship between chl *a* and occupancy (Table 1). Five species had significant estimates for the linear effect of date on detection probability, and 3 species had significant estimates for the quadratic effect of date on detection (Table 1, Fig. 2).

Surveys of the Nantucket Sound study plot conducted during the 2003–2004 winter season detected 17 species (see Table S3 in Section 4 of the Supplement), 12 of which were diving species and 5 of which were surface-feeding species. The model for Nantucket Sound had a good predictive accuracy, as suggested by the mean AUC value of 0.91. The only species with a significant relationship between occupancy and water depth was surf scoter *Melanitta perspicillata*, a diving species. There were no significant species-specific estimates of the relationship between

Table 1. Effects of environmental covariates on occupancy and detection probabilities of seabirds included in winter models for both study plots. Posterior means of species-specific coefficients are shown, with significant (95% credible intervals did not overlap zero) coefficient estimates indicated in bold. Dovekie was not included in the Nantucket Sound model but is shown here because some species-specific covariate effects were significant. SST = sea surface temperature, date = date of detection, date² = date of detection squared. *Surface-feeding species

Species	Rhode Island					Nantucket Sound				
	Occupancy			Detection		Occupancy			Detection	
	Water depth	SST	Chl a	Date	Date ²	Water depth	SST	Chl a	Date	Date ²
Common eider	1.24	-0.36	0.78	0.53	0.06	-0.18	-0.27	0.29	0.11	-0.11
Surf scoter	1.22	0.45	1.54	-0.04	-1.20	-0.82	-0.26	0.90	-0.43	-0.58
White-winged scoter	1.18	-1.47	2.15	-0.14	-0.54	-0.14	-0.67	-0.60	-0.12	-0.06
Black scoter	1.29	0.17	1.35	-0.06	-1.16	0.01	0.77	-1.24	-0.15	-0.52
Long-tailed duck	1.27	-0.33	1.24	0.54	-0.21	-0.50	0.72	0.001	0.91	0.26
Red-breasted merganser	1.32	0.16	1.21	0.40	-0.42	0.89	-0.97	-1.41	-0.82	-0.12
Red-throated loon	1.34	-0.89	1.04	-0.29	0.17	-1.01	0.81	-0.19	-0.23	-0.67
Common loon	1.04	-0.83	0.33	0.53	0.06	-0.84	-0.26	0.54	-0.39	-0.12
Northern gannet	0.90	1.27	0.89	-0.98	-0.43	0.68	-0.59	-2.01	-1.66	-0.33
Great cormorant	1.27	-0.82	0.66	-0.69	-0.13	-0.003	-0.02	-0.92	0.09	-0.54
Black-legged kittiwake*	0.93	1.04	0.10	-0.71	-1.00	-0.13	0.13	-1.92	-0.99	-0.94
Bonaparte's gull*	1.23	1.25	0.51	0.14	-1.05	-0.05	-0.07	-2.61	-1.12	-0.34
Herring gull*	1.04	2.08	1.25	0.09	0.07	0.18	0.91	-0.79	-0.40	-0.55
Great black-backed gull*	1.08	3.04	0.61	-0.20	0.02	0.40	0.58	-1.92	-0.74	-0.52
Dovekie	1.22	1.95	-1.52	-0.08	-2.41	NA	NA	NA	NA	NA
Razorbill	1.51	-0.40	-0.29	1.24	0.16	-0.41	-0.43	-1.02	0.32	0.01

SST and occupancy in this model. Species-specific estimates of the relationship between chl a concentration and occupancy were significant for 5 species, 3 of which were surface-feeding species (Table 1). Ten species had significant estimates for the relationship between date and detection, and 6 species had significant estimates for the quadratic effect of date on detection (Table 1, Fig. 2).

Within the occupancy component of the model, we found significant differences between the 2 study plots in the species-specific parameter estimates of water depth for 6 species, all of which were diving species (Table 2). The great black-backed gull was the only species for which we found a significant difference in the parameter estimates for the effect of SST on occupancy. We found a significant difference in the parameter estimates for the effect of chl a concentration on occupancy for 2 diving species, red-breasted merganser *Mergus serrator* and northern gannet *Morus bassanus*, and for 2 surface-feeding species, herring gull *Larus argentatus* and great black-backed gull (Table 2).

