

ABSTRACT

FLANDERS, NICHOLAS P. Using Occupancy Models to Estimate Temporal and Spatial Variation in Seabird Distributions. (Under the direction of Beth Gardner).

Comparisons of seabird distributions across time and space are of interest to ecologists. However, without formally accounting for the imperfect at-sea detection of seabirds, such comparisons are likely to contain bias due to variation in detection probability. Distance sampling methodology is an attractive analysis option but is not applicable when data is collected under strip-transect survey protocols. We analyzed aerial strip-transect survey data collected in southern New England using community occupancy models and dynamic occupancy models to make comparisons across space and time while formally accounting for imperfect detection probabilities. Predictions of species-specific winter distributions were made in two study plots, one off the coast of Rhode Island and the other in Nantucket Sound, using environmental covariate relationship estimates from two independent community occupancy models. We found larger differences between the two study plots in predicted diving species' distributions than predicted surface-feeding species' distributions. This result was largely explained by differences between the two foraging guilds in the relative strength of covariates as predictors of occupancy. We expected that diving species' winter distributions would show greater persistence over time than surface-feeding species' winter distributions. A three-year aerial strip-transect survey dataset collected in Nantucket Sound was analyzed using dynamic occupancy models where spatial variation in probabilities of initial occupancy, extinction, and colonization was modeled using environmental covariates. Results largely matched our expectations with the significant inter-annual shifts observed in predicted winter distributions of three diving species, common eider *Somateria mollissima*, northern gannet *Morus bassanus*, and razorbill *Alca torda*, as notable exceptions. Our results are directly relevant to

offshore spatial planning in the region, and by formally accounting for imperfect detection we ensured easy interpretability of these results for decision-makers.

Using Occupancy Models to Estimate Temporal and Spatial Variation in Seabird Distributions

by
Nicholas P. Flanders

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APPROVED BY:

Beth Gardner
Committee Chair

Allan O'Connell

Chris Moorman

Brian Reich

DEDICATION

I would like to dedicate this work to my grandmothers, Moma Lena and Moma Jean.

BIOGRAPHY

Nick grew up in Newport News, VA where his interest in the natural world began while spending time on the numerous water-bodies of the Hampton Roads region engaged in fishing and other recreational activities. After becoming an avid birdwatcher prior to finishing high school, Nick met contacts with the US Fish and Wildlife Service through friends in local bird clubs and worked as a Biological Technician at National Wildlife Refuges in eastern VA during the summers of his undergraduate years at Old Dominion University in Norfolk, VA. After graduating from that institution with a B.S. in Biology in 2011 Nick began pursuit of an M.S. at North Carolina State University.

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USING A COMMUNITY OCCUPANCY MODEL TO IDENTIFY KEY SEABIRD AREAS IN SOUTHERN NEW ENGLAND

ABSTRACT

Estimating the relationships between seabird distributions and environmental variables is a common goal in seabird studies. When distance data is not recorded, researchers may have difficulty estimating detection probability, which is known to vary by species. However, repeated sampling of aerial strip-transects and occupancy models can be used to account for species-specific detection rates less than one. To our knowledge, this approach has not been previously used to estimate seabird distributions. We applied single-season community occupancy models to datasets collected in two large study plots in southern New England. We estimated the influence of remotely-sensed environmental covariates including bathymetry, sea surface temperature, and chlorophyll *a* surface concentration on species-specific occupancy. Similarly, we modeled detection as a function of both survey date and effort. The two study plots were modeled separately to explore differences in predicted distributions and species-specific environmental covariate relationships. Diving species showed large differences between the two study plots in terms of their predicted winter distributions, which was largely explained by bathymetry acting as a stronger predictor of occupancy in Rhode Island than in Nantucket Sound. Conversely, similarities between the two 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 from the observed communities to detect "hot-spots" of seabird occupancy in the two study plots. Our results will be useful to biologists and planners interested in seabird conservation in the region.

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). A variety of 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 ancillary distance 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). Other approaches may be necessary if there is interest in species with too few observations to fit a detection function (Winiarski et al. 2014) or if data are collected utilizing strip-transect survey protocols when distance information is not recorded (Camphuysen et al. 2004).

Community occupancy models (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 some form of geographical closure can be assumed. These models do not estimate abundance, but instead the probability of site-occupancy by a species, and information is lost when reducing counts to binary detection/non-detection data (MacKenzie et al. 2002, 2006). However, community occupancy models account for the imperfect detection of species and allow for inference about species-specific habitat relationships and predicted distributions for species that are rare or difficult to detect (Russell et al. 2009, Ruiz-Gutiérrez et al. 2010). Community-level metrics such as species richness can also be estimated (Dorazio et al. 2006, Royle et al. 2007, Zipkin et al. 2009, 2010b). Traditional distance sampling techniques assume perfect detection at distance 0 from the transect (Buckland et al. 2001). Community occupancy models do not make this assumption and allow for the probability of a species being available for detection to be less than one (Tyre et al. 2003, MacKenzie 2005, MacKenzie et al. 2006, Kéry & Schaub 2012).

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 two study plots in the northwestern Atlantic Ocean. We expect these results to increase our knowledge of seabird ecology and distribution in the region, thereby supporting those responsible for decisions regarding ocean planning.

METHODS

Study area

Our study area encompassed two study plots in the northwestern North Atlantic in southern New England. One 3800-km² study plot located south of Rhode Island, USA, included Block Island Sound and Rhode Island Sound and portions of the Continental Shelf (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). Both study plots provide important habitat for a diversity of seabird species (Huettmann & Diamond 2000), including the federally-endangered roseate tern (*Sterna dougallii*) and species of conservation concern such as the common loon (*Gavia immer*), red-throated loon (*Gavia stellata*), least tern (*Sterna antillarum*), and great shearwater (*Puffinus gravis*; Kinlan et al. 2012a, Winiarski et al. 2013). The study area is also globally important for wintering sea ducks (Tribe 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. Aerial surveys of 24 transect lines within the Rhode Island study plot were conducted every 1-2 weeks from December 2009 to February 2010 (Winiarski et al. 2011). Mass Audubon conducted 54 aerial surveys of 15 transect lines within Nantucket Sound from August 2002 to March 2006. The transect lines in the Rhode Island study plot were positioned perpendicular to the coast, were separated by 3 kilometers (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 an 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.

For both study plots, transect lines were divided into 2.27-km long sections to form unique segments. 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 1065 m (SD = 640). All avian observations used in this analysis were identified to species and given the appropriate segment identification as an attribute. We defined the winter season as the months of December-February and selected the winter 2003-2004 data from the Nantucket Sound study plot to form two single-season datasets, where most segments had within-season temporal replication. Data were segregated by species and survey-specific counts were reduced to binary data to represent the detection or non-detection of a species within each segment.

Environmental covariates

Remotely-sensed data on sea surface temperature (SST), bathymetry, and chlorophyll *a* surface (chl *a*) concentration were used to model occupancy probability as a function of covariates in survey segments throughout the study area. These abiotic and biotic variables were used 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 x 4 km) grid cell resolution using Marine Geospatial Ecology Tools (Roberts et al. 2010) and averaged across the relevant winter seasons. 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 (“GEODAS Grid Translator-Design-a-Grid” 2006) 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 spatially with the transect segments and weighted average covariate values for each segment were calculated (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 bathymetry values in the Rhode Island study plot covered a larger range of values and the overall mean was deeper than in the Nantucket Sound study plot (Fig. 1). Ranges of SST and chl *a* concentration values were similar between the two study plots for both seasons (Appendix Sec. 1.1). 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.

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. The latent state z_{ik} represents this process, as $z_{ik} = 1$ if segment i is occupied by species k and $z_{ik} = 0$ 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 as a function of bathymetry and seasonal averages of both SST and chl *a* concentration (chlA) at the segment level (Kéry & Royle 2008a, 2008b, Russell et al. 2009) such that

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

where occint_k is the species-specific intercept.

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 two 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, $y_{ijk} | z_{ik} \sim \text{Bern}(p_{ijk} * z_{ik})$; thus, when $z_{ik} = 0$ the probability of a detection is 0 and when $z_{ik} = 1$ the probability of a detection is p_{ijk} .

We modeled variation in p as a function of date and observer effort (Kéry & Royle 2008a, 2008b, Russell et al. 2009). Differences in estimates of observer effort collected under the two sampling protocols for the study areas led to the construction of two 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, Gardner et al. 2011). For the Rhode Island data, we accounted for reduced observer effort at survey locations with significant glare by including an indicator variable $glare_{ij} = 0$ when only one observer was recording data and $glare_{ij} = 1$ at normal double observer survey occasions such that

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

where $pint_{1,k}$ is the intercept for species k with glare (only one observer on survey) and $pint_{2,k}$ is the intercept for species k when there is no glare effect (both observers on survey).

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

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

where $pint_k$ is the species-specific intercept.

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 was a random effect arising from a Normal prior distribution (Sauer & Link 2002, Dorazio & Royle 2005, Royle & Dorazio 2006):

$$\beta_{1,k} \sim \text{Normal}(\mu_{\beta_1}, \sigma_{\beta_1}^2)$$

The means and variances of the Normal prior distributions 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 similar to the common prior distribution and of course precision is 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 means 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 Appendix Sec. 1.2. Posterior distributions of parameters were approximated using 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.

Making predictions and comparisons

We used grids with 4-km² (2 x 2 km) cells for spatial predictions of occupancy probability across the two 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 standardized with the original covariate means and standard deviations used in the analysis. To map means and standard deviations of 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 and were summed across species at each iteration to approximate the posterior distribution of the grid cell-specific predictions.

We compared seabird habitat 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 habitat relationship differed between the two study plots for a given species. These probabilities were calculated following Ruiz-Gutiérrez et al. (2010). We considered there was a significant difference between species-specific estimates from the two study plots if the probability of this difference was ≥ 0.95 .

To generalize observed similarities or differences in species-specific habitat relationships between the two study plots, we placed all species included in the models into one of two *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 (Appendix Sec. 1.3). These foraging guilds were not used during the modeling process but rather for qualifying consistent relationships across species with similar natural history.

RESULTS

Surveys of the Rhode Island study plot conducted during the 2009-2010 winter season detected 17 species (Appendix Sec. 1.4), 13 of which were diving species and four of which were surface-feeding species. Species-specific estimates of the relationship between bathymetry and occupancy were significant for eight species, all of which were diving species. 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 relationship between date and detection, and three species had significant estimates for the quadratic effect of date on detection (Table 1, Fig. 2).

Bathymetry was the strongest predictor of the distributions of diving species in the Rhode Island study plot in the winter (Table 1), which is not surprising as foraging sea ducks and some other diving species are typically associated with shallow depths (Guillemette et al. 1993, Nehls & Ketzenberg 2002, Zipkin et al. 2010a). SST was an important predictor of occupancy for species that forage on the surface during winter (Table 1), also matching our expectations. One surprising result was that a sea duck, the common eider, had a significantly positive estimate for the coefficient corresponding to the relationship of chl *a* concentration with its winter occupancy (Table 1).

Surveys of the Nantucket Sound study plot conducted during the 2003-2004 winter season detected a total of 17 species (Appendix Sec. 1.5), 12 of which were diving species and five of which

were surface-feeding species. The only species with a significant relationship between bathymetry and its occupancy was surf scoter (*Melanitta perspicillata*), a diving species. There were no significant species-specific estimates of the relationship between SST and occupancy in this model. Species-specific estimates of the relationship between chl *a* concentration and occupancy were significant for five species, three of which were surface-feeding species (Table 1). Ten species had significant estimates for the relationship between date and detection, and six species had significant estimates for the quadratic effect of date on detection (Table 1, Fig. 2).

We found a significant difference in our estimates of species-specific relationships between bathymetry and occupancy from the two study plots for six species, all of which were diving species. The great black-backed gull was the only species for which we found a significant difference in the parameter estimates for SST from the two study plots. We found a significant difference in the estimates of species-specific relationships between chl *a* concentration and occupancy from the two study plots for red-breasted merganser (*Mergus serrator*), a diving species, and for three surface-feeding species: herring gull (*Larus argentatus*), northern gannet (*Morus bassanus*), and great black-backed gull (Table 2).

We documented large differences in patterns of predicted occupancy between the two study plots for common eider (Fig. 3), 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*; Appendix Sec. 2). Specifically, areas of high predicted occupancy in the RIOSAMP 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-throated loon, common loon (Fig. 3), red-breasted merganser, and great cormorant (*Phalacrocorax carbo*) were similar to those for sea ducks, with areas of high predicted occupancy occurring near the mainland and near islands (Appendix Sec. 2). 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, another diving piscivore, 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 (Fig. 3).

Patterns of predicted occupancy were much more similar between the two 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 (Appendix Sec. 2). In both study plots, areas of high predicted occupancy were large and concentrated away from the mainland. The razorbill (*Alca torda*) was the only alcid included in both winter models and predicted distributions were similar to those of the sea ducks (Fig. 3). 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 (Appendix Sec. 2).

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 two study plots (Appendix Sec. 3). 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. Such hot-spots in Nantucket Sound encompassed much of the southern half of the study plot.

Detection probability was modeled as a quadratic function of date to account for changes in species abundance across the two three-month seasons. Species-specific detection probabilities were expected to reach a maximum when the species was at peak abundance in the study plot. Thus, it is interesting that the predicted detection of long-tailed duck in the Nantucket Sound study plot reached its maximum at the end of the winter season, while the maximum predicted detection of northern gannet in the Rhode Island and Nantucket Sound study plots occurred at the beginning of the winter season (Fig. 2).

DISCUSSION

We used community occupancy models to draw inference on habitat relationships for seasonal seabird communities that included uncommon species with few detections. This approach appears suitable 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 two foraging guilds. Comparisons of parameter estimates and predicted distributions for the same species also showed considerable differences between the two 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 must use predicted seabird distributions that are based on survey data from the area in question.

By using the temporal replication of these two datasets to account for imperfect detection, we avoided bias in our estimates and predictions that is incurred when perfect or constant detection is

assumed (MacKenzie et al. 2002, Tyre et al. 2003). The two species with significant estimates of both linear and quadratic effects of date on detection in both winter models, northern gannet and black-legged kittiwake, showed significantly different detection probability estimates between the two study plots for some portion of the winter season. By allowing detection probability to vary among both species and study plots we avoided potential confounding of ecological parameter differences with differences in detection rate (Kéry et al. 2008, Ruiz-Gutiérrez et al. 2010).

Environmental covariate relationships and predicted seabird distributions

Primary productivity tends to be concentrated in certain areas of the ocean, usually related to levels of nutrient enrichment (Kinlan et al. 2012b). These areas tend to concentrate seabird prey and provide important habitat for foraging seabirds (Hyrenbach et al. 2000, Spear et al. 2001, Ballance et al. 2006, Louzao et al. 2006, Bost et al. 2009, Louzao 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 surface-feeding species. However, diving piscivores present in the study region were able to forage at a variety of depths in the water column, and a number of surface water characteristics could predict foraging habitat for these species as well (Harrison 1983, Winiarski et al. 2013).

Nantucket Sound model results did not exhibit the consistent relationships between bathymetry and diving species' winter occupancy that was evident in the Rhode Island study plot, likely because Nantucket Sound shows far less variation in water depth than the Rhode Island study plot. Winter occupancy of some diving species in this model was explained by chl *a* concentration, a covariate that showed greater variation in the study area 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 a surprise, although it was a notable departure from patterns in results from the Rhode Island model.

Differences and similarities in patterns of predicted occupancy for the two study plots can be explained by species-specific covariate relationship estimates from the two models. Large differences in predicted distributions of winter diving species can be explained by bathymetry 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 two 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 as 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 two study plots.

Our spatial predictions of the number of observed species occupying grid cells across the two 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 (Fig. 6). 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. Efforts are taken to reduce double counting of individuals and incorporation of spatially explicit covariates may reduce the impacts 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 survey counts to binary data, our goal was to minimize the effect of misidentification and false positives in our analyses.

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 inter-specific 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.

Conservation implications

Offshore wind resources in the northeastern United States provide a viable option for generating renewable energy (Kempton et al. 2007). Two offshore wind energy development projects (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 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. Seabirds that use both nearshore (<5 km) and offshore waters in the northwestern Atlantic Ocean are potentially vulnerable to any proposed OWED (Drewitt & Langston 2006, Langston 2013). Thus, the results of this study should be relevant to the conservation-minded siting of OWED in these two study plots and to the design of future seabird surveys in anticipation of OWED.

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Table 1. Effects of environmental covariates on occupancy and detection probabilities of seabirds included in both winter models. Posterior means of species-specific coefficients are shown, with significant 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.

Species	Rhode Island study plot					Nantucket Sound study plot					
	Occupancy			Detection		Occupancy			Detection		
	Bathymetry	SST	Chl <i>a</i>	Date	Date ²	Bathymetry	SST	Chl <i>a</i>	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	-1.2	-0.82	-0.26	0.9	-0.43	-0.58	
White-winged scoter	1.18	-1.47	2.15	-0.14	-0.54	-0.14	-0.67	-0.6	-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	-0.5	0.72	0.001	0.91	0.26	
Red-breasted merganser	1.32	0.16	1.21	0.4	-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	0.9	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	0.1	-0.71	-1	-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	-0.4	-0.55	
Great black-backed gull	1.08	3.04	0.61	-0.2	0.02	0.4	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	-0.4	-0.29	1.24	0.16	-0.41	-0.43	-1.02	0.32	0.01	

Table 2. Significant probabilities of differences between Rhode Island study plot and Nantucket Sound study plot estimates of relationships between covariates and occupancy in winter.

Species	Pr(RI coefficient > Nantucket Sound coefficient)		
	Bathymetry	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	--	--

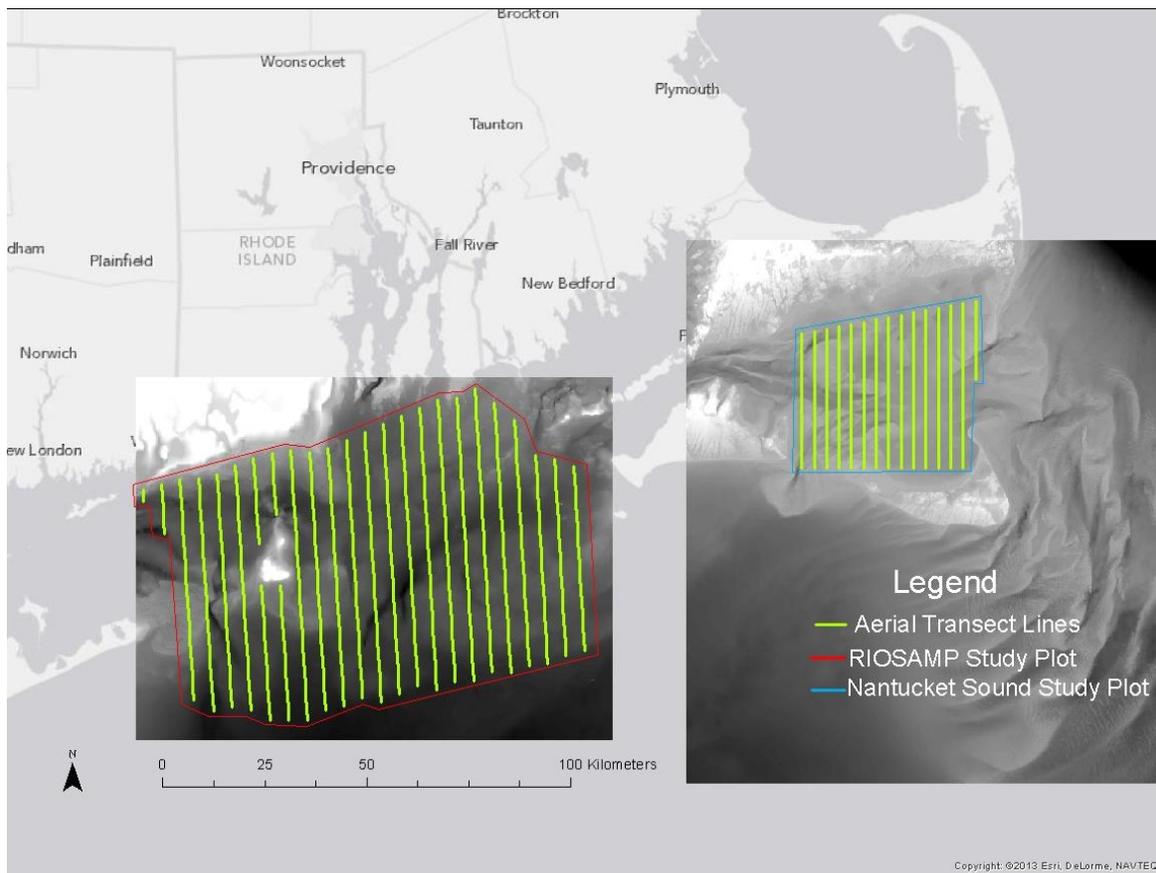


Figure 1. Rhode Island (left) and Nantucket Sound (right) study plots, transect lines, and bathymetry maps.