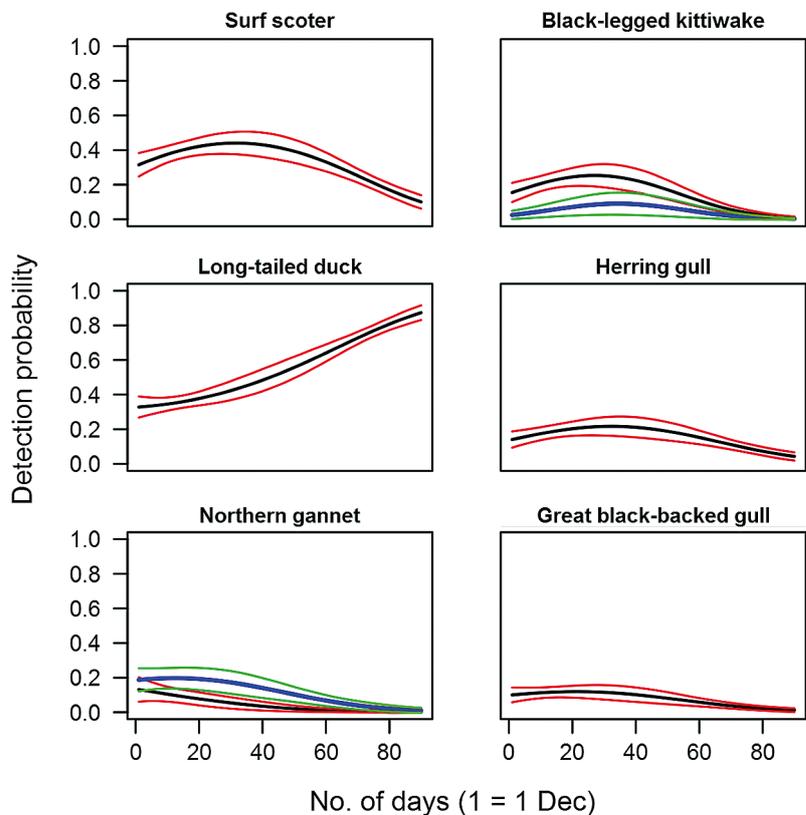


Fig. 2. Means (thick black and blue lines) and 95% credible intervals (thin red and green lines) of predicted detection probabilities (p) across winter season dates for seabird species with significant linear and quadratic effects of date (see Table 1) on p in the Nantucket Sound study plot 2003–2004 (black and red lines) and the Rhode Island study plot 2009–2010 (blue and green lines)

Table 2. Significant probabilities of differences between Rhode Island (RI) study plot and Nantucket Sound (NS) study plot estimates of relationships between covariates (water depth, SST, chl *a*) and seabird occupancy in winter

Species	Pr(RI coeff. > NS coeff.)		
	Water depth	SST	Chl <i>a</i>
Common eider	0.99	–	–
Surf scoter	0.99	–	–
Long-tailed duck	0.98	–	–
Red-breasted merganser	–	–	0.95
Red-throated loon	0.99	–	–
Common loon	0.99	–	–
Northern gannet	–	–	0.96
Herring gull	–	–	0.97
Great black-backed gull	–	0.96	0.95
Razorbill	0.98	–	–

We documented large differences in the patterns of predicted occupancy between the 2 study plots for common eider (Fig. 3A), which is representative of our findings for other sea ducks: surf scoter, white-winged scoter *Melanitta fusca*, black scoter *Melanitta americana*, and long-tailed duck *Clangula hyemalis* (see Figs. S1–S10 in Section 5 of the Supplement). Specifically, areas of high predicted occupancy in the RIOSAMP (Rhode Island) study plot were closely associated with shorelines and islands for these species, whereas areas of high predicted occupancy in the Nantucket Sound study plot were much more dispersed, covering nearly the entire study plot.

Predicted distributions across the Rhode Island study plot for diving piscivores such as red-breasted merganser, red-throated loon, common loon (Fig. 3B), and great cormorant *Phalacrocorax carbo* were similar

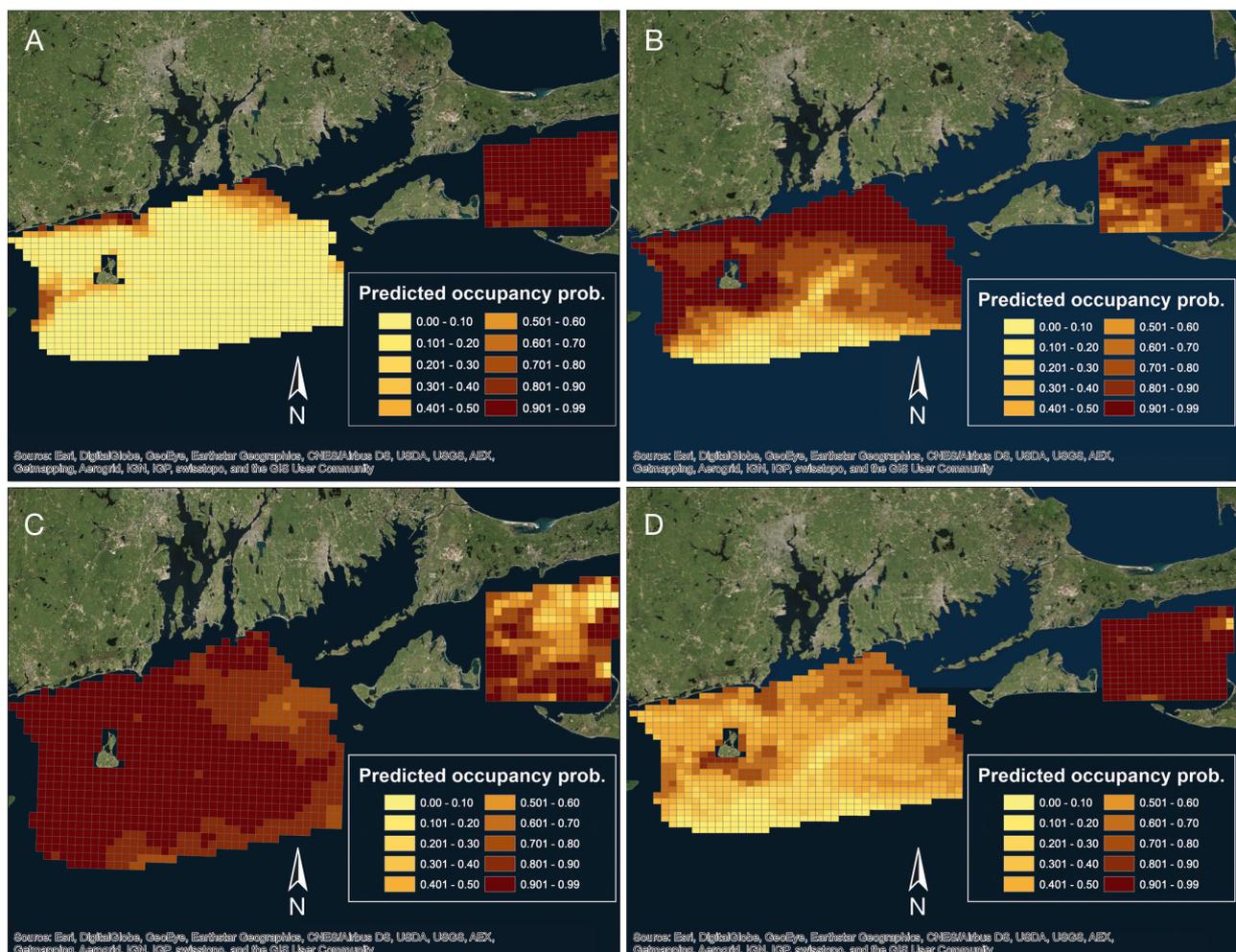


Fig. 3. Predicted winter occupancy estimates (posterior means) for 4 species of diving seabirds in 2 study plots off southern New England, USA. (A) Common eider *Somateria mollissima*, (B) common loon *Gavia immer*, (C) northern gannet *Morus bassanus*, and (D) razorbill *Alca torda*