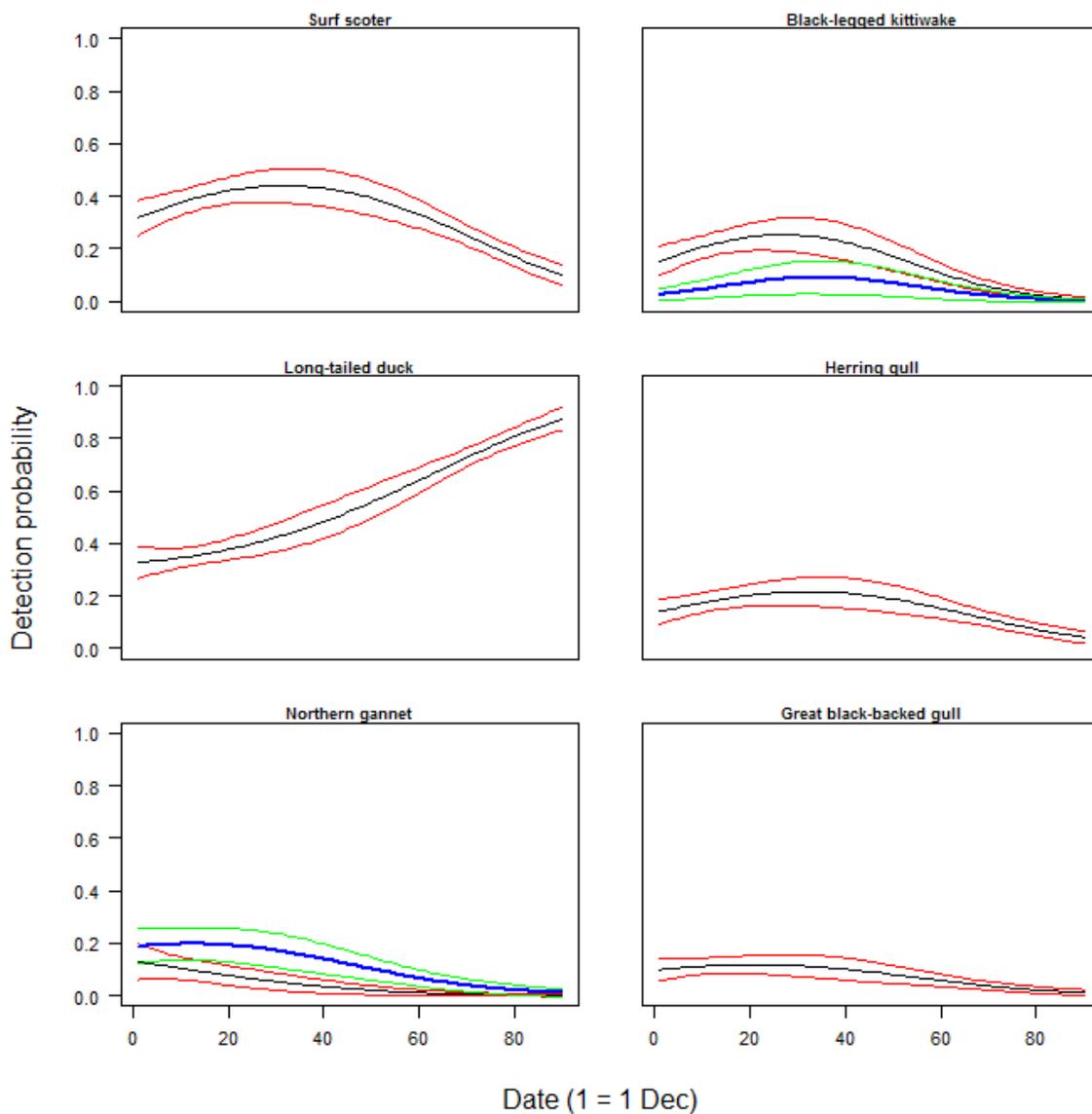


Figure 2. Means and 95% credible intervals of predicted detection probabilities across winter season dates for species with significant linear and quadratic effects of date on p . Black and red lines for Nantucket Sound study plot winter 2003-2004, blue and green lines for Rhode Island study plot winter 2009-2010.

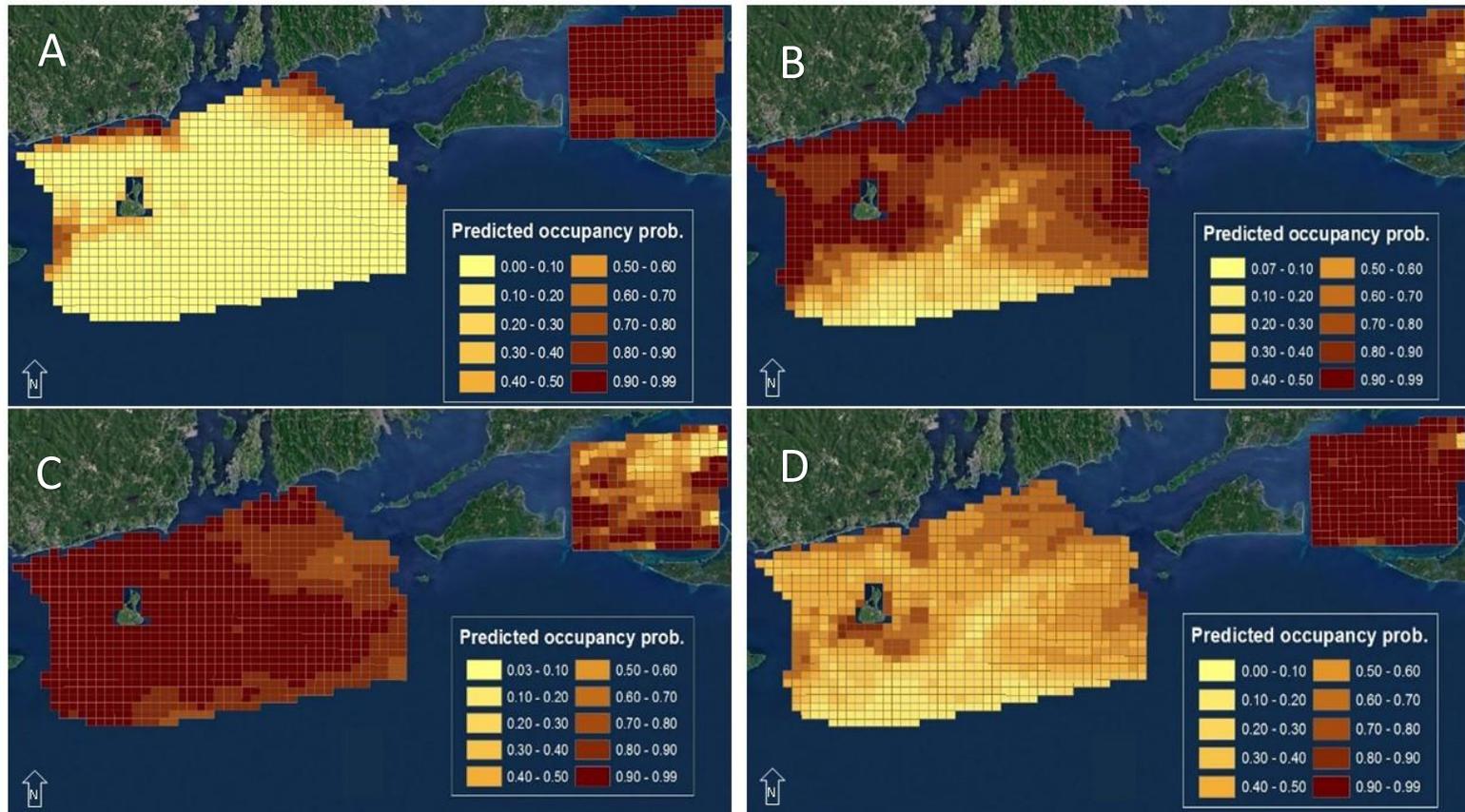


Figure 3. Map of the posterior means of predicted winter occupancy for selected diving species; A: common eider, B: common loon, C: northern gannet, D: razorbill.

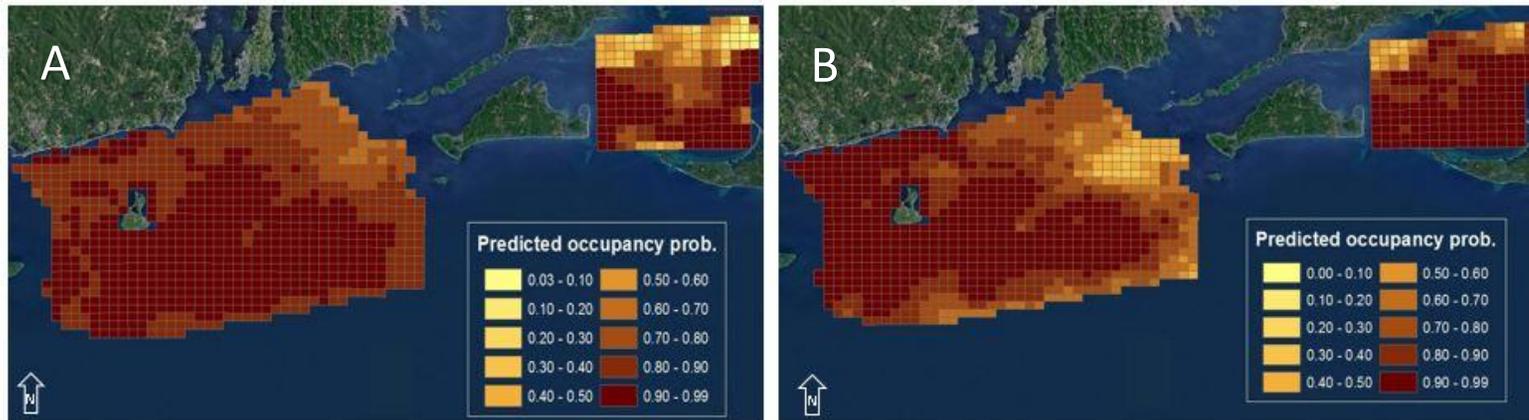


Figure 4. Map of the posterior means of predicted winter occupancy for selected surface-feeding species; A: black-legged kittiwake, B: herring gull.

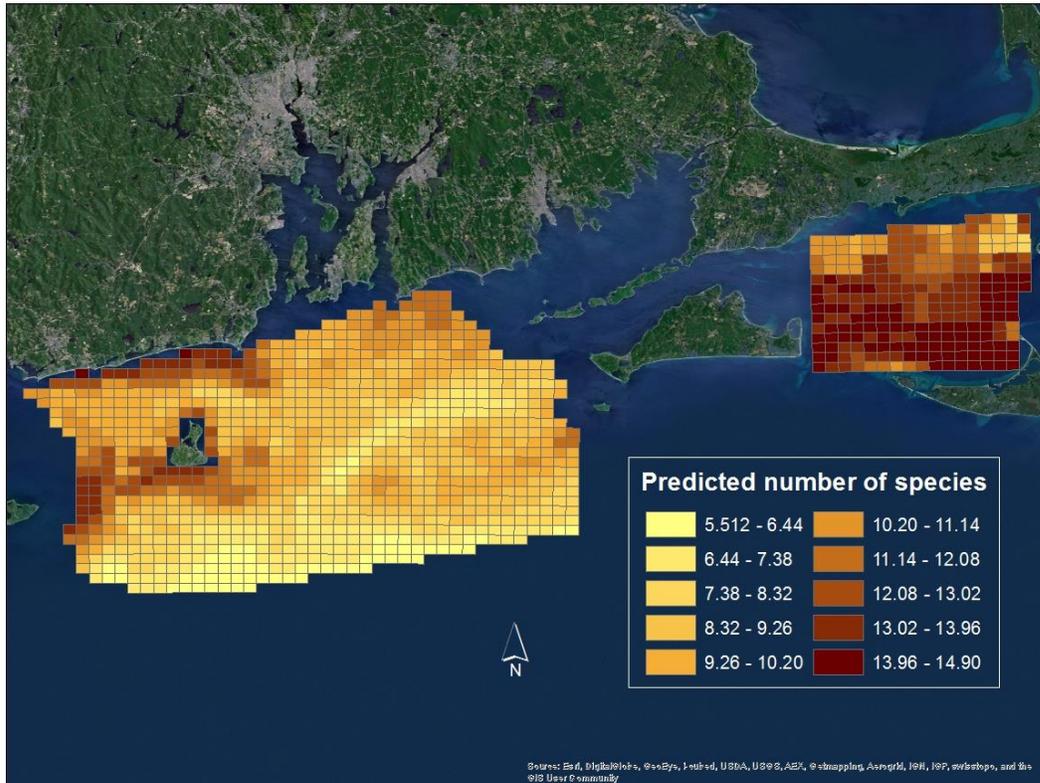


Figure 5. Map of the posterior means of the predicted number of species in the observed communities for the winter season.

APPENDIX

Sec. 1.1. Comparison of means and ranges of covariate values used for seasonal analysis of Rhode Island Ocean SAMP (RIOSAMP) and Nantucket Sound datasets. RIOSAMP data from winter 2009-2010 and Nantucket Sound data from winter 2003-2004.

	Bathymetry	
	Mean (SD)	Range
RIOSAMP	-35.44 (8.50)	(-55.86, -10.33)
Nantucket Sound	-11.53 (3.27)	(-19.32, -0.92)

	Winter SST		Winter chl-A	
	Mean (SD)	Range	Mean (SD)	Range
RIOSAMP	5.79 (0.58)	(4.23, 6.73)	2.96 (0.51)	(1.88, 5.60)
Nantucket Sound	3.28 (0.23)	(2.66, 4.12)	4.88 (0.58)	(3.57, 7.44)

Sec. 1.2. Example BUGS code for community occupancy model

```

sink("commmodel15.txt")
cat("
model {

# Priors
for(k in 1:(nspec)){
  lpsi[k] ~ dnorm(mu.lpsi, tau.lpsi)
  betalpsi1[k] ~ dnorm(mu.betalpsi1, tau.betalpsi1)
  betalpsi2[k] ~ dnorm(mu.betalpsi2, tau.betalpsi2)
  betalpsi3[k] ~ dnorm(mu.betalpsi3, tau.betalpsi3)

  lp[k] ~ dnorm(mu.lp, tau.lp)
  betalp1[k] ~ dnorm(mu.betalp1, tau.betalp1)
  betalp2[k] ~ dnorm(mu.betalp2, tau.betalp2)
  betalp3[k] ~ dnorm(mu.betalp3, tau.betalp3)
}

mu.lpsi ~ dnorm(0,0.01)
tau.lpsi <- pow(sd.lpsi, -2)
sd.lpsi ~ dunif(0,20)

mu.betalpsi1 ~ dnorm(0,0.01)
tau.betalpsi1 <- pow(sd.betalpsi1, -2)
sd.betalpsi1 ~ dunif(0,20)

mu.betalpsi2 ~ dnorm(0,0.01)
tau.betalpsi2 <- pow(sd.betalpsi2, -2)

```

```
sd.betalpsi2 ~ dunif(0,20)
```

```
mu.betalpsi3 ~ dnorm(0,0.01)
tau.betalpsi3 <- pow(sd.betalpsi3, -2)
sd.betalpsi3 ~ dunif(0,20)
```

```
mu.lp ~ dnorm(0,0.01)
tau.lp <- pow(sd.lp, -2)
sd.lp ~ dunif(0,20)
mu.betalp1 ~ dnorm(0,0.01)
tau.betalp1 <- pow(sd.betalp1, -2)
sd.betalp1 ~ dunif(0,20)
mu.betalp2 ~ dnorm(0,0.01)
tau.betalp2 <- pow(sd.betalp2, -2)
sd.betalp2 ~ dunif(0,20)
mu.betalp3 ~ dnorm(0,0.01)
tau.betalp3 <- pow(sd.betalp3, -2)
sd.betalp3 ~ dunif(0,20)
```

```
# Likelihood
```

```
for(k in 1:(nspec)){
  for (i in 1:nsite) {
    psi[i,k] <- exp(lp[k] + betalpsi1[k] * bath[i] + betalpsi2[k] * SST[i] + betalpsi3[k] *
chla[i])/(1+exp(lp[k] + betalpsi1[k] * bath[i] + betalpsi2[k] * SST[i] + betalpsi3[k] * chla[i]))
    z[i,k] ~ dbern(psi[i,k])
  }
}
```

```
for(k in 1:(nspec)){
  for (i in 1:nsite){
    for(j in 1:J[i]){
      p[i,j,k] <- exp(lp[k] + betalp1[k] * date[i,j] + betalp2[k] * pow(date[i,j],2) + betalp3[k] *
leng[i,j])/(1+exp(lp[k] + betalp1[k] * date[i,j] + betalp2[k] * pow(date[i,j],2) + betalp3[k] * leng[i,j]))
      p.eff[i,j,k] <- z[i,k] * p[i,j,k]
      Y[i,j,k] ~ dbern(p.eff[i,j,k])
    }
  }
}
```

```
for(k in 1:(nspec)){
  for(j in 1:npredsite){
```

```

    predocc[j,k]<-exp(lpsi[k] + betalpsi1[k] * bathpred[j] + betalpsi2[k] * SSTpred[j] + betalpsi3[k] *
    chlapred[j])/(1+exp(lpsi[k] + betalpsi1[k] * bathpred[j] + betalpsi2[k] * SSTpred[j] + betalpsi3[k] *
    chlapred[j]))
    newz[j,k] ~ dbern(predocc[j,k])
  }
}

for(j in 1:npredsite){
  predspecies[j]<-sum(newz[j,1:nspec])
}
}
",fill = TRUE)
sink()

```

Sec. 1.3. Classification of species included in models based on foraging method

Winter

Diving species

common eider (*Somateria mollissima*)
 surf scoter (*Melanitta perspicillata*)
 white-winged scoter (*Melanitta fusca*)
 black scoter (*Melanitta americana*)
 long-tailed duck (*Clangula hyemalis*)
 red-breasted merganser (*Mergus serrator*)
 red-throated loon (*Gavia stellata*)
 common loon (*Gavia immer*)
 red-necked grebe (*Podiceps grisegena*)
 northern gannet (*Morus bassanus*)
 great cormorant (*Phalacrocorax carbo*)
 dovekie (*Alle alle*)
 common murre (*Uria aalge*)
 razorbill (*Alca torda*)

Surface-feeding species

brant (*Branta bernicla*)
 black-legged kittiwake (*Rissa tridactyla*)
 bonaparte's gull (*Chroicocephalus philadelphia*)
 herring gull (*Larus argentatus*)
 great black-backed gull (*Larus marinus*)

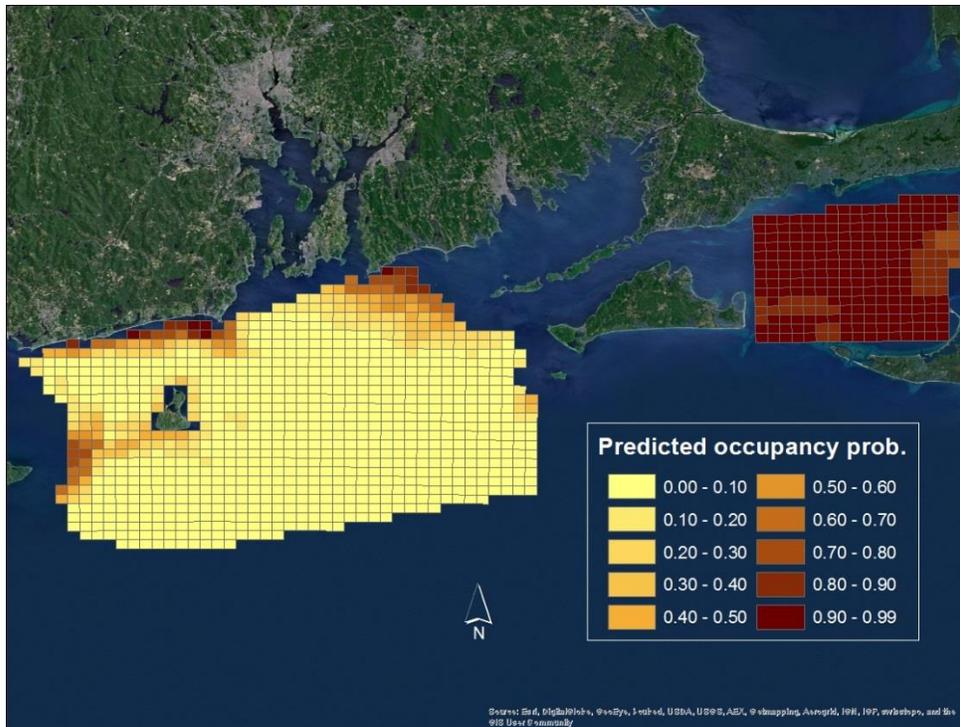
Sec. 1.4. Detected species and number of detections at the segment level, Rhode Island Ocean SAMP study plot winter 2009-2010

Species	Number of detections
common eider (<i>Somateria mollissima</i>)	44
surf scoter (<i>Melanitta perspicillata</i>)	1
white-winged scoter (<i>Melanitta fusca</i>)	10
black scoter (<i>Melanitta americana</i>)	1
long-tailed duck (<i>Clangula hyemalis</i>)	1
red-breasted merganser (<i>Mergus serrator</i>)	2
red-throated loon (<i>Gavia stellata</i>)	15
common loon (<i>Gavia immer</i>)	232
northern gannet (<i>Morus bassanus</i>)	105
great cormorant (<i>Phalacrocorax carbo</i>)	2
black-legged kittiwake (<i>Rissa tridactyla</i>)	47
bonaparte's gull (<i>Chroicocephalus philadelphia</i>)	1
herring gull (<i>Larus argentatus</i>)	152
great black-backed gull (<i>Larus marinus</i>)	92
dovekie (<i>Alle alle</i>)	24
common murre (<i>Uria aalge</i>)	1
razorbill (<i>Alca torda</i>)	11