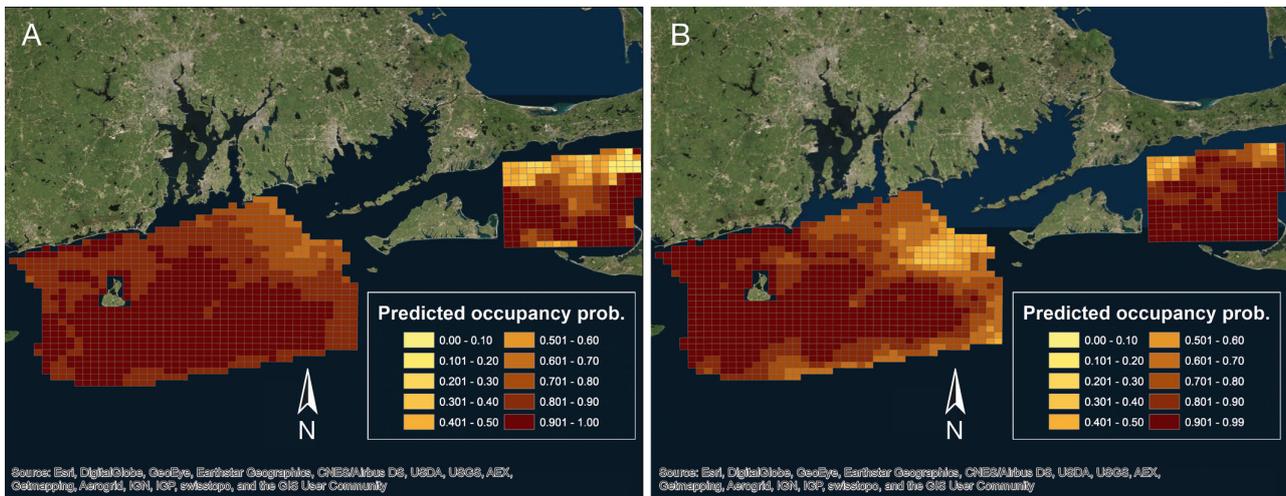


Fig. 4. Predicted winter occupancy estimates (posterior means) for 2 species of surface-feeding seabirds in 2 study plots off southern New England, USA. (A) Black-legged kittiwake *Rissa tridactyla* and (B) herring gull *Larus argentatus*

to those for sea ducks, with areas of high predicted-occupancy occurring near the mainland and near islands (see Figs. S11–S20 in Section 5 of the Supplement). No consistent pattern in predicted occupancy for these diving piscivore species was evident in the Nantucket Sound study plot. The predicted distribution of northern gannet, a piscivore that forages primarily by plunge diving (Haney & Stone 1988), in the Rhode Island study plot included areas of high occupancy across most of the study plot, with a patchier pattern of high occupancy predicted in the Nantucket Sound study plot (Figs. 3C, S17 & S18 in Section 5 of the Supplement).

Patterns of predicted occupancy were more similar between the 2 study plots for black-legged kittiwake *Rissa tridactyla* and herring gull (Fig. 4), which is representative of our findings for other surface-feeding species included in both winter models (see Figs. S21–S28 of Section 5 of the Supplement). In both study plots, areas of high predicted occupancy were large and concentrated away from the mainland. The razor-bill *Alca torda* was the only alcid included in both winter models and predicted distributions were similar to those of the sea ducks (Figs. 3D, S31 & S32 in Section 5 of the Supplement). In contrast, dovekie was only detected in the Rhode Island study plot and its predicted distribution was strongly concentrated in the south-central portion of the study plot (see Figs. S29 & S30 in Section 5 of the Supplement).

Model-specific and species-specific habitat relationship estimates were also used to predict the number of species from the observed communities occupying each grid cell and the respective standard errors across the 2 study plots (see Figs. S33 & S34 in

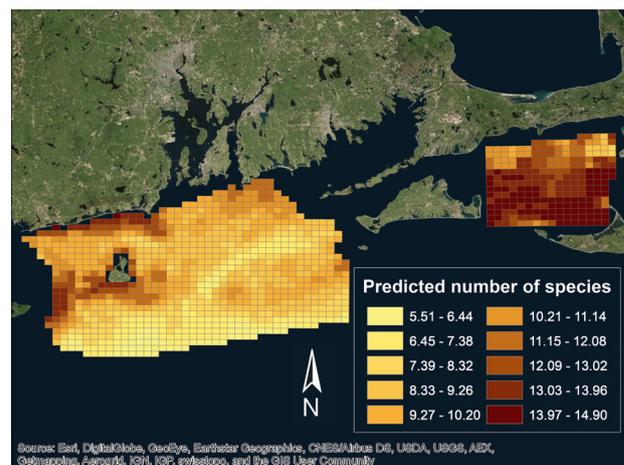


Fig. 5. Predicted number of species in the observed seabird communities for the winter season (posterior means) in 2 study plots off southern New England

Section 6 of the Supplement). The Nantucket Sound study plot was predicted to host a greater number of observed species than the Rhode Island study plot (Fig. 5). ‘Hot-spots’ of observed species diversity in the Rhode Island study plot were predicted near Block Island and in the western and northwestern near-shore portions of the study plot, whereas hot-spots in Nantucket Sound encompassed much of the southern half of the study plot.

DISCUSSION

We used community occupancy models to draw inference on habitat relationships for seasonal sea-

bird communities that included uncommon species with few detections. This approach appears useful for analyzing data from aerial seabird surveys that include temporal and spatial replication, as our model results largely agreed with both our *a priori* expectations and findings from other analyses in southern New England (Winiarski et al. 2013, 2014). We found considerable variation among species in estimates of relationships between occupancy and environmental covariates, much of which concurred with our *a priori* placement of species into 2 foraging guilds. Comparisons of parameter estimates and predicted distributions for the same species from the 2 study plots also showed considerable differences between the 2 study plots. This finding confirms that species-specific habitat relationships and distributions can be area-specific and extrapolating patterns from one area to another, even if areas are close geographically, may prove problematic. Regulators making offshore development decisions should use caution when making prediction of seabird distributions and 'hot spots' based on survey data from an area outside that of the region of development interest. Note however, that our 2 study areas were surveyed in different years, thus we may be seeing some differences due to inter-annual variation as opposed to true biological differences.

By using the temporal replication of these 2 datasets we were able to account for imperfect detection (MacKenzie et al. 2002, Tyre et al. 2003), which in these surveys appears to be an important issue as many of the species we modeled had <0.5 detection probability (see Fig. 2). Some species had a maximum detection probability of 0.2, which means 10 temporal replicates would need to be conducted to detect the species once with a probability of 0.9. This has large implications for designing future aerial studies for seabirds, particularly when the species of interest may be rare or hard to detect. Additionally, 2 species, northern gannet and black-legged kittiwake, showed significantly different detection probability estimates between the 2 study plots. These results suggest that not only can detection probability vary by species, but also that species can have regionally varying detection probabilities. Detection probability was modeled as a quadratic function of date to account for changes in species abundance that might occur during the season. Species-specific detection probabilities were expected to reach a maximum when the species was at peak abundance in the study plot. We found that the predicted detection of long-tailed ducks in the Nantucket Sound study plot reached its maximum at the end of the winter season (Fig. 2), which may have been due to birds returning

from more southerly wintering grounds at that time (White et al. 2009). The maximum predicted detection of northern gannets in the Rhode Island and Nantucket Sound study plots occurred at the beginning of the winter season (Fig. 2), likely due to birds moving farther south as the season progressed and northward movements occurring even later in the year (Powers 1983, Mowbray 2002). We found that species level detection varied across the winter season and between species and study plots, suggesting that the use of raw count data may not be a reliable way to make comparisons across species, seasons, or regions.