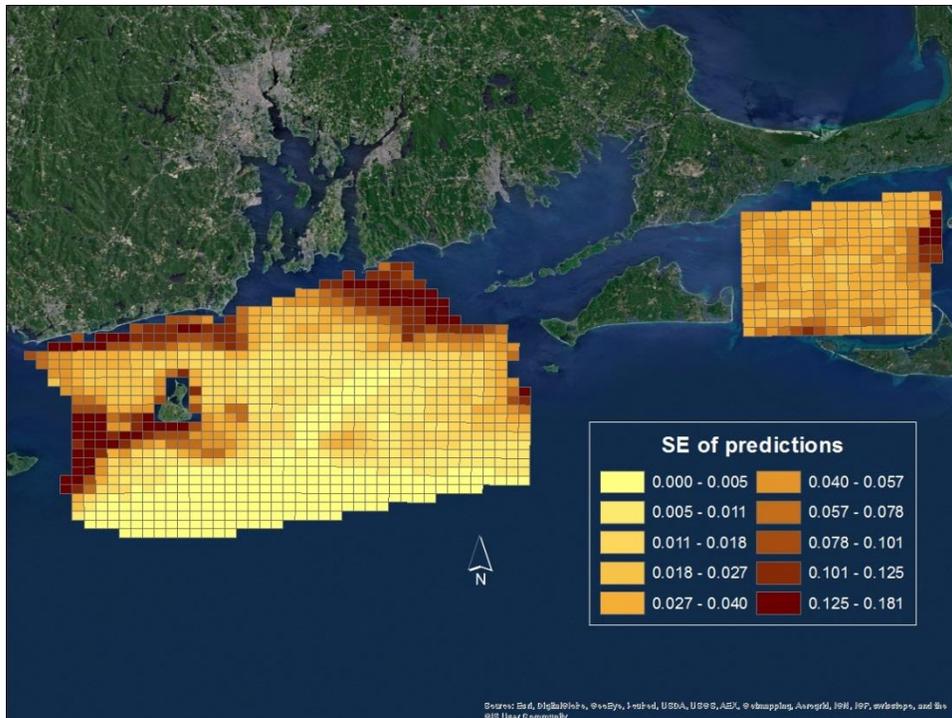
Sec. 1.5. Detected species and number of detections at the segment level, Nantucket Sound study plot winter 2003-2004

Species	Number of detections
brant (<i>Branta bernicla</i>)	1
common eider (<i>Somateria mollissima</i>)	463
surf scoter (<i>Melanitta perspicillata</i>)	365
white-winged scoter (<i>Melanitta fusca</i>)	146
black scoter (<i>Melanitta americana</i>)	21
long-tailed duck (<i>Clangula hyemalis</i>)	779
red-breasted merganser (<i>Mergus serrator</i>)	12
red-throated loon (<i>Gavia stellata</i>)	38
common loon (<i>Gavia immer</i>)	57
red-necked grebe (<i>Podiceps grisegena</i>)	1
northern gannet (<i>Morus bassanus</i>)	51
great cormorant (<i>Phalacrocorax carbo</i>)	1
black-legged kittiwake (<i>Rissa tridactyla</i>)	147
bonaparte's gull (<i>Chroicocephalus philadelphia</i>)	21
herring gull (<i>Larus argentatus</i>)	183
great black-backed gull (<i>Larus marinus</i>)	93
razorbill (<i>Alca torda</i>)	179

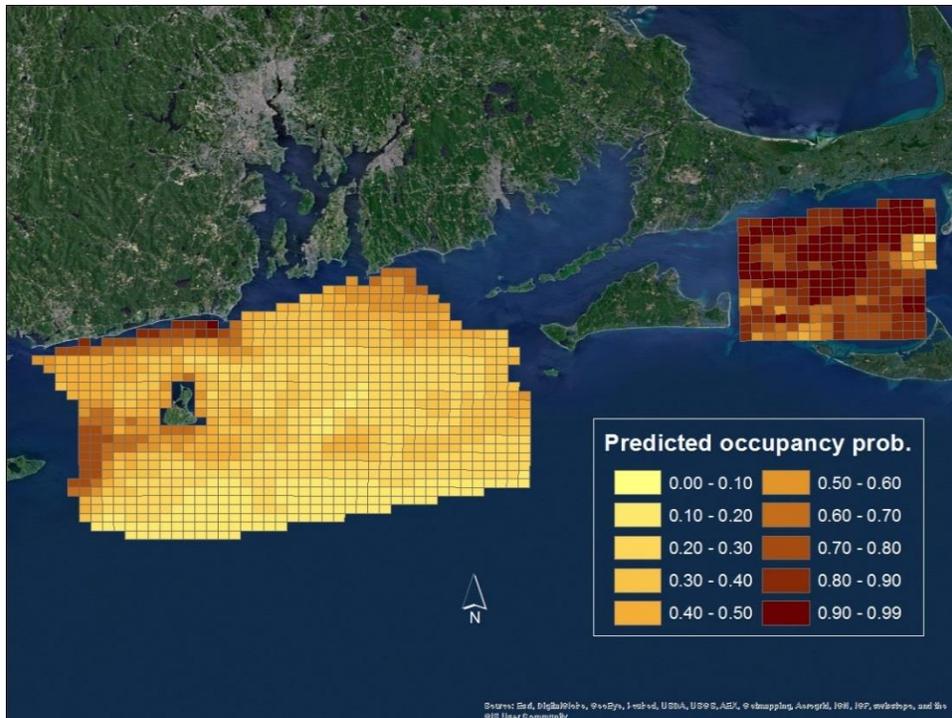
Sec. 2.1. Posterior means of predicted common eider occupancy, winter.



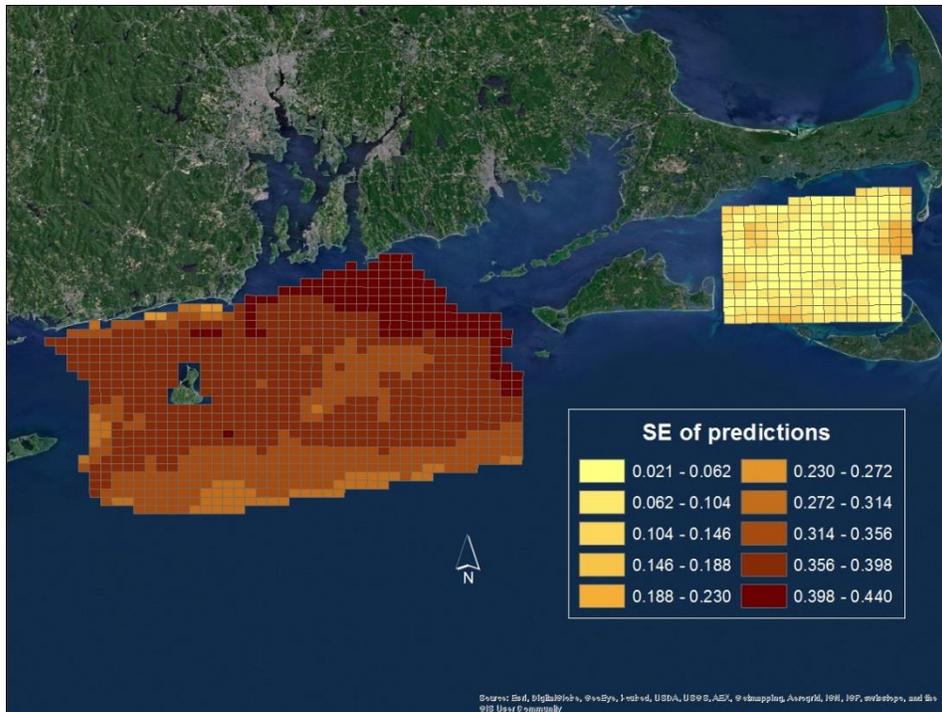
Sec. 2.2. Standard errors of predicted common eider occupancy, winter.



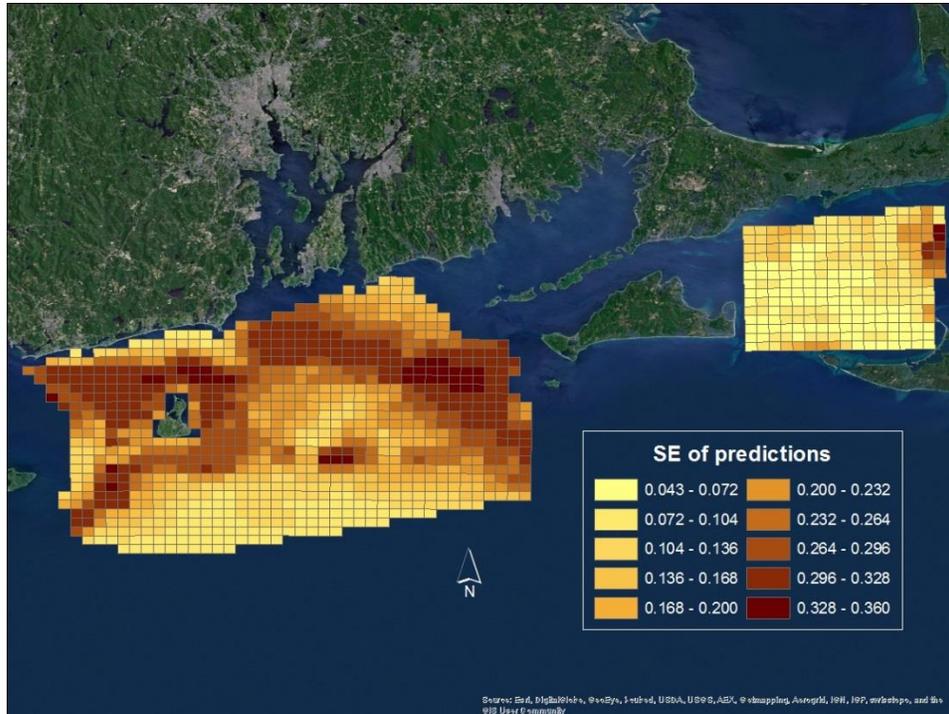
Sec. 2.3. Posterior means of predicted surf scoter occupancy, winter.



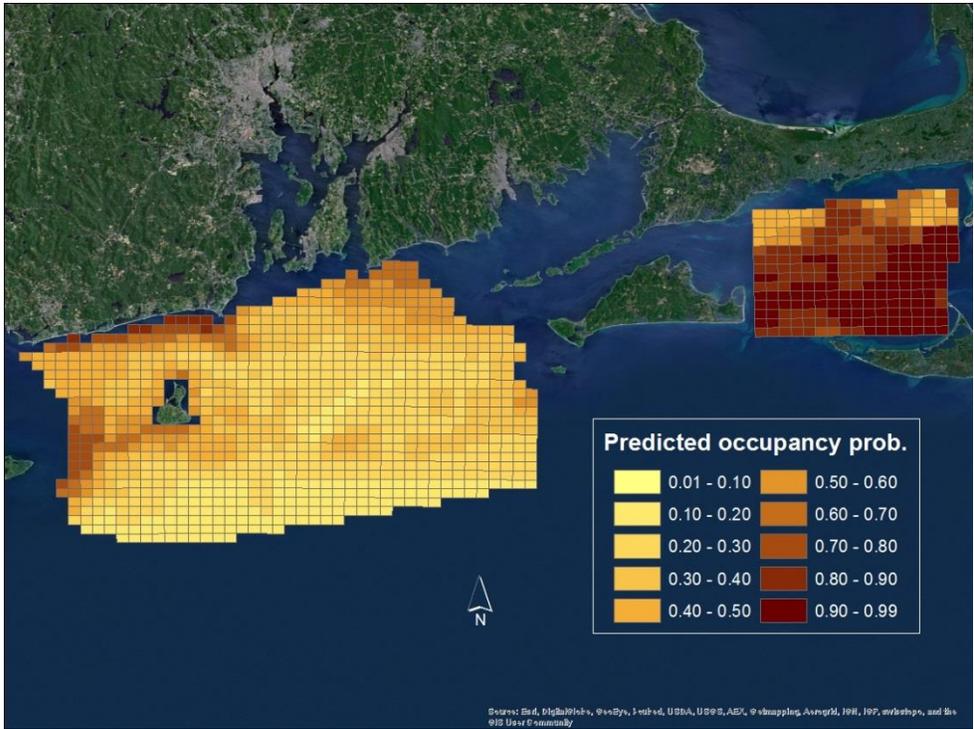
Sec. 2.4. Standard errors of predicted surf scoter occupancy, winter.



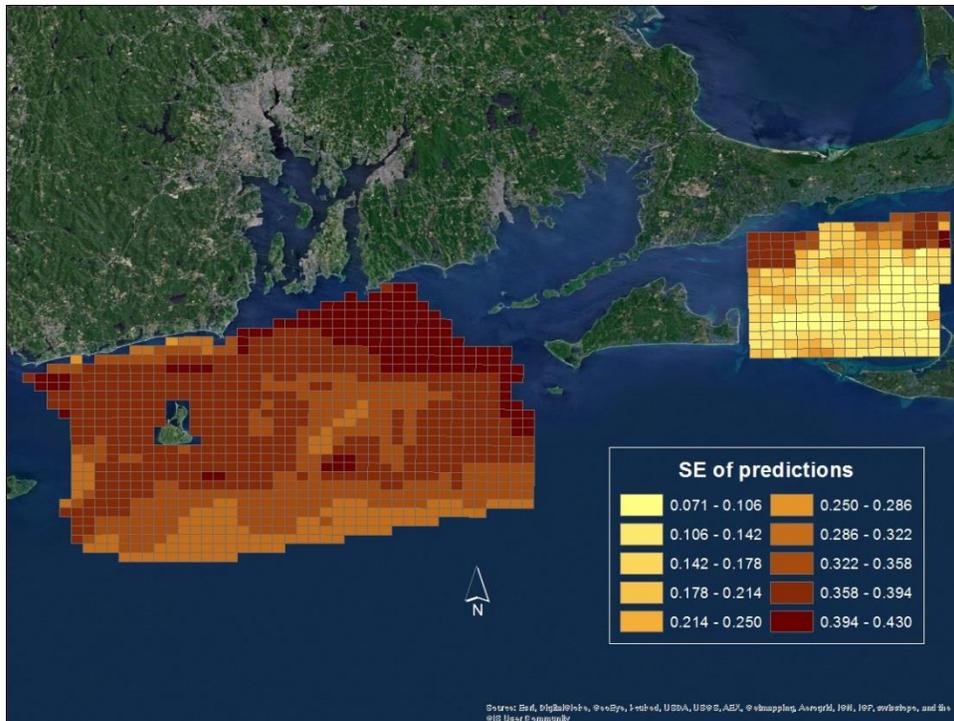
Sec. 2.6. Standard errors of predicted white-winged scoter occupancy, winter.



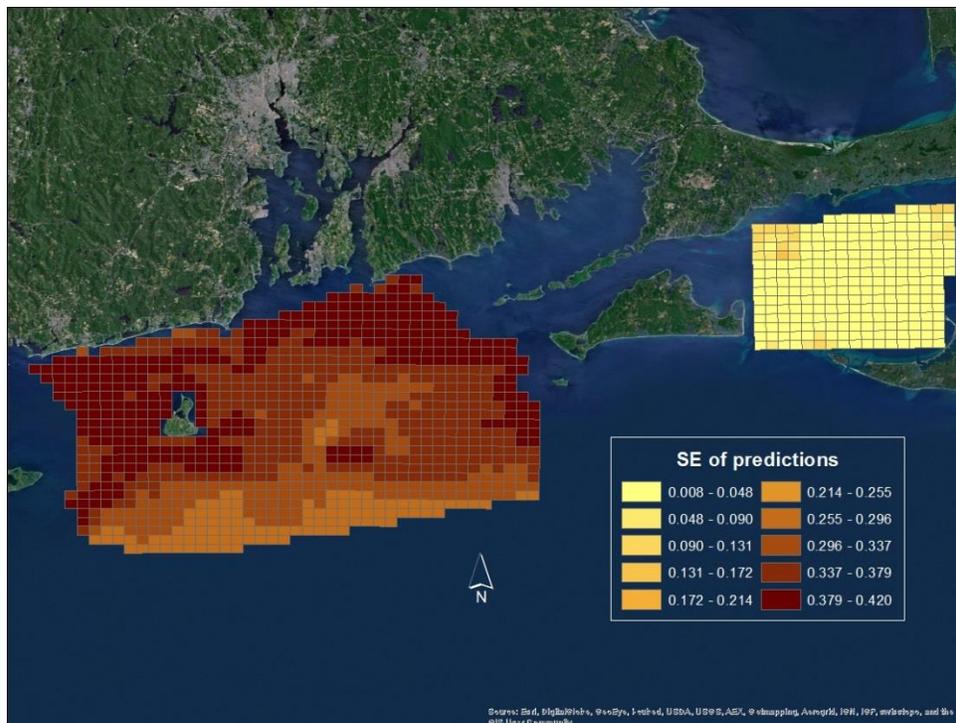
Sec. 2.7. Posterior means of predicted black scoter occupancy, winter.



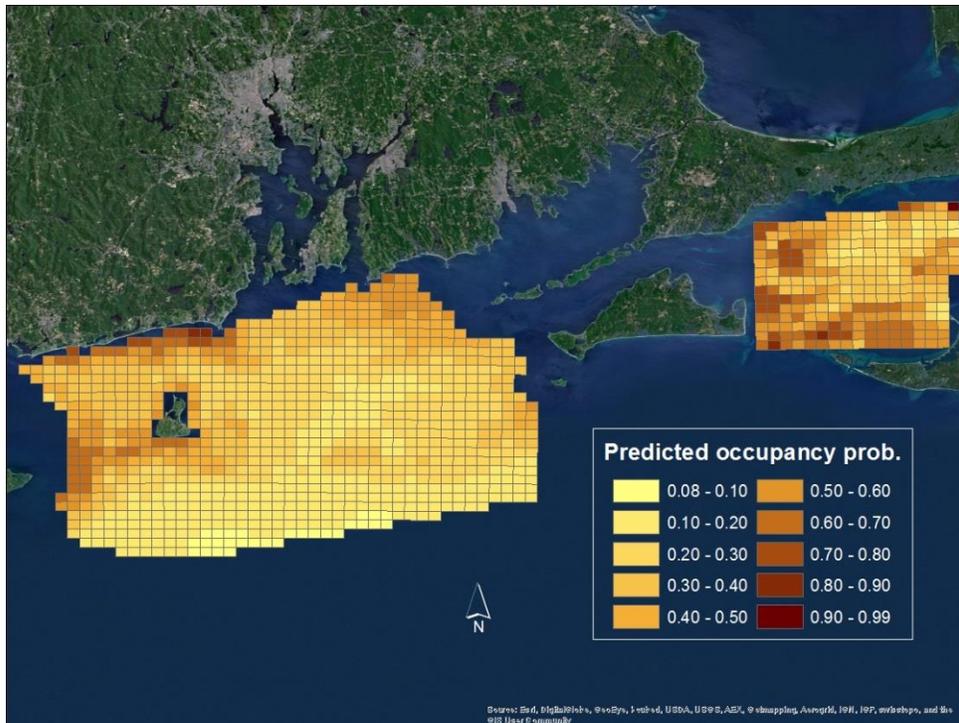
Sec. 2.8. Standard errors of predicted black scoter occupancy, winter.



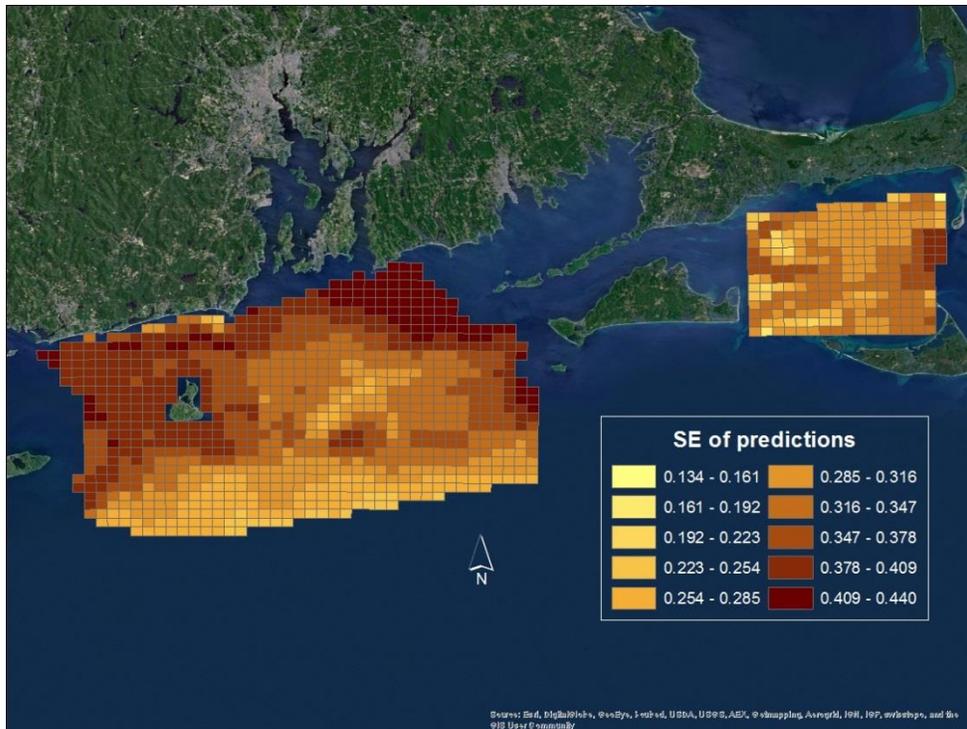
Sec. 2.10. Standard errors of predicted long-tailed duck occupancy, winter.



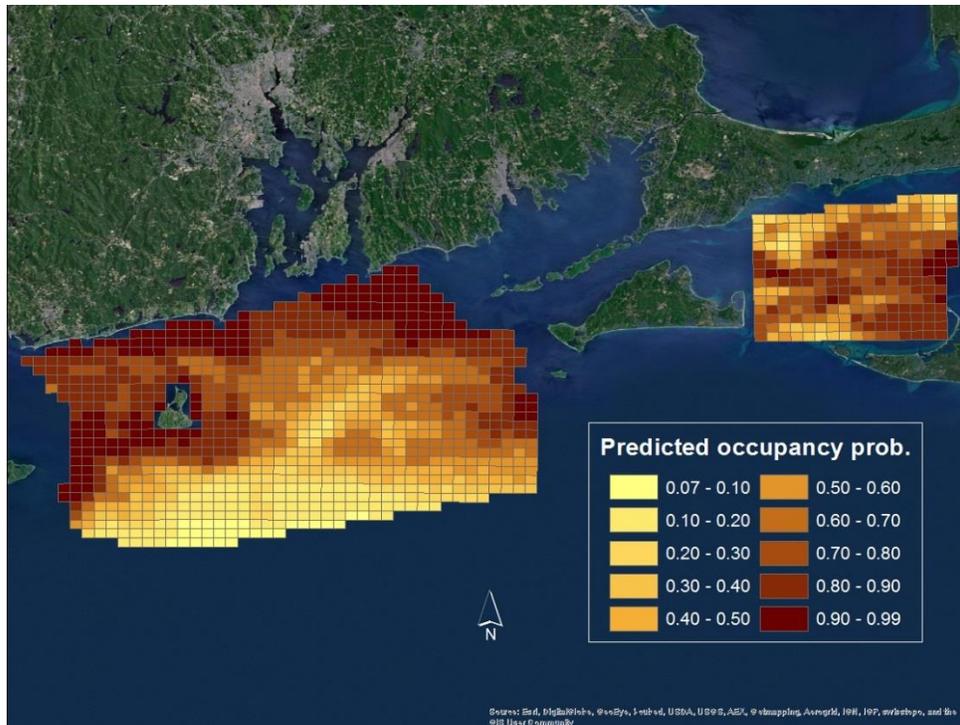
Sec. 2.11. Posterior means of predicted red-breasted merganser occupancy, winter.



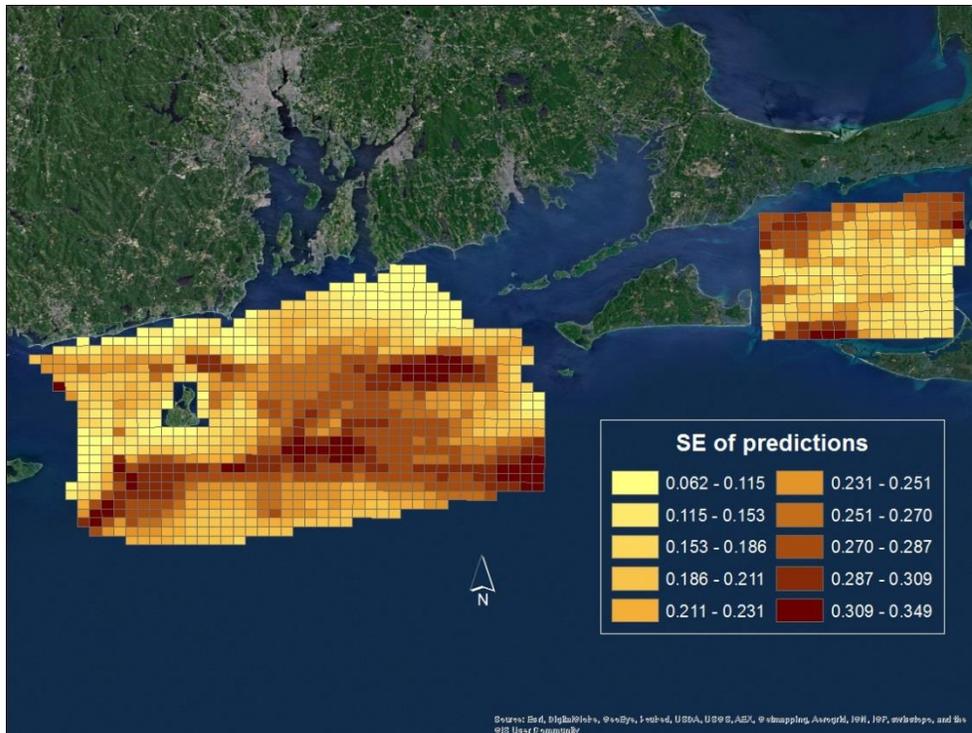
Sec. 2.12. Standard errors of predicted red-breasted merganser occupancy, winter.



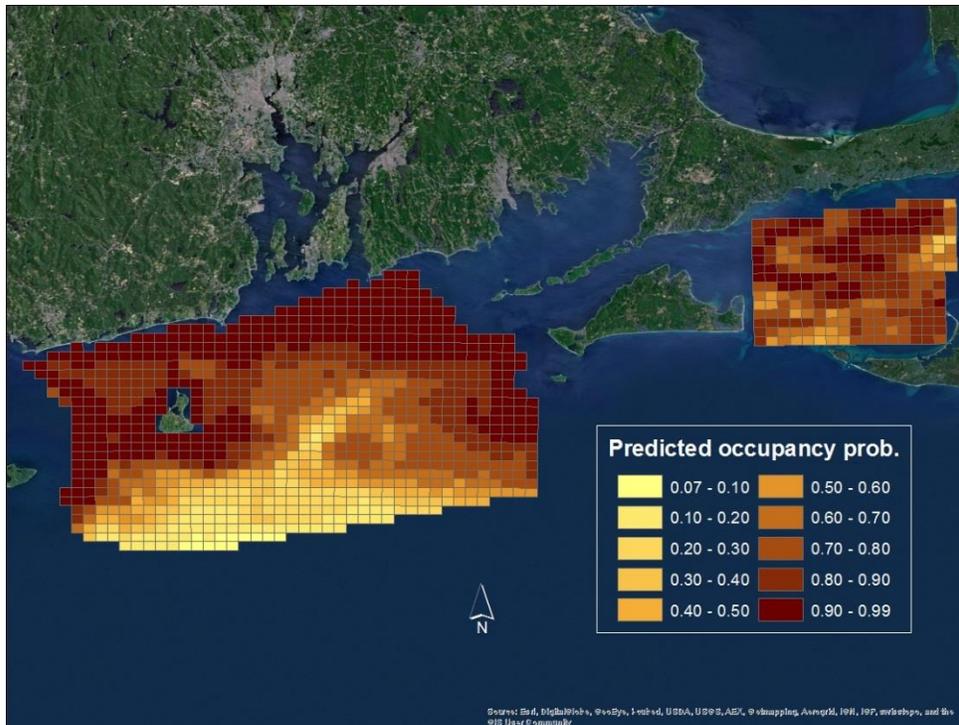
Sec. 2.13. Posterior means of predicted red-throated loon occupancy, winter.



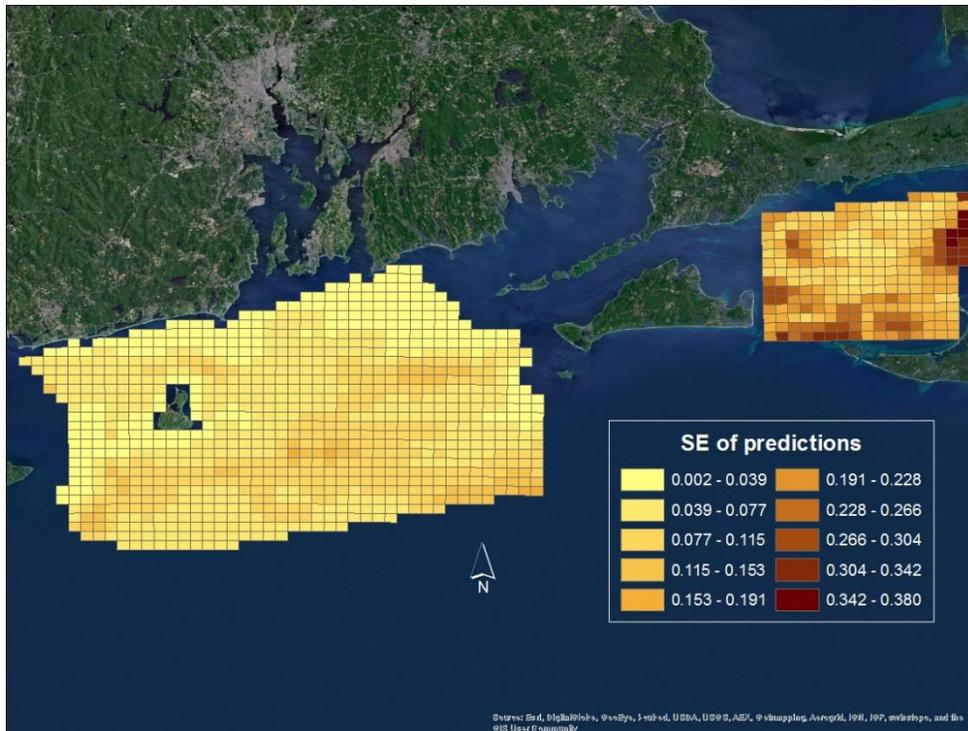
Sec. 2.14. Standard errors of predicted red-throated loon occupancy, winter.



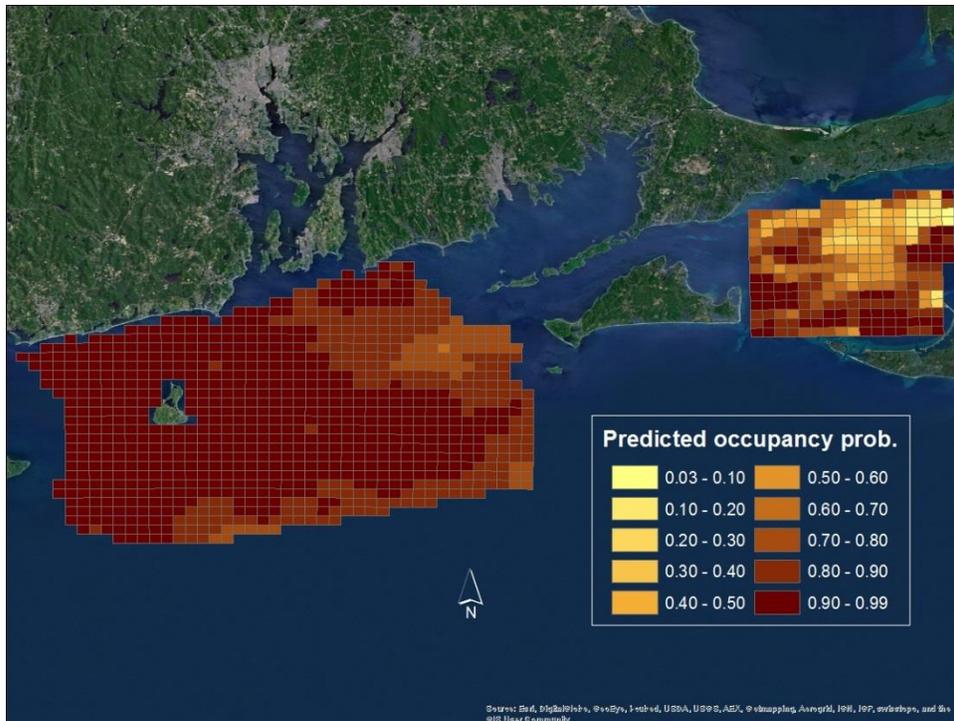
Sec. 2.15. Posterior means of predicted common loon occupancy, winter.



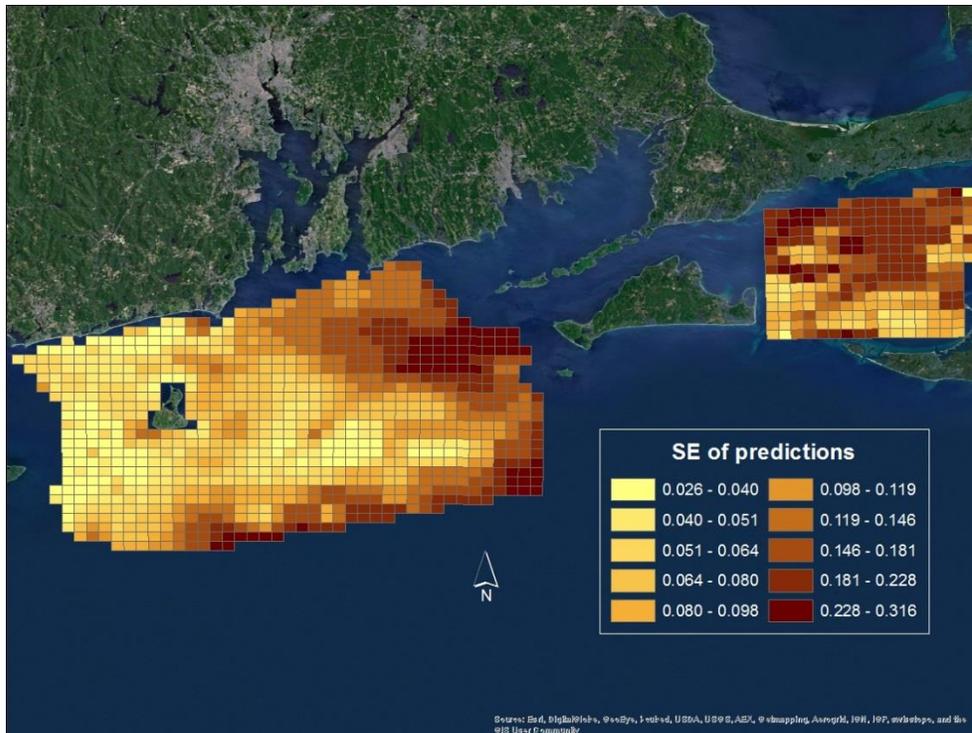
Sec. 2.16. Standard errors of predicted common loon occupancy, winter.



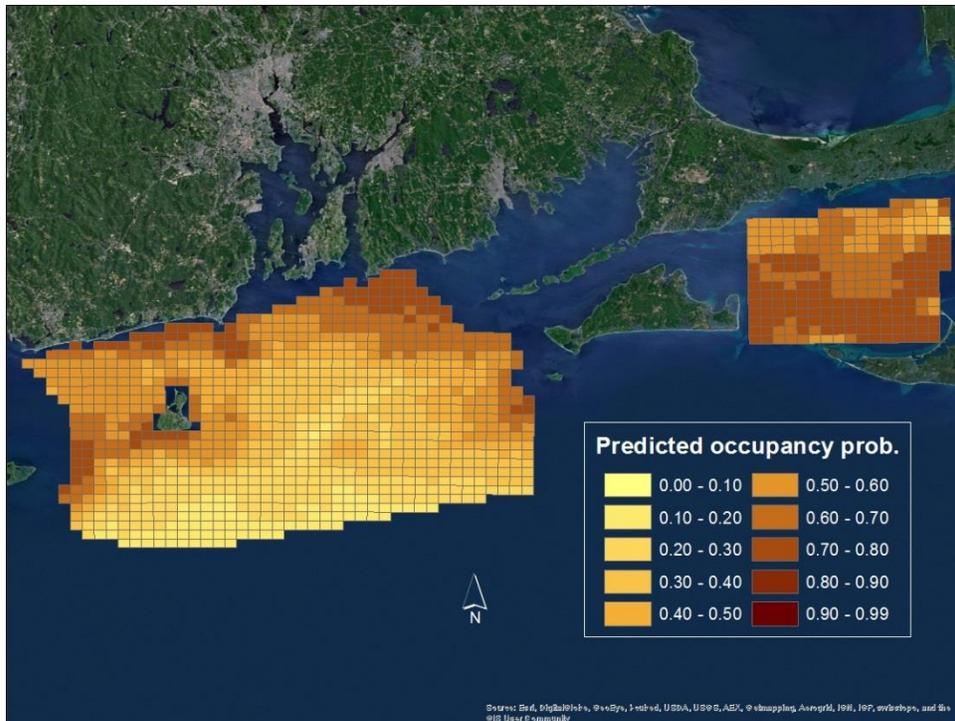
Sec. 2.17. Posterior means of predicted northern gannet occupancy, winter.



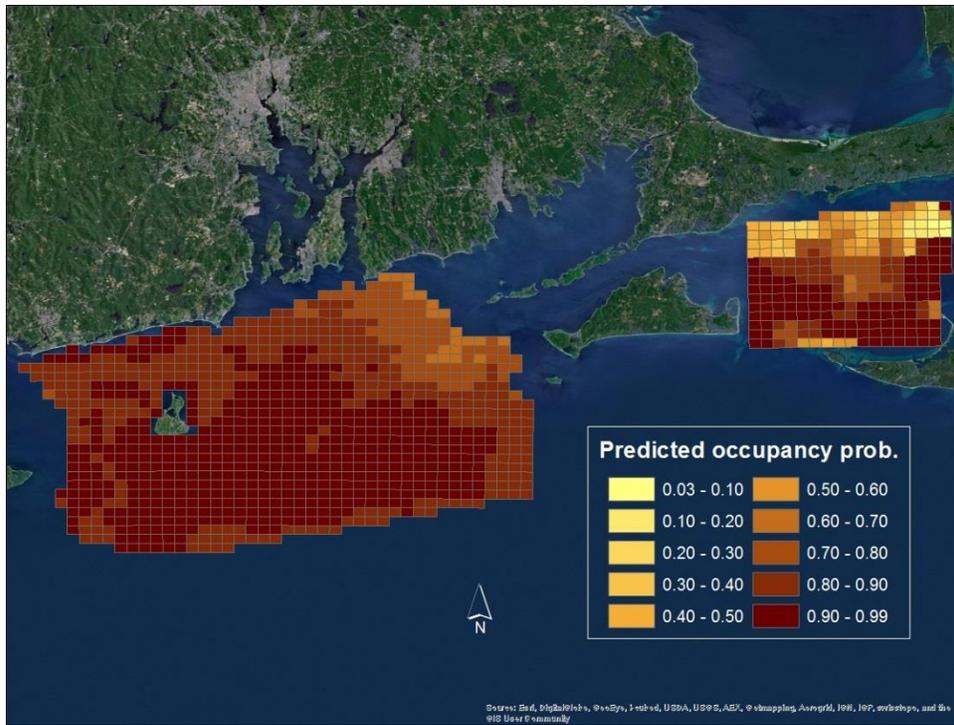
Sec. 2.18. Standard errors of predicted northern gannet occupancy, winter.



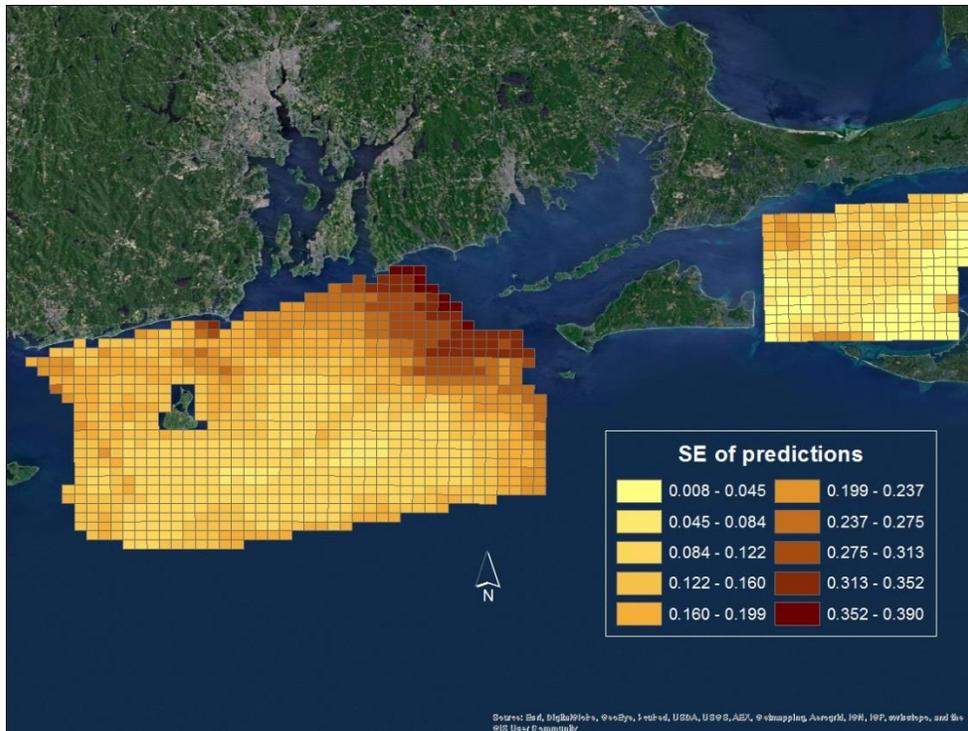
Sec. 2.19. Posterior means of predicted great cormorant occupancy, winter.