Environmental covariate relationships and predicted seabird distributions

Community occupancy models based on data collected in Nantucket Sound did not exhibit the consistent relationships between water depth and diving species' winter occupancy that was evident in the Rhode Island study plot. This was likely because Nantucket Sound shows far less variation in water depth than the Rhode Island study plot. Suitable foraging habitat for sea ducks and some other diving species in the Rhode Island study plot is restricted to near-shore areas whereas a majority of the Nantucket Sound study plot is shallow enough to be suitable. Winter occupancy of some diving species in the Nantucket Sound model was explained by chl *a* concentration, a covariate that showed greater variation than water depth in this study plot and a significant positive relationship to surf scoter occupancy. Overall, chl *a* concentration appeared to be the only consistently strong predictor of winter surface-feeding species' occupancy in Nantucket Sound. This result was not unexpected (Hyrenbach et al. 2002), although it was a notable departure from results in the Rhode Island model.

Differences and similarities in patterns of species-specific estimates of predicted occupancy for the 2 study plots can be explained by species-specific covariate relationship estimates from the 2 models. Large differences in predicted distributions of winter diving species can be explained by water depth showing up as a much stronger predictor of species' occupancy in the Rhode Island study plot than in the Nantucket Sound study plot. Predicted winter distributions of surface-feeding species are more similar between the 2 study plots. This can be explained by either SST or chl *a* concentration showing up as strong predictors of species' occupancy in both study

plots. Specifically, the covariate relationship driving these species' distributions in the Rhode Island model shows a positive effect for SST, whereas the relationship driving these species' distributions in the Nantucket Sound model is a negative effect of chl *a* concentration. At the level of spatial resolution we used, winter values of SST and chl *a* concentration appear negatively correlated in the study region.

It was surprising to see significant negative relationships between chl *a* concentration and surface-feeding species' occupancy in the Nantucket Sound model because chl *a* concentration is believed to be a proxy for primary productivity and thus prey density (Hyrenbach et al. 2002). However, the spatial resolution of the covariate data may have been too coarse to allow the model to detect associations between seabird occupancy and small patches of primary productivity represented by high local chl *a* concentration values (Huettmann & Diamond 2006). Instead, extensive variation in chl *a* concentration at the spatial resolution used here follows a gradient of high near-shore values to lower values farther from the mainland. Negative estimates of the relationship between chl *a* concentration and some surface-feeding species' occupancy may have little biological meaning, but instead be an artifact of these species' distributions being concentrated farther from the mainland. Similarly, the significantly positive relationships between chl *a* concentration and the winter occupancy of some sea ducks are likely a result of winter chl *a* concentration values at this level of spatial resolution serving as an effective proxy of distance to shore rather than a proxy of local prey patches, as these sea ducks are associated with benthic, sessile prey in shallow and near-shore areas (Guillemette et al. 1993). Nevertheless, these coefficients are useful for predicting patterns of occupancy of these species across the 2 study plots.

Our spatial predictions of the number of observed species occupying grid cells across the 2 study plots are directly relevant to conservation efforts in the region. The pattern of this metric across the Rhode Island study plot resembles the general spatial pattern of predicted occupancy for diving species in this plot, while the pattern of this metric across the Nantucket Sound study plot resembles the spatial pattern of predicted occupancy for surface-feeding species. It appears that the predicted occupancy of diving species is driving the spatial distribution of this metric in the Rhode Island study plot and the predicted occupancy of surface-feeding species is driving such patterns in the Nantucket Sound study plot. The usefulness of such a metric may increase by weighting

species differently based on species-specific levels of conservation concern (Winiarski et al. 2014).