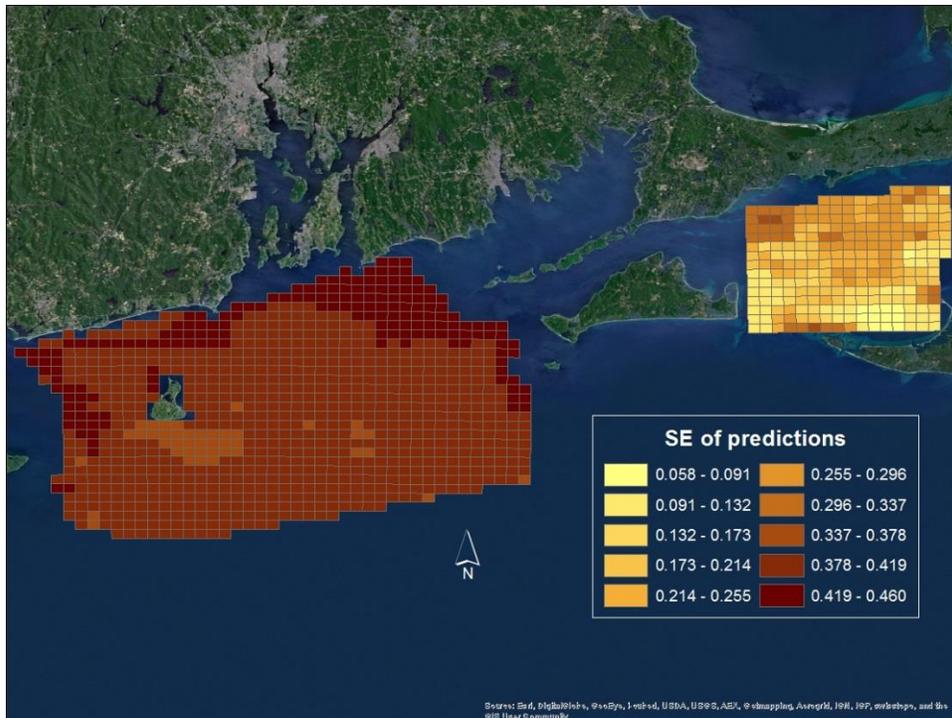
Sec. 2.21. Posterior means of predicted black-legged kittiwake occupancy, winter.



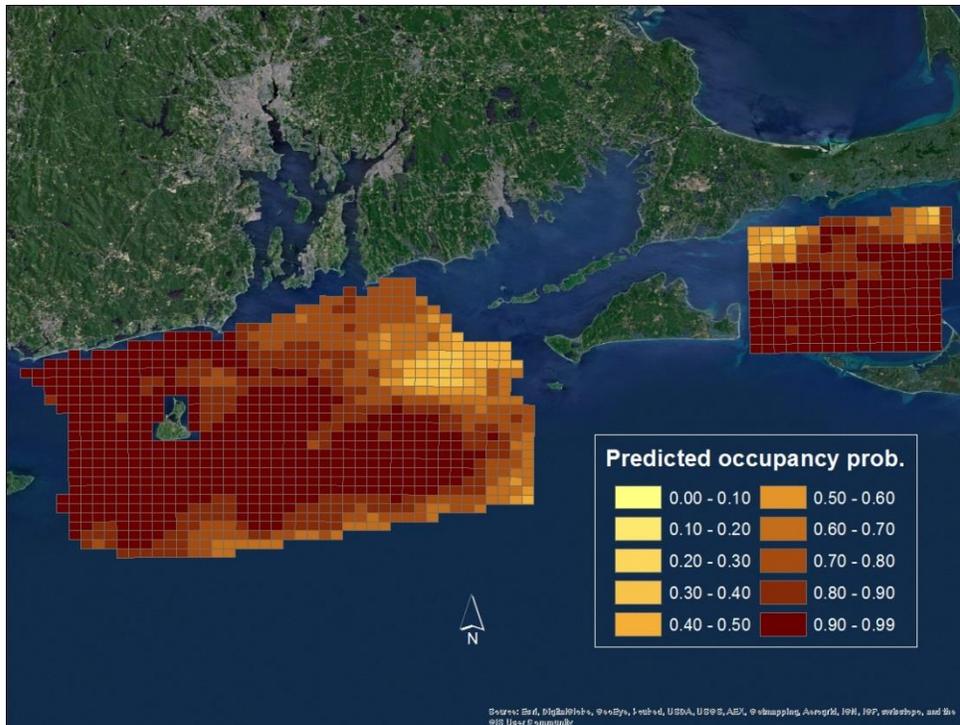
Sec. 2.22. Standard errors of predicted black-legged kittiwake occupancy, winter.



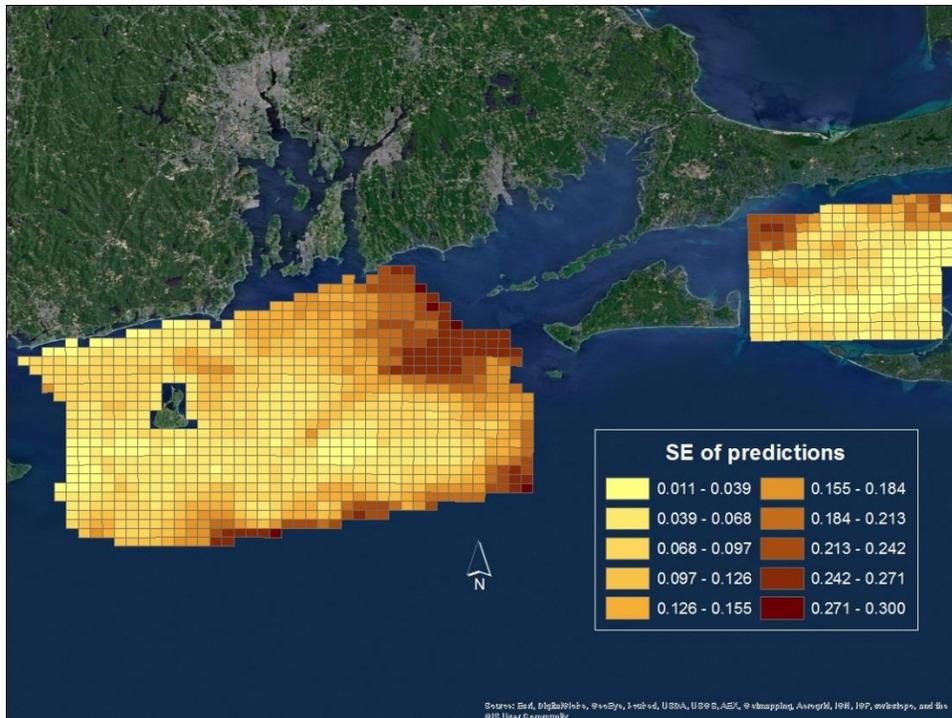
Sec. 2.24. Standard errors of predicted bonaparte's gull occupancy, winter.



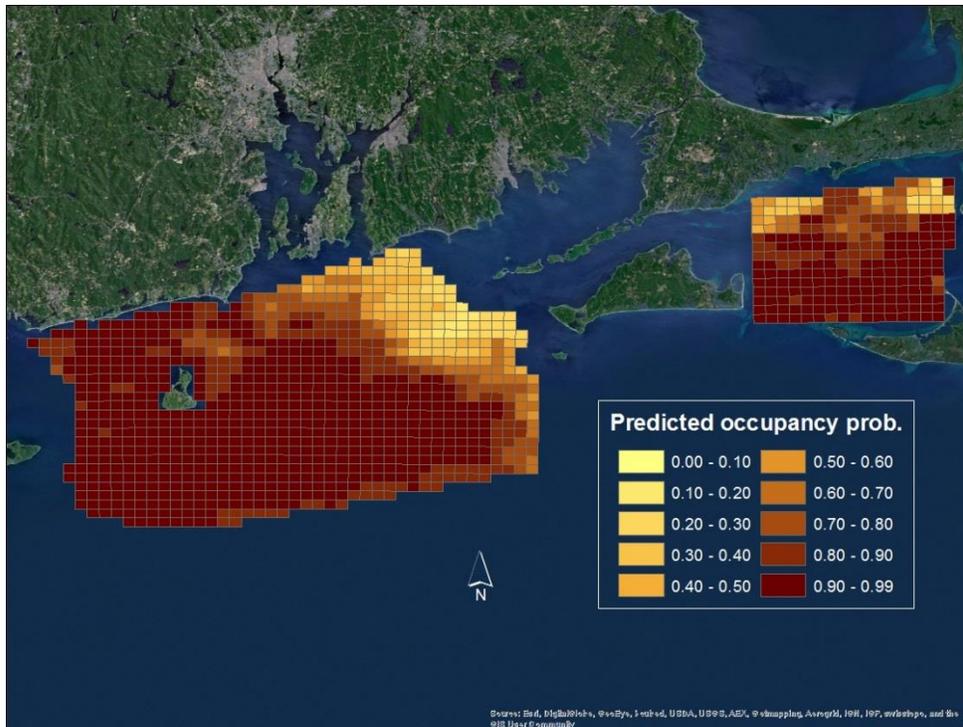
Sec. 2.25. Posterior means of predicted herring gull occupancy, winter.



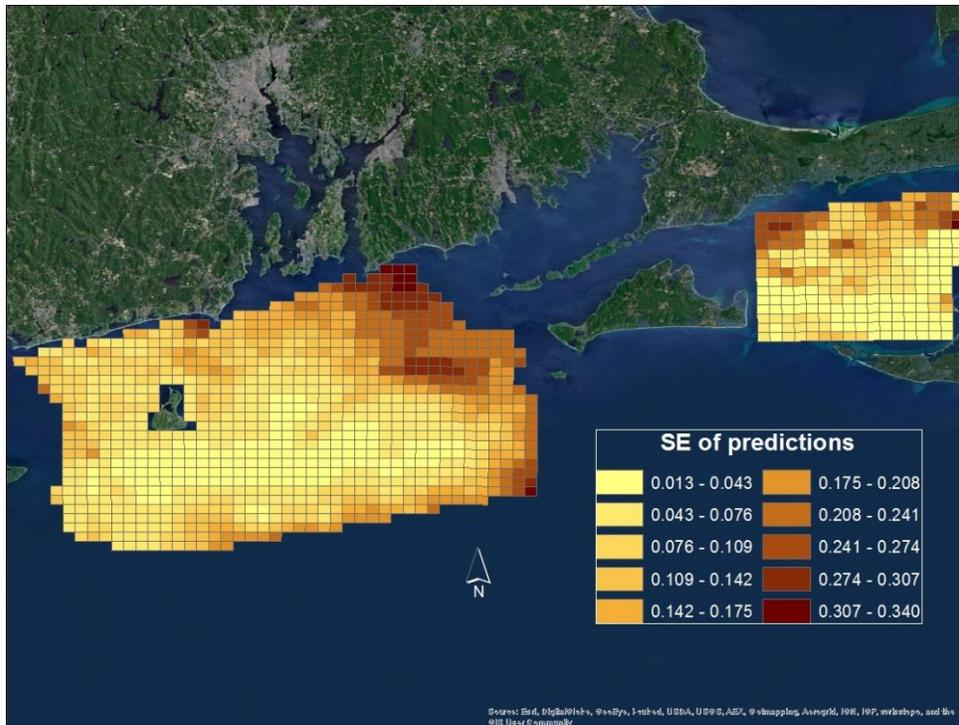
Sec. 2.26. Standard errors of predicted herring gull occupancy, winter.



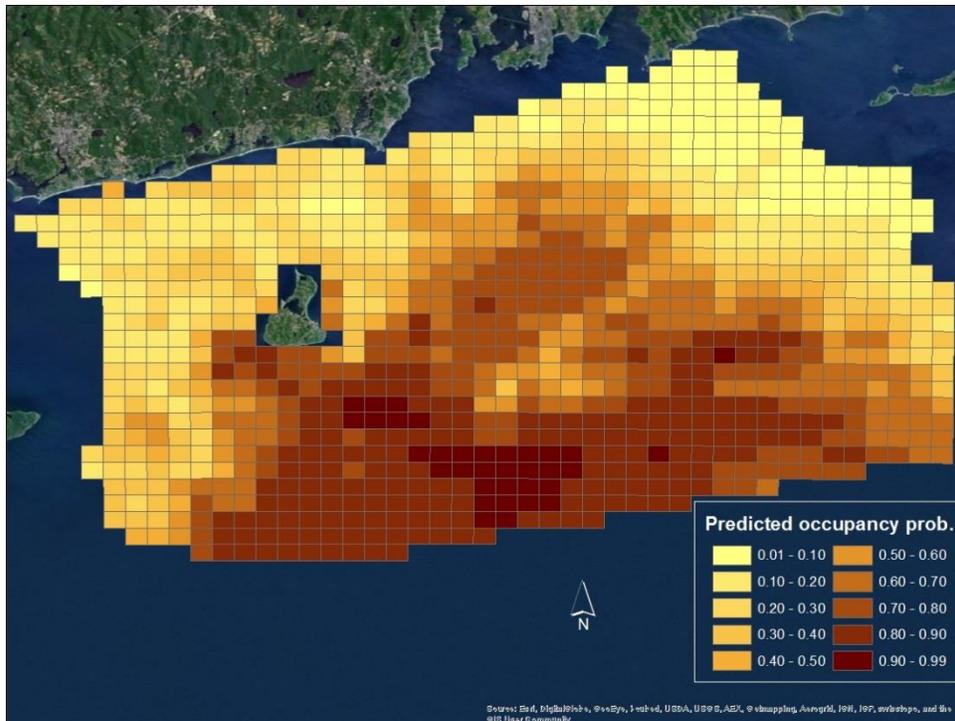
Sec. 2.27. Posterior means of predicted great black-backed gull occupancy, winter.



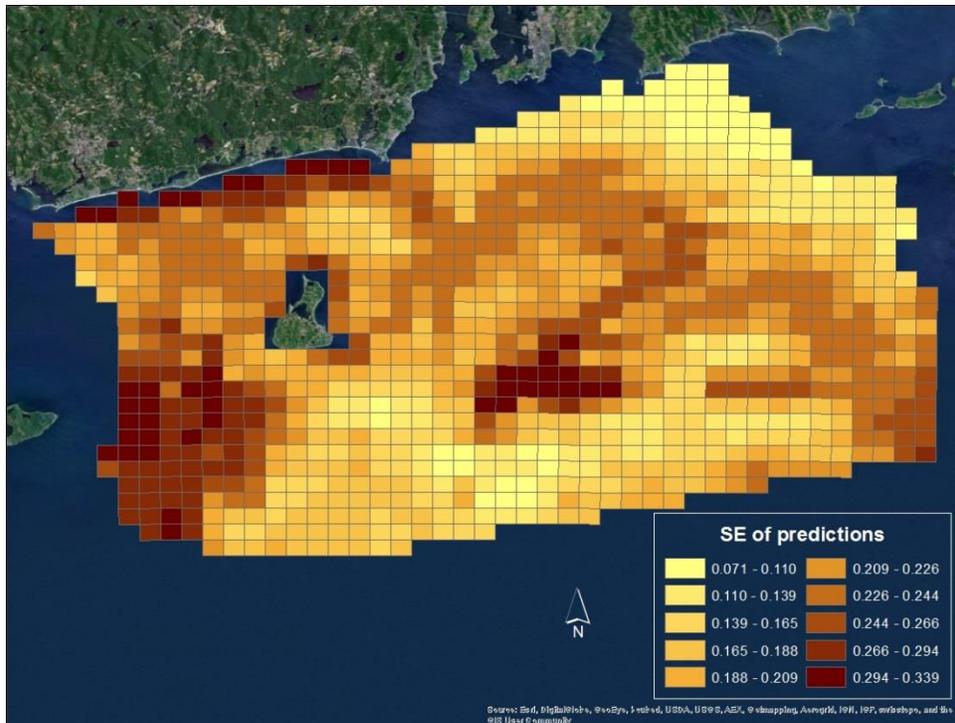
Sec. 2.28. Standard errors of predicted great black-backed gull occupancy, winter.



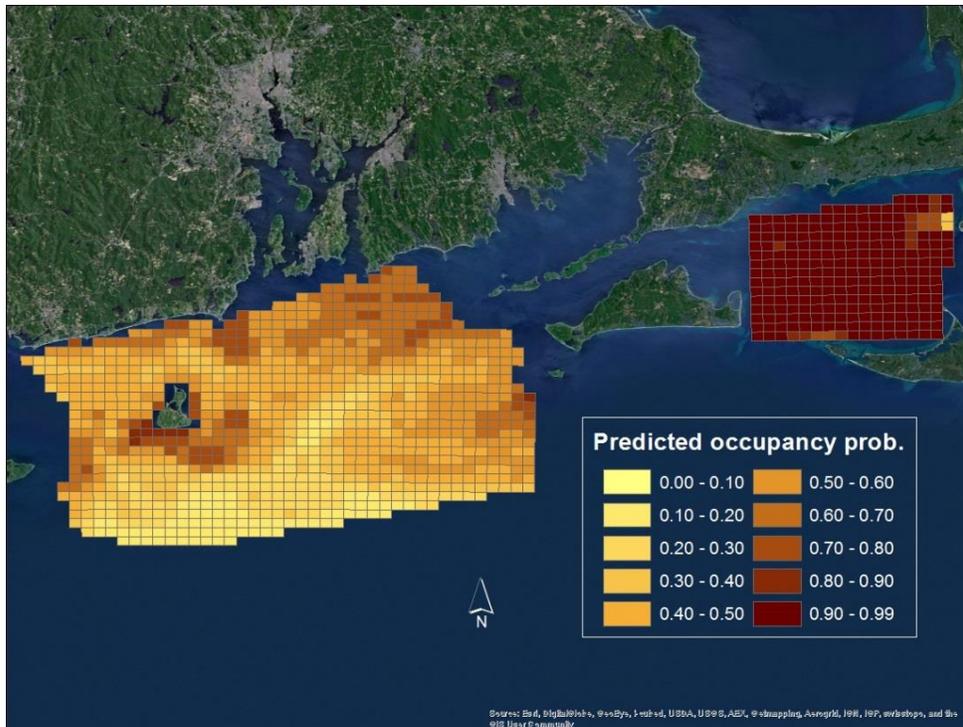
Sec. 2.29. Posterior means of predicted dovekie occupancy, winter.



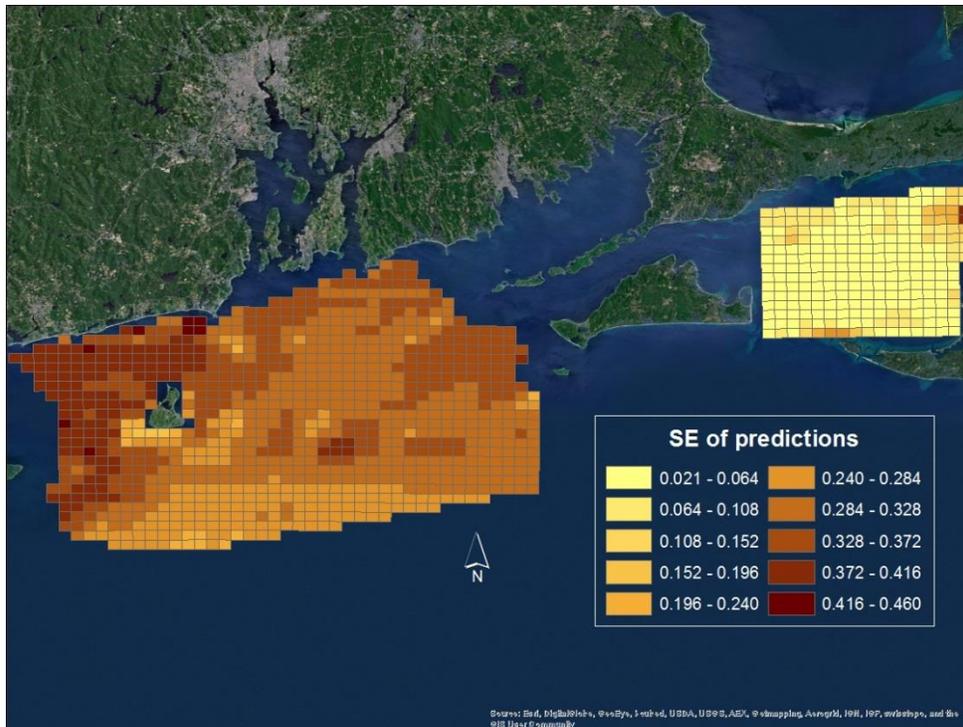
Sec. 2.30. Standard errors of predicted dovekie occupancy, winter.



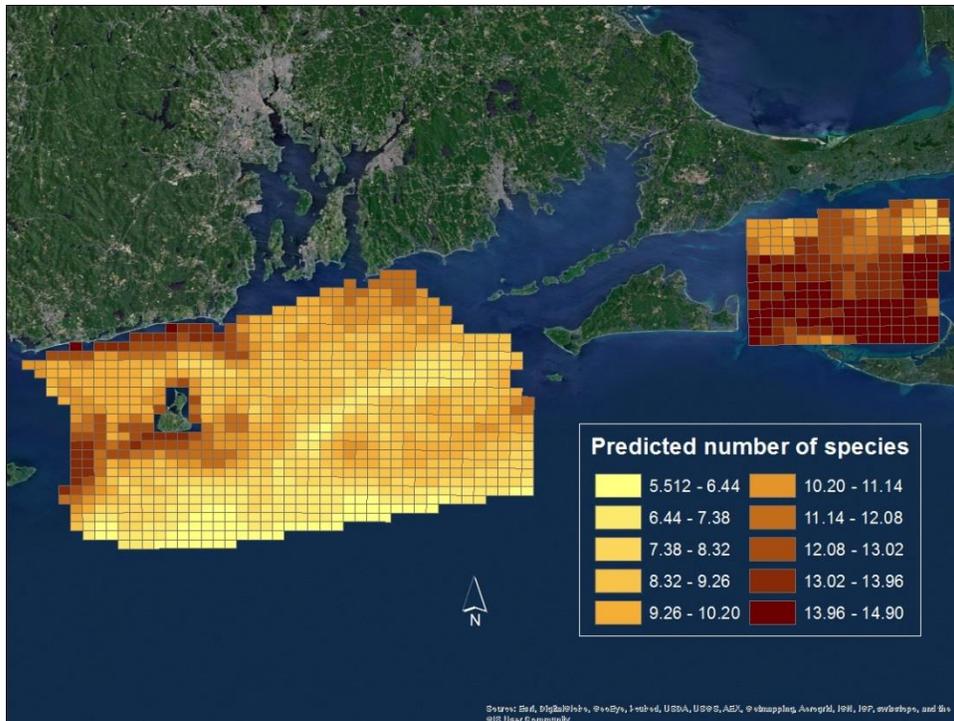
Sec. 2.31. Posterior means of predicted razorbill occupancy, winter.



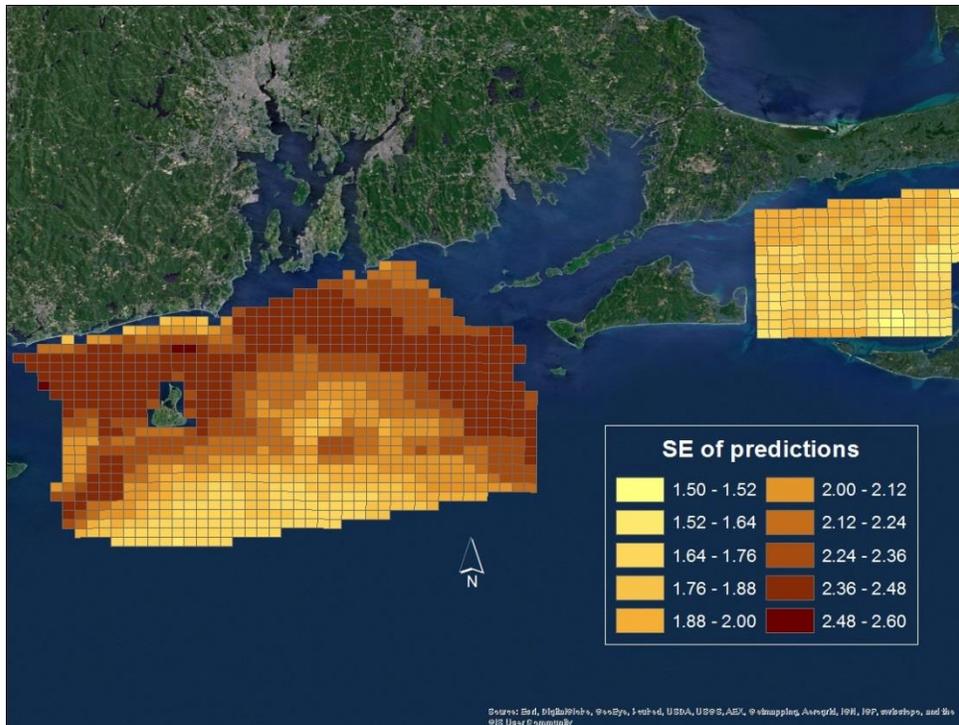
Sec. 2.32. Standard errors of predicted razorbill occupancy, winter.



Sec. 3.1. Posterior means of the predicted number of species in the observed communities, winter.



Sec. 3.2. Standard errors of the predicted number of species in the observed communities, winter.



USING DYNAMIC OCCUPANCY MODELS TO INVESTIGATE INTER-ANNUAL SHIFTS IN SEABIRD DISTRIBUTIONS IN SOUTHERN NEW ENGLAND

ABSTRACT

Inter-annual variation must be taken into account when studying seabird distributions, with important areas, or “hotspots,” for diving species expected to be more persistent across time than those for surface-feeding species. We avoided confounding seabird distribution dynamics with changes in year-specific detection rates by analyzing a three-year winter-season aerial seabird survey dataset from southern New England using dynamic occupancy models. We allowed for spatial variation in probabilities of site-occupancy, extinction, and colonization using the environmental covariates bathymetry, sea surface temperature, and chlorophyll *a* surface concentration. We allowed detection probability to vary by year and as a function of survey date. Across eleven modeled species we saw high variation in the degree to which predicted hotspot locations shifted between years. Loons (*Gavia* spp.) and sea ducks (Tribe Mergini), with the exception of common eider (*Somateria mollissima*), showed relatively stable distributions across years. Other diving species and all three surface-feeding species showed substantial inter-annual shifts in their distributions. Four species showed significant differences between year-specific detection probability intercept estimates, suggesting that in some cases failing to account for imperfect detection will lead to biased results in studies examining the temporal stability of seabird hotspot locations.

INTRODUCTION

Given the dynamic nature of seabird habitat (Louzao et al. 2006, 2009; Kinlan et al. 2012) it is important to consider inter-annual variability when investigating seabird distributions. The distribution of foraging seabirds is a result of individual habitat selection choices made in a manner that maximizes predatory efficiency (Kirk et al. 2008, Stephens 1986). Thus, the distribution of wintering seabirds in the northwestern Atlantic Ocean is largely dictated by the availability of prey. Prey of sea ducks and other seabirds that forage by diving to considerable depths below the ocean surface are often sessile with distributions tied to bathymetry (Guillemette et al. 1993, Schneider 1997, Bost et al. 2009, Kinlan et al. 2012). Prey of surface-feeding species (Flanders et al. in review) often have distributions associated with more ephemeral features (Hyrenbach et al. 2000). Thus, we expected less inter-annual variation in distributions of diving species than those of surface-feeding species (Louzao et al. 2006, Zipkin et al. 2010, Silverman et al. 2013).

The spatial scale of studies is a crucial parameter to consider when interpreting predicted dynamics in seabird distributions (Ballance et al. 2006, Weimerskirch 2007). At the broad scales used for planning marine protected areas (MPAs), important areas for seabirds, or “hotspots,” appear to be related to bathymetry and relatively persistent across time (Hyrenbach et al. 2000, Nur et al. 2011, Zipkin et al. 2010, Silverman et al. 2013). Information on the persistence of hotspots in the northwestern Atlantic Ocean is needed at finer spatial scales to reflect the resolution at which offshore planning decisions are made (Kinlan et al. 2012). We expected that at these finer spatial scales, inter-annual shifts in surface-feeding species’ distributions would become apparent.

Most published studies on inter-annual variation in seabird distributions fail to account for imperfect detection. In these cases, estimated dynamics can be confounded with changes in detection rates between years caused by variation in species’ behavior and abundance, human

observers' skill level, or logistical details of surveys (MacKenzie et al. 2003, Ruiz-Gutiérrez et al. 2010). Occupancy modeling is a method used to account for imperfect detection when strip-transect seabird surveys include both spatial and temporal replication (Flanders et al. in review). Dynamic occupancy models extend analyses to data from multiple years collected under a robust design (Pollock 1982, MacKenzie et al. 2003). These models estimate initial occupancy rates as well as probabilities of site colonization and extinction, all of which can be allowed to vary spatially using covariates (MacKenzie et al. 2003). By formally accounting for detection, researchers can provide accurate, easily-interpretable information on seabird distribution dynamics.

Here, we applied dynamic occupancy models to estimate seabird distributions in three consecutive winter seasons across a study site in the northwestern Atlantic Ocean. We accounted for imperfect detection and made predictions at spatial scales relevant to offshore planning. Our results should provide information on species-specific inter-annual variation in distribution that is easily interpreted by decision-makers evaluating the long-term stability of predicted seabird hotspots.

METHODS

Study site

Our study site located in Massachusetts, USA was approximately 1870 km² and included much of the Nantucket Sound (Fig. 1). Nantucket Sound is a relatively shallow offshore area bordered to the north by Cape Cod and to the south by Nantucket and Martha's Vineyard. Huettmann & Diamond (2000) describe the Cape Cod area as providing important foraging habitat for wintering northern gannet (*Morus bassanus*), herring gull (*Larus argentatus*), and great black-backed gull (*Larus marinus*) populations. This region is also globally important for wintering sea ducks (Tribe Mergini; Silverman et al. 2013), a guild of conservation concern (Zipkin et al. 2010).

Aerial strip-transect surveys

The Massachusetts Audubon Society collected data using aerial surveys flown at an altitude of 152 m over 15 transect lines within Nantucket Sound (Fig. 1). For details on data collection protocols see Flanders et al. (in review). The survey data selected for this analysis came from the winter 2003-2004, winter 2004-2005, and winter 2005-2006 seasons, with the winter season defined as the months of December-February. We chose only the winter season in each year as closure-related assumptions of occupancy models were expected to be more easily satisfied than in spring or fall and summer data were scarce and likely affected by breeding colony locations. Most segments had within-season temporal replication in all three years, with a maximum number of 9 surveys at a segment in winter 2003-2004, 6 in winter 2004-2005, and 3 in winter 2005-2006.

Environmental covariates

Monthly composites of winter sea surface temperature (SST) and winter chlorophyll *a* surface (chl *a*) concentration values collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite were retrieved at a 4 km x 4 km grid cell resolution using Marine Geospatial Ecology Tools (Roberts et al. 2010) and averaged across each winter season to make three single-season raster grids. We acquired a 1/3 arc-second resolution bathymetry digital elevation model (DEM) of Nantucket Sound from the National Oceanic and Atmospheric Administration (NOAA; Eakins et al. 2009). These grids were overlaid spatially with the transect segments and weighted average covariate values for each segment (Zipkin et al. 2010) were obtained using Spatial Analyst Tools in ArcMap10 (ESRI 2011; Appendix Sec. 1). The segment-level covariate values were standardized by subtracting from the mean and dividing by the standard deviation (Appendix Sec. 1).

Dynamic occupancy model

We exploited the temporal and spatial replication inherent to the Nantucket Sound survey design and analyzed the data with single-species dynamic occupancy models (MacKenzie et al. 2003). We assumed that each segment was either occupied or not by a given species over the course of each winter season. The latent state z_{it} represents this process, as $z_{it} = 1$ if segment i is occupied during season t and $z_{it} = 0$ if segment i is not occupied during season t (MacKenzie et al. 2002, MacKenzie et al. 2006). These binary latent states were modeled as Bernoulli random variables with success probability Ψ_t , which represents the occupancy probability during season t . In our sub-model for initial occupancy we used a logit link to model Ψ_1 , species-specific initial occupancy, as a function of bathymetry and seasonal averages of both SST and chl a concentration (MacKenzie et al. 2003, MacKenzie et al. 2006) such that

$$\text{logit}(\Psi_{i1}) = \alpha_{psi} + \beta_1 \text{bathymetry}_i + \beta_2 \text{SST}_{i1} + \beta_3 \text{chla}_{i1}$$

where α_{psi} is the species-specific intercept.

Dynamic occupancy models allow the occupancy state to change between seasons such that segments unoccupied at time t could become colonized at time $t + 1$ with probability γ and segments occupied at time t could go extinct at time $t + 1$ with probability ϵ (MacKenzie et al. 2003). We allowed for spatial variation in extinction and colonization probabilities using a logit link and covariates that varied by year (MacKenzie et al. 2003, MacKenzie et al. 2006). In our sub-model for extinction probability we modeled ϵ as a function of segment-level averages of SST and chl a such that

$$\text{logit}(\epsilon_{it}) = \alpha_\epsilon + \beta_4 \text{SST}_{i,t+1} + \beta_5 \text{chla}_{i,t+1}$$

where α_ϵ is the species-specific intercept. Our sub-model for species-specific colonization probability had identical structure to extinction with coefficients for SST and chl a concentration. We chose the variables bathymetry, SST, and chl a concentration as covariates as they are readily available at adequate spatial and temporal scales and are known to be important predictors of seabird distributions (Ballance et al. 2006, Nur et al. 2011, Kinlan et al. 2012). We did not include bathymetry as a covariate on colonization and extinction probabilities as it made more intuitive sense to model these processes as functions of the temporally dynamic covariates SST and chl a concentration.

Dynamic occupancy models assume an imperfect observation process (MacKenzie et al. 2002, 2006). Specifically, $y_{ijt}|z_{it} \sim \text{Bern}(p_{ijt} * z_{it})$; thus, when $z_{it} = 0$ the probability of a detection is 0 and when $z_{it} = 1$ the probability of a detection is p_{ijt} . We allowed p to vary by year and as a function of date and observer effort (MacKenzie et al. 2003). We included both linear and quadratic effects of date on p , as we expected a temporal trend in detection probability across a survey season due to intra-seasonal changes in abundance (Kendall 1999, MacKenzie et al. 2003, Royle & Nichols 2003, Zipkin et al. 2009, Gardner et al. 2011). The lengths of the Nantucket Sound survey flight tracks through a given segment showed significant variation, so we modeled p as a function of survey length such that

$$\text{logit}(p_{ijt}) = \text{pint}_t + \alpha_1 \text{date}_{ijt} + \alpha_2 \text{date}_{ijt}^2 + \alpha_3 \text{length}_{ijt}$$

where pint_t is the species and season-specific intercept.

We adopted a different interpretation of the occupancy parameter to allow for more flexibility in meeting the closure assumption of occupancy models. 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). For more details on this interpretation see Flanders et al. (in review).

Implementation and model selection

All dynamic occupancy models were fitted using the R package “unmarked” (Fiske & Chandler 2011). For species with more than fifty detections in at least one winter season (Appendix Sec. 1), we ran the global model described above and then an additional 127 nested models with all possible combinations of covariates on initial occupancy, colonization, and extinction probabilities. We fitted only nine models for species with between thirty and fifty detections in at least one winter season (Appendix Sec. 1). In all cases, we included the global detection probability models as we expected both survey length and survey date to be important predictors of detection for many species (Flanders et al. in review). Convergent models were ranked by Akaike’s Information Criterion (AIC) and parameter estimates were averaged based on models within two delta AIC of the best model (Burnham & Anderson 2002). We used the R package “AICcmodavg” to obtain model-averaged point estimates and standard errors of the parameters (Mazerolle 2013).

Making predictions

We used a grid with 2 km x 2 km cell size resolution for spatial predictions of occupancy probability in winter 2003-2004, winter 2004-2005, and winter 2005-2006 for each modeled species. 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 standardized with the original covariate means and standard deviations used in the analysis. We then used model-averaged estimates and the standardized covariate values to obtain predictions and standard errors of initial occupancy probability for each grid cell. We followed the same procedure to obtain model-averaged predictions of colonization and extinction probabilities at each grid cell for the two open

periods of winter 2003-2004 to winter 2004-2005 and winter 2004-2005 to winter 2005-2006.

Predicted occupancy for winter 2004-2005 and winter 2005-2006 was then derived at each grid cell using predicted initial occupancy, colonization, and extinction probabilities as described in MacKenzie et al. 2003.

RESULTS

Ten species had a sufficient number of winter season detections allowing us to run the complete dynamic model set of 128 models (Appendix Sec. 1). We fitted only 9 models for red-throated loon *Gavia stellata* due to a lower number of detections. Brant (*Branta bernicla*), black scoter (*Melanitta americana*), red-breasted merganser (*Mergus serrator*), red-necked grebe (*Podiceps grisegena*), great cormorant (*Phalacrocorax carbo*), and bonaparte's gull (*Chroicocephalus philadelphia*) had too few detections to allow any modeling. The number of models that converged for each species was highly variable and complete model selection results for each species are in Appendix Sec. 2.

The average of ocean depth values from the study site was 11.56 meters (m) below mean high water (Appendix Sec. 1). The average of SST values from the study site was 3.75 degrees Celsius and the average of chl *a* concentration values from the study site was 4.25 mg m⁻³. From winter 2003-2004 to winter 2005-2006 seasonal SST values in the study site increased on average; seasonal winter chl *a* concentration values in the study plot decreased and then increased again on average over the three years (Appendix Sec. 1).

We found significantly negative model-averaged estimates of the effect of bathymetry on initial occupancy for common loon (*Gavia immer*), surf scoter (*Melanitta perspicillata*), and red-throated loon (Table 1). Model-averaged estimates of the effect of SST on initial occupancy were significantly negative for white-winged scoter (*Melanitta fusca*) and significantly positive for herring gull, and model-averaged estimates of the effect of chl-A on initial occupancy were significantly negative for

black-legged kittiwake (*Rissa tridactyla*) and significantly positive for surf scoter. Model-averaged estimates of the effect of SST on extinction were significantly positive for razorbill (*Alca torda*) and significantly negative for herring gull, and model-averaged estimates of the effect of chl *a* on extinction were significantly negative for northern gannet and significantly positive for herring gull. We did not find significant model-averaged estimates of the effects of either SST or chl *a* on colonization for any of the modeled species.

Two species, long-tailed duck (*Clangula hyemalis*) and white-winged scoter, showed little change in their predicted distributions across years (Fig. 2, Appendix Sec. 2). Other species showed dynamics that were relatively constant across the study plot, leaving the spatial configuration of high and low rates of predicted occupancy intact. Common loon, red-throated loon, and surf scoter were three such species that showed overall declines in predicted occupancy across years without significant spatial variation in extinction rate (Fig. 2, Appendix Sec. 2).

All species with significant model-averaged estimates of relationships between covariates and extinction rate showed noticeable spatial variation in predicted occupancy dynamics. The general increase in predicted herring gull and black-legged kittiwake occupancy observed across the study plot showed such spatial variation (Fig. 2, Appendix Sec. 2). Similarly, changes in predicted occupancy of common eider (*Somateria mollissima*), razorbill, and great black-backed gull showed spatial variation, but for these species a general decrease in predicted occupancy across the study plot was observed (Appendix Sec. 2). Larger changes were observed for northern gannet, with noticeable increases and decreases in predicted occupancy at varying intensities across the study plot.

Four species that showed this third pattern of occupancy dynamics also experienced notable shifts in the locations of areas of high predicted occupancy across the three years. Two gull species, black-

legged kittiwake and herring gull, had predicted distributions in winter 2003-2004 that included distinct areas of high occupancy in southwestern and eastern portions of the study plot, which disappeared in subsequent winters, as predicted occupancy became uniformly high across the study plot (Fig. 2). An area of relatively low predicted black-legged kittiwake occupancy did remain across years in the northeastern portion of the study plot. Areas of low predicted common eider occupancy in winter 2003-2004 located in southwestern and eastern portions of the study plot were not present in winter 2004-2005, with an additional area of low predicted occupancy in the northwestern corner of the study plot appearing in winter 2005-2006. Finally, areas of low predicted northern gannet occupancy in winter 2003-2004 located in the eastern portion of the study plot became areas of high predicted occupancy in subsequent winters.

Most species showed noticeable variation in detection probability among years (Appendix Sec. 2), with significantly different year-specific intercept estimates for four species (Fig. 3). For both razorbill and common eider, estimates of winter 2003-2004 intercepts were lower than in winter 2005-2006. The winter 2003-2004 intercept estimate for long-tailed duck was lower than both winter 2004-2005 and winter 2005-2006 estimates, while the winter 2003-2004 intercept estimate for surf scoter was higher than the 2004-2005 estimate for this species.

DISCUSSION

Many diving species (Flanders et al. in review), especially sea ducks, associate with benthic features where they consume relatively sessile prey (Guillemette et al. 1993, Winiarski et al. 2013), leading us to expect small changes in the location of predicted hotspots for this group (Zipkin et al. 2010, Silverman et al. 2013). Even at the relatively fine spatial scale of our study, this expectation matched our results for five diving species with common eider, razorbill, and northern gannet as notable exceptions. Persistent areas of high predicted occupancy for common loon and surf scoter

were concentrated in the north of the study plot, while such areas for red-throated loon were concentrated in the east. Predicted occupancy of long-tailed duck and white-winged scoter was persistently high across the study plot, with an area of lower predicted white-winged scoter occupancy located in the eastern portion of the study plot each year.

Shifts in common eider distribution may be a result of year-to-year changes in foraging habitat suitability (Guillemette et al. 1993, 1996; Merkel et al. 2007). Some of these changes may be due to the heavy consumption of sessile prey by common eiders at one location over the course of a winter season leading to decreased prey density the following year. Mobile prey are more important in the diets of northern gannet and razorbill than most sea ducks, possibly explaining inter-annual variation in distributions of these diving species.

Prey of surface-feeding species are associated with more ephemeral features than prey of most diving species (Hyrenbach et al. 2000), explaining noticeable inter-annual shifts in surface-feeding species' distributions at the spatial resolution used here (Louzao et al. 2006). Investigations of surface-feeding species' distributions at much broader spatial scales would likely overlook these predicted dynamics. In contrast, inter-annual variation in the predicted winter distribution of northern gannet, a diving piscivore, was large enough to show up in studies conducted at a variety of spatial scales.