Improving models for predicting seabird distributions

The analysis of temporally replicated aerial seabird survey data with occupancy models is an improvement over other distribution modeling techniques, such as those using presence-only data, that do not formally account for imperfect detection probabilities (Yackulic et al. 2013). We note that occupancy models require several assumptions, including the spatial independence of detections between sites (MacKenzie et al. 2002). The rapid movement of seabird individuals across a dynamic ocean landscape could lead to violations of this assumption if the same individuals are detected at multiple sites during a given survey flight. It is sometimes difficult for observers to avoid double counting of individuals for highly mobile species, thus incorporation of spatially explicit covariates may reduce the impact of this correlation. Occupancy models also assume that no false positives, or misidentification errors, occur (MacKenzie et al. 2002, Tyre et al. 2003, MacKenzie 2005, Kéry & Royle 2008a, Kéry & Schaub 2012). Large seabird datasets collected by aerial surveys are likely to contain some errors as it can be difficult to identify individuals under such challenging conditions. In using 2.27 km-long segments and reducing counts to binary data, our goal was to minimize the effect of misidentification and false positives in our analyses. In doing so, it can also be argued that we lose information from the count data when reducing it to binary.

Another important assumption specific to community occupancy models is independence among the occurrence of different species at a site (Kéry & Royle 2008b). Although we acknowledge that the presence of certain seabird species may influence the occurrence of other species in these communities (e.g. competitive exclusion), we assume that the spatial scale of the transect segments is large enough to minimize such effects in most cases. The development of community occupancy models that estimate interspecific interactions, or that derive information about the occupancy of a site by a species from the occurrence of other species at that site, could relax this assumption. Co-occurrence occupancy models have been developed and applied to several taxa (Bailey et al. 2009). Exploring these areas offers promising avenues for future work in the application of community occupancy models to seabird survey data. For

example, with seasonal data from multiple years dynamic models could be built to examine permanence of hot-spots of species-specific occupancy (Hyrenbach et al. 2000, Kinlan et al. 2012a). It may also be useful to determine the best way to incorporate data collected at taxonomic levels higher than species.

As we noted above, one limitation of our study is that our plots were surveyed in different years and this may lead to some of the differences that we see between the species in the 2 areas. For some species the distinction of changes in distribution between study plots and changes in distribution between years may be confounded, yet we still expect species-specific covariate relationships to remain consistent across time and thus the comparisons are valid. We selected the closest spatial and temporal data that were available, but for future studies, we would recommend trying to reduce the temporal heterogeneity to improve the inference regarding covariate relationships.

CONCLUSIONS

Two OWEDs are currently proposed in the Rhode Island study plot, a 5-turbine facility about 5 km southeast of Block Island that may be constructed starting as early as fall 2015 and a 150 to 200-turbine OWED in the middle of Rhode Island Sound that is still in the permitting process. In the Nantucket Sound study plot a 130-turbine facility is proposed in Horseshoe Shoals that is nearing the final stages of development. These and other proposed facilities could pose risks to seabird populations along the eastern coast of the USA (Drewitt & Langston 2006, Langston 2013). In order to minimize potential risks, one step is for decision makers to better understand the distribution and abundance of seabirds in and around OWED areas (Kinlan et al. 2012a, Winiarski et al. 2013). By using a community occupancy model we were able to provide this type of information by estimating occupancy and detection of all species observed during the study, even those with very few detections. The results provided spatially explicit estimates of species-specific occupancy probability, allowing us to examine the use of areas by different species throughout the study area. This study also provided estimates of species richness across study plots, which is another metric of interest in evaluating potential risks to seabird communities (Nur et al. 2011, Kinlan et al. 2012a, Winiarski et al. 2014).

Finally, repeated sampling combined with the community occupancy framework allowed us to see that there is a great deal of variation in detection probability across species and date. By correcting for detection, this approach allows for valid comparisons between species and areas (MacKenzie et al. 2002, Tyre et al. 2003, Kéry et al. 2008, Ruiz-Gutiérrez et al. 2010). Based on our findings, detection probability was low for many species, suggesting that if only one survey was conducted we would likely miss a number of species but more so, we would miss individuals. We acknowledge that occupancy models do not estimate abundance, a common parameter of interest. Thus, when abundance-based methods that can account for detection are available (such as distance sampling), we suggest the use of those methods.

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