Species-specific relationships between initial occupancy rate and covariates match findings in Flanders et al. (in review). Bathymetry appears to be a more important predictor of diving species' initial occupancy rate than that of surface-feeding species, while either SST or chl a concentration appear to be important predictors for surface-feeding species. The significantly positive estimate of the relationship between razorbill extinction rate and SST suggests that wintering razorbills select areas with lower SST, behavior observed elsewhere in the northwestern Atlantic Ocean (Patteson

pers. comm.). The significantly negative estimate of the relationship between northern gannet extinction rate and chl *a* concentration suggests that wintering northern gannets select areas with higher chl *a* concentration. This pattern was expected as chl *a* concentration is believed to be positively correlated with prey density (Hyrenbach et al. 2002). Significant estimates of relationships between covariates and herring gull extinction rate are not as easily explained, and we caution that the relatively coarse spatial resolution of our covariate data decreases the biological interpretability of covariate relationship estimates.

Dynamic occupancy models appear to be an effective tool for examining the persistence of seabird distributions using aerial strip-transect survey data while accounting for imperfect detection. The assumptions required to apply occupancy models to seabird data discussed in Flanders et al. (in review) apply to the dynamic case here. For very widespread species, such as long-tailed ducks wintering in Nantucket Sound, dynamic occupancy models are not very useful. Other techniques are needed for such species to look for possible inter-annual shifts in density that are not evident in our modeling results. Dynamic multi-species occupancy models would be a useful extension to our methods, allowing inference on rare species' dynamics and possibly on temporal variation in hotspots of species diversity (Ruiz-Gutiérrez et al. 2010, Flanders et al. in review). We felt that data collected under a study design with more than three primary periods (Pollock 1982) would be more appropriate for analysis with these models.

We analyzed a multi-year seabird survey dataset using dynamic occupancy models to examine the permanence of seabird distributions in a study site in the northwestern Atlantic Ocean. Our results show a diversity of patterns in predicted inter-annual dynamics, with patterns for most species following expectations based on foraging guild. Four diving species showed significant differences between year-specific detection probability intercept estimates. Significant changes in detection

probability for these species was likely caused by variation in annual abundance or foraging behavior in the study area. By formally accounting for imperfect detection we avoided potential bias in our estimates of temporal variation in seabird distributions (MacKenzie et al. 2003, Ruiz-Gutiérrez et al. 2010).

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Table 1. Model-averaged estimates (SE) of species-specific relationships between bathymetry (bath), sea surface temperature (SST), and chlorophyll *a* surface concentration (chlA) and initial occupancy (psi), colonization (col), and extinction (ext). Bold indicates significant estimate; coefficients not estimated by any top model are represented with --.

	psi(bath)	psi(SST)	psi(chlA)	col(SST)	col(chlA)	ext(SST)	ext(chlA)
Black-legged kittiwake	-0.09(0.36)	.08(.3)	-1.77(.51)	-.7(.61)	.36(.75)	-.85(.87)	.44(.5)
Common eider	-.21(.28)	-.38(.29)	.27(.31)	-.39(1.05)	-.61(.39)	-.19(.25)	.07(.17)
Common loon	-.89(.41)	-.4(.51)	.9(.55)	-7.02(9.33)	1.34(1.88)	-2.23(4.02)	-.31(2.45)
Long-tailed duck	-.83(.5)	.99(.52)	.25(.57)	-1.65(1.94)	1.18(1.17)	.59(.39)	-.02(.37)
Northern gannet	2.37(2.03)	-3.03(2.3)	-4.29(2.93)	1.31(0.79)	--	.62(.78)	-.95(.43)
Razorbill	-.38(.58)	-.37(.42)	-1.03(.63)	--	-.22(.92)	1.29(.6)	.59(.77)
Surf scoter	-.86(.26)	-.08(.36)	.79(.28)	-1.05(1.14)	.55(.79)	.27(.49)	-.09(.3)
White-winged scoter	.07(.48)	-1.7(.67)	--	--	-.42(1.06)	.96(1.87)	5.26(4.49)
Herring gull	.15(.32)	1.19(.34)	--	--	--	-2.49(1.03)	1.51(.66)
Great black-backed gull	.45(.98)	--	-3.9(2.03)	--	--	.42(.64)	-.16(1.55)
Red-throated loon	-2.3(1.12)	1.27(.65)	-.03(.39)	--	--	--	--

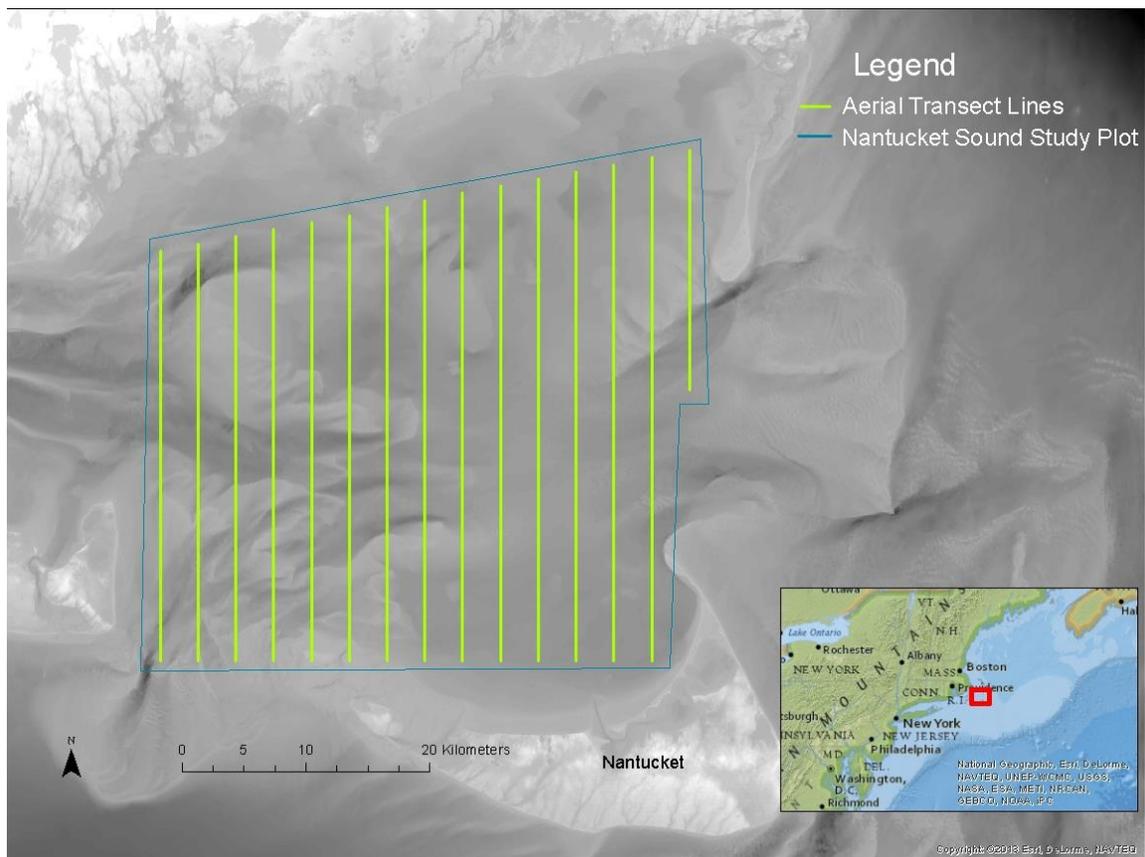


Figure 1. Map of Nantucket Sound study plot, aerial survey transect lines, and bathymetry raster.

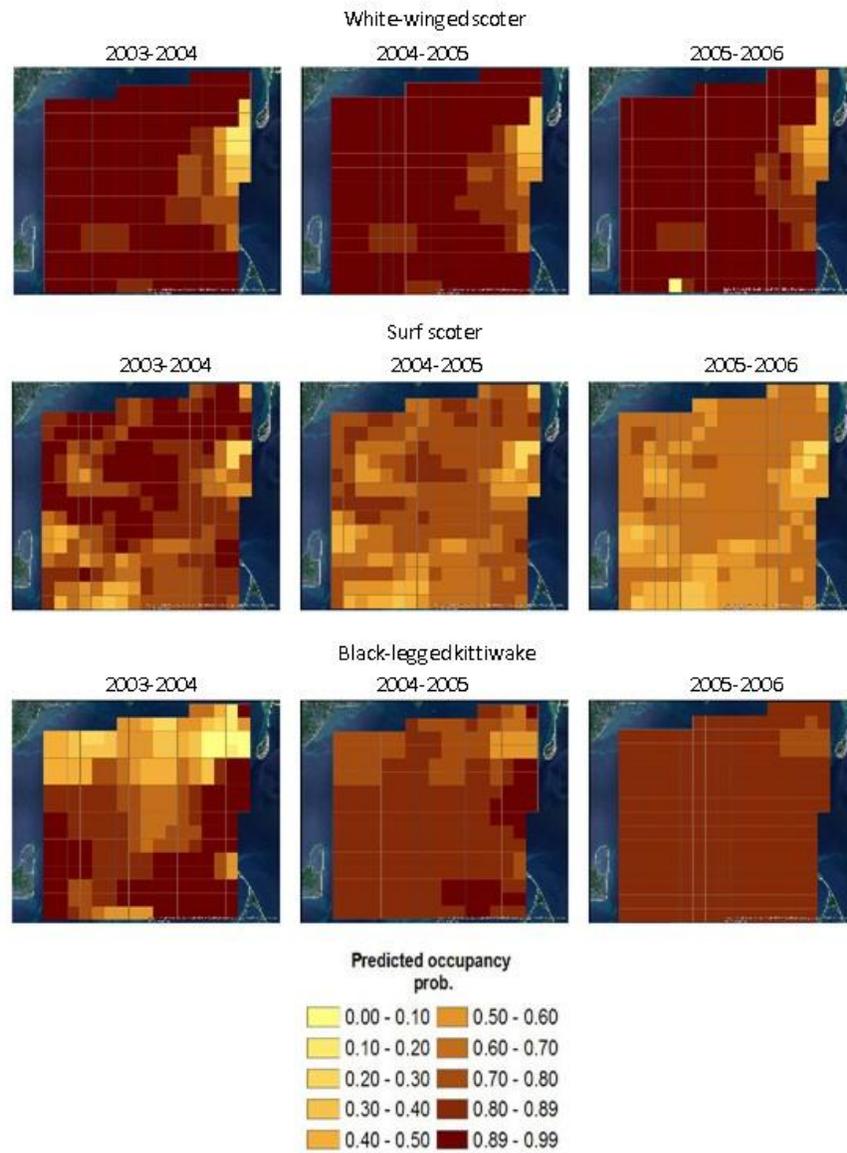


Figure 2. Predicted occupancy probabilities of white-winged scoter, surf scoter, and black-legged kittiwake across Nantucket Sound study plot in winter 2003-2004, winter 2004-2005, and winter 2005-2006.

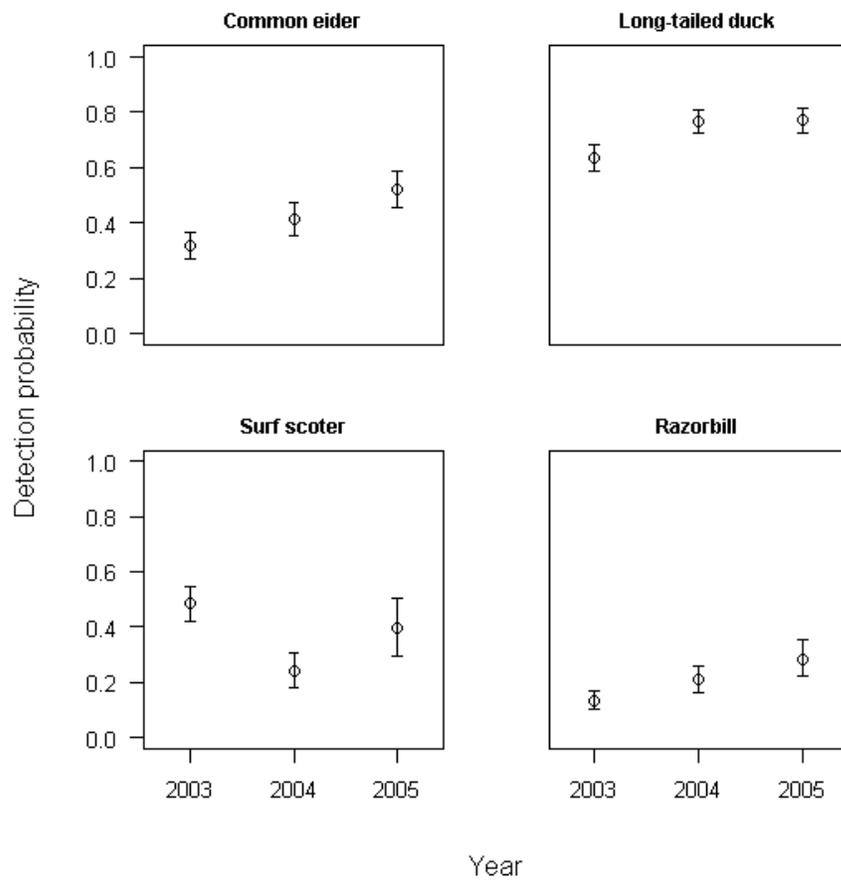


Figure 3. Year-specific detection probability intercept estimates for common eider, long-tailed duck, surf scoter, and razorbill in winter 2003-2004, winter 2004-2005, and winter 2005-2006.

APPENDIX

SECTION 1. DESCRIPTIVE INFORMATION.

This section contains means and ranges of covariate values used in the modeling, the number of detections of modeled species, and the classification of modeled species into two foraging guilds.

Table 1. Overall means and ranges of covariate values used in dynamic occupancy models for Nantucket Sound seabird dataset. Bathymetry in meters below mean high water, sea surface temperature (SST) in degrees Celsius, and chlorophyll *a* surface concentration (chl-A) in mg m⁻³.

	Mean (SD)	Range
Bathymetry	-11.56 (3.26)	(-19.32, -0.92)
SST	3.75 (0.51)	(2.66, 5.86)
chl-A	4.25 (0.74)	(2.73, 7.44)

Table 2. Season-specific means and ranges of dynamic covariate values used in modeling for Nantucket Sound seabird dataset. Sea surface temperature (SST) in degrees Celsius and chlorophyll *a* surface concentration (chl-A) in mg m⁻³.

	winter 2003-2004		winter 2004-2005		winter 2005-2006	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
SST	3.28 (.23)	(2.66,4.12)	3.68 (.36)	(3.24,5.25)	4.30 (.25)	(4.00,5.86)
chl-A	4.89 (0.58)	(3.57,7.44)	3.66 (.50)	(2.73,4.99)	4.20 (.53)	(3.05,6.16)

Table 3. Modeled species and number of detections at the segment level.

Species	Number of detections		
	winter 2003-2004	winter 2004-2005	winter 2005-2006
common eider (<i>Somateria mollissima</i>)	463	363	256
surf scoter (<i>Melanitta perspicillata</i>)	365	99	77
white-winged scoter (<i>Melanitta fusca</i>)	146	70	22
long-tailed duck (<i>Clangula hyemalis</i>)	779	692	391
red-throated loon (<i>Gavia stellata</i>)	38	18	20
common loon (<i>Gavia immer</i>)	57	47	22
northern gannet (<i>Morus bassanus</i>)	51	57	16
black-legged kittiwake (<i>Rissa tridactyla</i>)	147	110	63
herring gull (<i>Larus argentatus</i>)	183	181	80
great black-backed gull (<i>Larus marinus</i>)	93	98	19
razorbill (<i>Alca torda</i>)	179	198	136

Table 4. Classification of wintering seabird species into two groups based on foraging guild.

Diving species	Winter Surface-feeding species
common eider (<i>Somateria mollissima</i>)	black-legged kittiwake (<i>Rissa tridactyla</i>)
surf scoter (<i>Melanitta perspicillata</i>)	herring gull (<i>Larus argentatus</i>)
white-winged scoter (<i>Melanitta fusca</i>)	great black-backed gull (<i>Larus marinus</i>)
long-tailed duck (<i>Clangula hyemalis</i>)	
red-throated loon (<i>Gavia stellata</i>)	
common loon (<i>Gavia immer</i>)	
northern gannet (<i>Morus bassanus</i>)	
razorbill (<i>Alca torda</i>)	

SECTION 2. MODEL RESULTS.

This section contains model selection results for each species (Tables 1-11), maps of predicted initial occupancy, occupancy in winters 2004-2005 and 2005-2006, and standard errors of initial occupancy predictions for each species (Figures 1-11), and plots of year-specific detection probability intercept estimates for each species.

Table 1. Dynamic model selection results for common eider; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g = global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(.)gam(c)eps(.)p(g)	3763.91	0	0.045935
psi(s)gam(c)eps(.)p(g)	3764.05	0.140644	0.042816
psi(.)gam(.)eps(.)p(g)	3764.741	0.831078	0.030316
psi(s)gam(.)eps(.)p(g)	3764.911	1.000781	0.02785
psi(c)gam(c)eps(.)p(g)	3764.935	1.02534	0.02751
psi(b)gam(c)eps(.)p(g)	3765.287	1.377414	0.02307
psi(.)gam(c)eps(s)p(g)	3765.31	1.399829	0.022813
psi(s)gam(c)eps(s)p(g)	3765.467	1.557374	0.021084
psi(b+s)gam(c)eps(.)p(g)	3765.661	1.750807	0.019141
psi(s+c)gam(c)eps(.)p(g)	3765.661	1.750817	0.019141

Table 2. Dynamic model selection results for surf scoter; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(b+c)gam(.)eps(.)p(g)	2486.277	0	0.16317
psi(b+c)gam(s)eps(.)p(g)	2487.374	1.097654	0.094251
psi(b+c)gam(c)eps(.)p(g)	2487.728	1.451808	0.078956
psi(b+c)gam(.)eps(s)p(g)	2488.07	1.793474	0.066557
psi(b+c)gam(.)eps(c)p(g)	2488.195	1.9185	0.062523
psi(b+s+c)gam(.)eps(.)p(g)	2488.223	1.946119	0.061666
psi(b+c)gam(s)eps(s)p(g)	2489.238	2.961526	0.037115
psi(b+s+c)gam(s)eps(.)p(g)	2489.31	3.033585	0.035802
psi(b+c)gam(s)eps(c)p(g)	2489.315	3.038394	0.035716
psi(b+c)gam(s+c)eps(.)p(g)	2489.326	3.04943	0.035519

Table 3. Dynamic model selection results for white-winged scoter; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(s)gam(c)eps(c)p(g)	1612.786	0	0.394545
psi(s)gam(c)eps(s+c)p(g)	1614.497	1.710775	0.167728
psi(b+s)gam(c)eps(c)p(g)	1614.767	1.981005	0.14653
psi(s+c)gam(c)eps(s+c)p(g)	1616.206	3.419813	0.071366
psi(b+s)gam(c)eps(s+c)p(g)	1616.474	3.68781	0.062416
psi(c)gam(.)eps(s)p(g)	1617.996	5.209339	0.029168
psi(b+s+c)gam(c)eps(s+c)p(g)	1618.049	5.262729	0.028399
psi(c)gam(.)eps(.)p(g)	1618.481	5.694881	0.022881
psi(c)gam(.)eps(s+c)p(g)	1619.627	6.841201	0.012899
psi(b+c)gam(.)eps(s)p(g)	1619.918	7.131968	0.011153
psi(.)gam(.)eps(.)p(g)	1621.285	8.499098	0.00563

Table 4. Dynamic model selection results for long-tailed duck; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

model	AIC	delta	AICwt
psi(b+s)gam(.)eps(.)p(g)	3633.148	0	0.03949
psi(b+s)gam(c)eps(.)p(g)	3633.409	0.260825	0.034661
psi(s)gam(.)eps(.)p(g)	3633.511	0.362892	0.032937
psi(b+s)gam(.)eps(s)p(g)	3633.706	0.55794	0.029876
psi(b+s)gam(c)eps(s)p(g)	3633.887	0.7389	0.027292
psi(b+s)gam(s)eps(.)p(g)	3634.017	0.869353	0.025569
psi(s)gam(c)eps(.)p(g)	3634.092	0.9442	0.024629
psi(s)gam(.)eps(s)p(g)	3634.17	1.021699	0.023693
psi(b)gam(.)eps(.)p(g)	3634.38	1.231764	0.021331
psi(b+s)gam(s)eps(s)p(g)	3634.519	1.371475	0.019892
psi(.)gam(.)eps(.)p(g)	3635.035	1.887156	0.015371
psi(b+s+c)gam(s+c)eps(s+c)p(g)	3639.362	6.213804	0.001767

Table 5. Dynamic model selection results for red-throated loon; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(b+s+c)gam(.)eps(.)p(g)	682.1524	0	0.754011
psi(b)gam(.)eps(.)p(g)	685.1127	2.96032	0.171614
psi(.)gam(.)eps(.)p(g)	687.0603	4.907944	0.064808
psi(.)gam(s)eps(s)p(g)	690.8865	8.734114	0.009567

Table 6. Dynamic model selection results for common loon; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(b+s+c)gam(s)eps(s)p(g)	1041.24	0	0.159916
psi(b+s)gam(s)eps(s)p(g)	1041.77	0.529583	0.122714
psi(b+c)gam(.)eps(.)p(g)	1041.796	0.555316	0.121145
psi(b+s)gam(s)eps(s+c)p(g)	1042.017	0.776066	0.108486
psi(b+c)gam(c)eps(.)p(g)	1042.343	1.102798	0.092135
psi(b+c)gam(c)eps(c)p(g)	1042.94	1.699829	0.068356

psi(b+c)gam(.)eps(s)p(g)	1043.3	2.05989	0.057094
psi(b+c)gam(c)eps(s)p(g)	1043.891	2.650613	0.042493
psi(s)gam(s)eps(.)p(g)	1044.461	3.220695	0.031954
psi(.)gam(s)eps(.)p(g)	1045.15	3.909838	0.02264

Table 7. Dynamic model selection results for northern gannet; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(b+s+c)gam(s)eps(c)p(g)	933.8997	0	0.368406
psi(b+s+c)gam(s)eps(s+c)p(g)	935.3048	1.405149	0.182475
psi(b+s+c)gam(s)eps(s)p(g)	936.1628	2.26316	0.11882
psi(s+c)gam(s)eps(c)p(g)	936.7342	2.83453	0.089293
psi(s+c)gam(s)eps(s+c)p(g)	938.1363	4.236597	0.044296
psi(b+s+c)gam(.)eps(c)p(g)	938.4484	4.548745	0.037895
psi(s+c)gam(s)eps(s)p(g)	939.7028	5.803112	0.020239
psi(b+s+c)gam(.)eps(.)p(g)	939.9009	6.001274	0.01833
psi(b+c)gam(.)eps(.)p(g)	940.0627	6.163024	0.016906
psi(b+s+c)gam(.)eps(s+c)p(g)	940.2468	6.34712	0.015419

Table 8. Dynamic model selection results for black-legged kittiwake; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(c)gam(.)eps(.)p(g)	1858.076	0	0.118217
psi(c)gam(s)eps(.)p(g)	1858.861	0.784729	0.079851
psi(c)gam(.)eps(c)p(g)	1859.33	1.253992	0.063151
psi(c)gam(.)eps(s)p(g)	1859.69	1.613974	0.052749
psi(c)gam(c)eps(.)p(g)	1859.796	1.719724	0.050032
psi(c)gam(s)eps(c)p(g)	1859.883	1.807004	0.047895
psi(s+c)gam(.)eps(.)p(g)	1860.009	1.932651	0.044979
psi(b+c)gam(.)eps(.)p(g)	1860.011	1.934754	0.044932
psi(c)gam(s)eps(s)p(g)	1860.063	1.987127	0.04377
psi(s+c)gam(s)eps(.)p(g)	1860.76	2.68335	0.030903
psi(b+s+c)gam(s+c)eps(s+c)p(g)	1866.195	8.118847	0.00204
psi(.)gam(.)eps(.)p(g)	1879.36	21.28421	2.82E-06

Table 9. Dynamic model selection results for herring gull; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(s)gam(.)eps(s+c)p(g)	2335.563	0	0.643866
psi(b+s)gam(.)eps(s+c)p(g)	2337.359	1.795834	0.262322
psi(s+c)gam(s+c)eps(c)p(g)	2339.415	3.852404	0.093812

Table 10. Dynamic model selection results for great black-backed gull; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(c)gam(.)eps(.)p(g)	1439.674055	0	0.392878
psi(c)gam(.)eps(s)p(g)	1441.33032	1.656266	0.171634
psi(b+c)gam(.)eps(.)p(g)	1441.454959	1.780904	0.161265
psi(c)gam(.)eps(c)p(g)	1441.665308	1.991253	0.145165
psi(b+c)gam(.)eps(s)p(g)	1443.137072	3.463017	0.069546
psi(b+c)gam(.)eps(c)p(g)	1443.448723	3.774669	0.059511

Table 11. Dynamic model selection results for razorbill; model names follow MacKenzie et al. 2003: . = null model, b = bathymetry, s = sea surface temperature, c = chlorophyll-A concentration, g= global, psi = initial occupancy probability, gam = colonization, eps = extinction, p = detection probability. Top ten models are shown along with null and global models if convergent.

Model	AIC	delta	AICwt
psi(c)gam(.)eps(s)p(g)	2650.377	0	0.096275
psi(c)gam(.)eps(.)p(g)	2650.802	0.425644	0.077819
psi(s+c)gam(.)eps(s)p(g)	2651.623	1.245871	0.051639
psi(s+c)gam(.)eps(.)p(g)	2651.691	1.313875	0.049912
psi(c)gam(.)eps(s+c)p(g)	2651.791	1.413952	0.047476
psi(b+c)gam(.)eps(s)p(g)	2651.97	1.593741	0.043395
psi(c)gam(c)eps(s)p(g)	2652.308	1.931099	0.036659
psi(.)gam(.)eps(c)p(g)	2652.49	2.112834	0.033475
psi(b+c)gam(.)eps(.)p(g)	2652.632	2.255121	0.031176
psi(c)gam(.)eps(c)p(g)	2652.667	2.290284	0.030633

Figure 1. Common eider predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

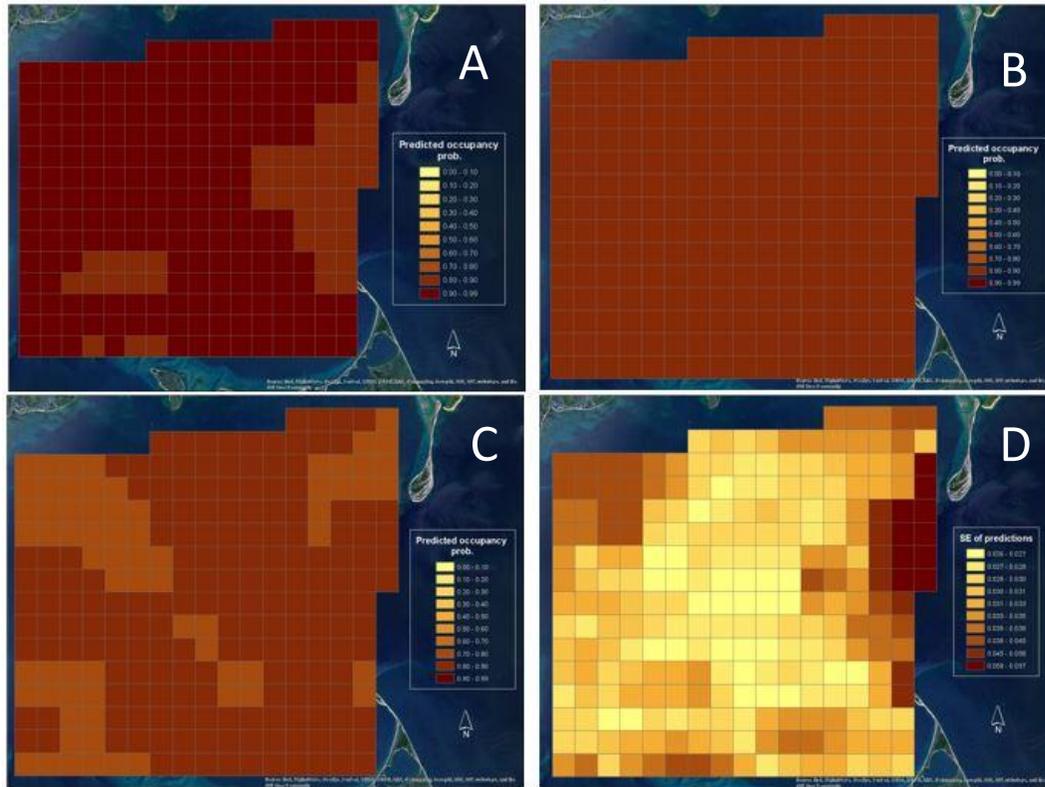


Figure 2. Surf scoter predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

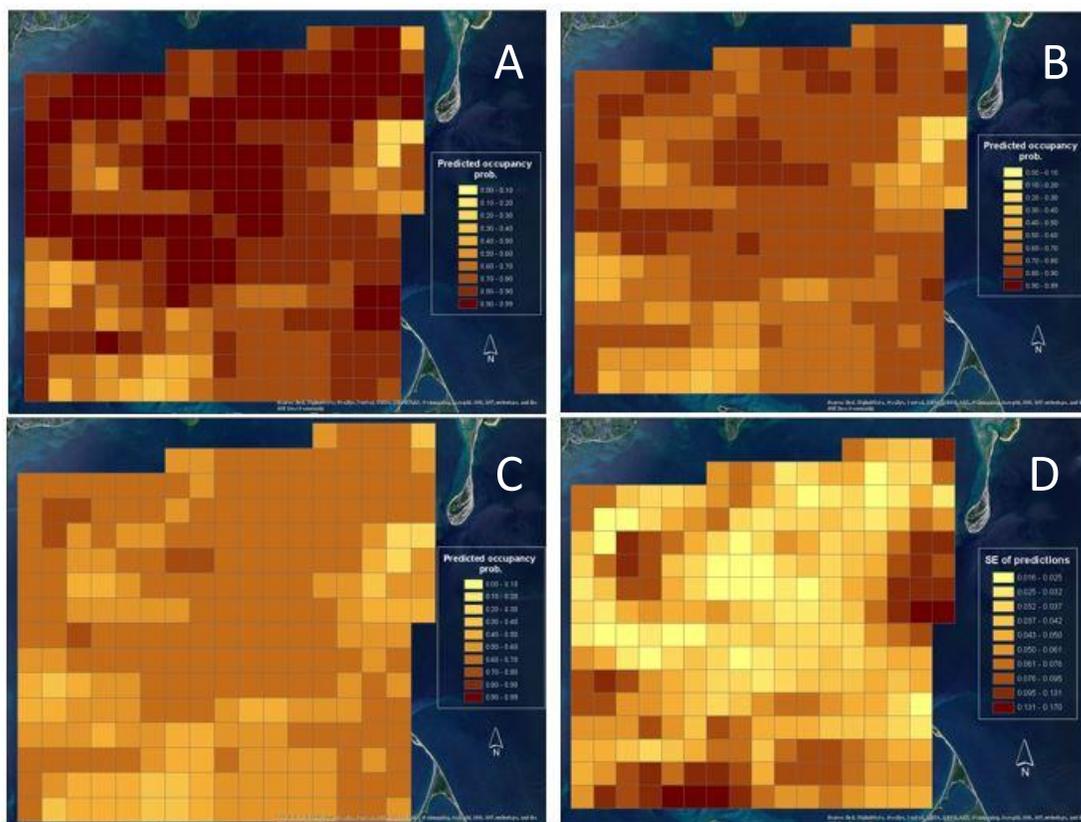


Figure 3. White-winged scoter predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

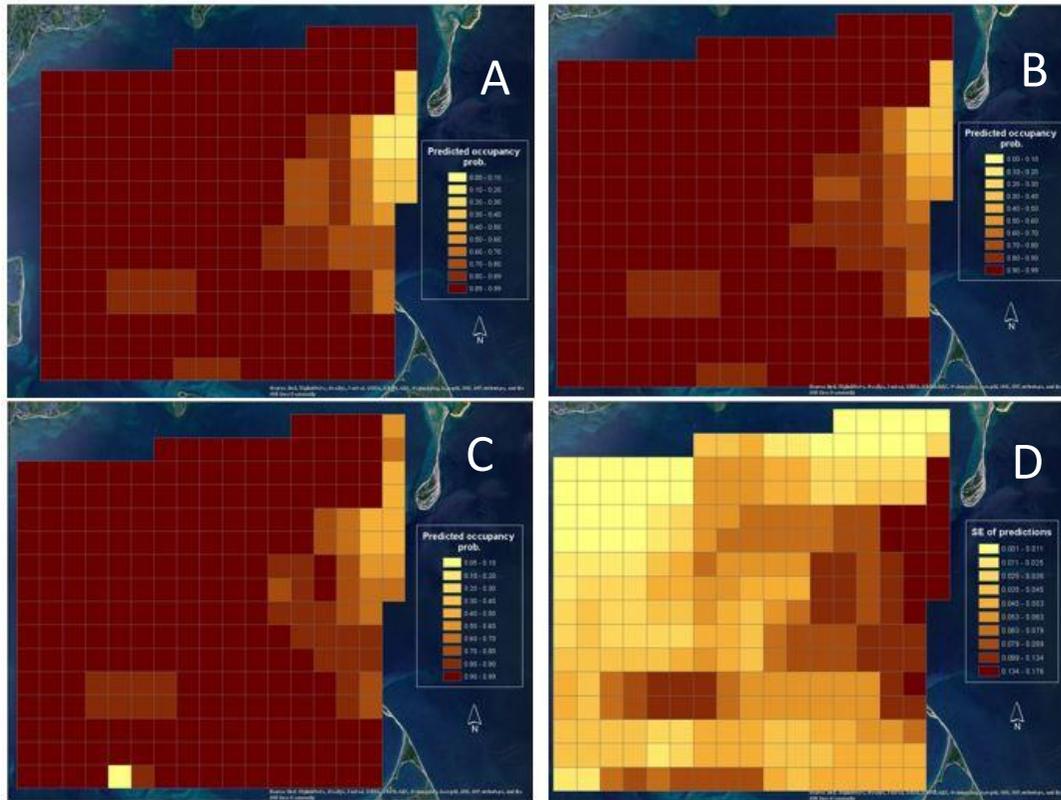


Figure 4. Long-tailed duck predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

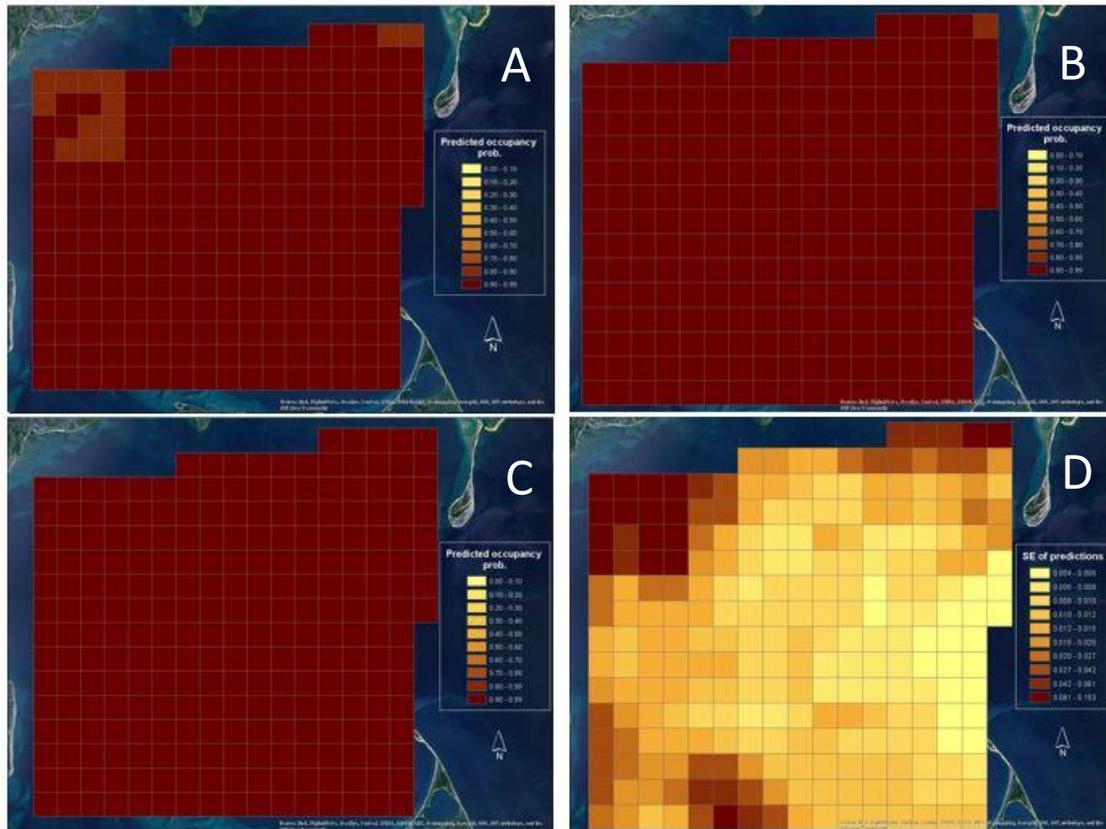


Figure 5. Red-throated loon predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

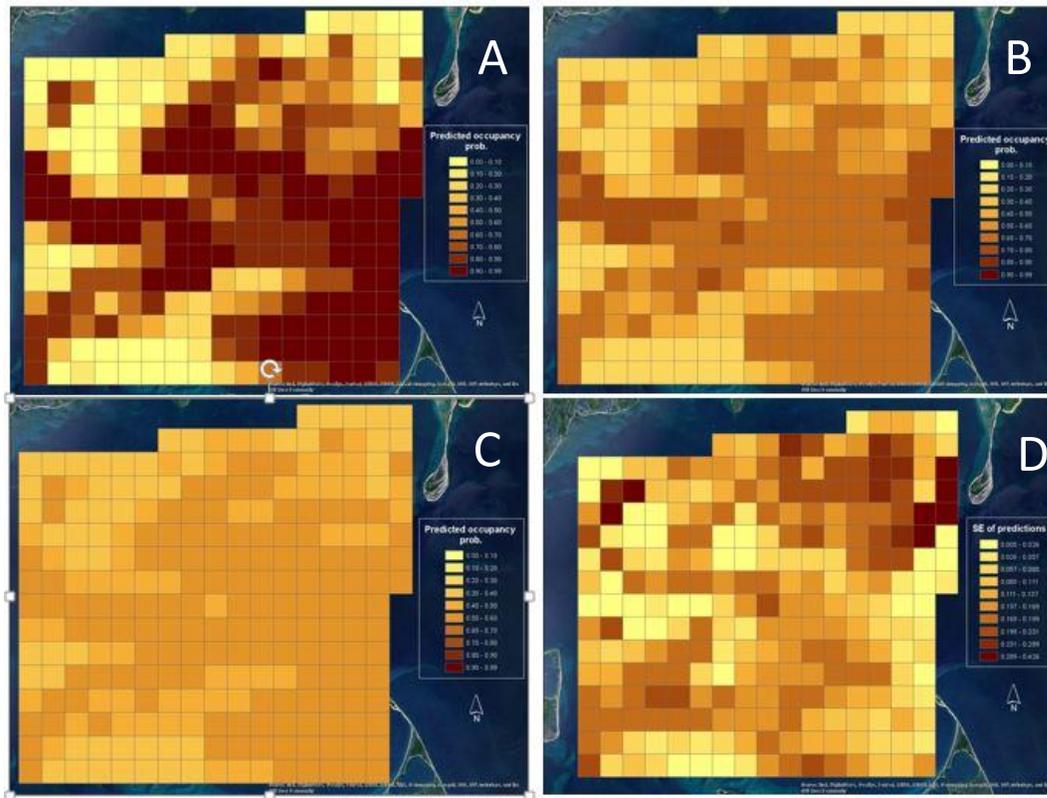


Figure 6. Common loon predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

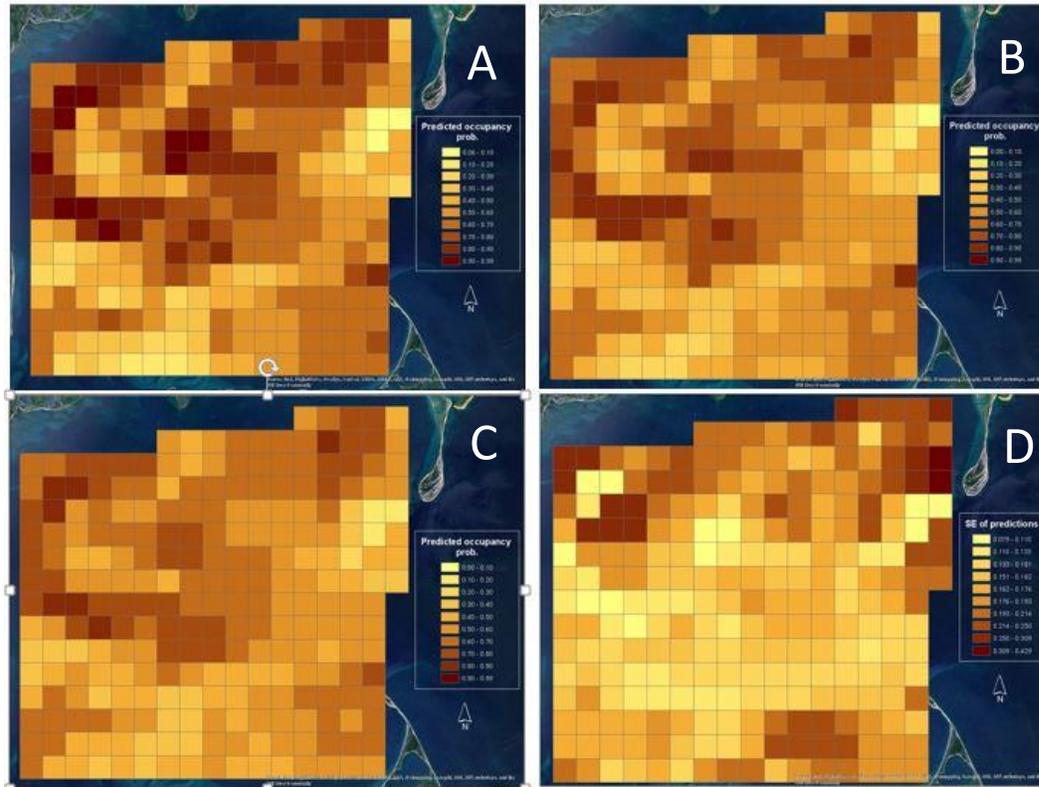


Figure 7. Northern gannet predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

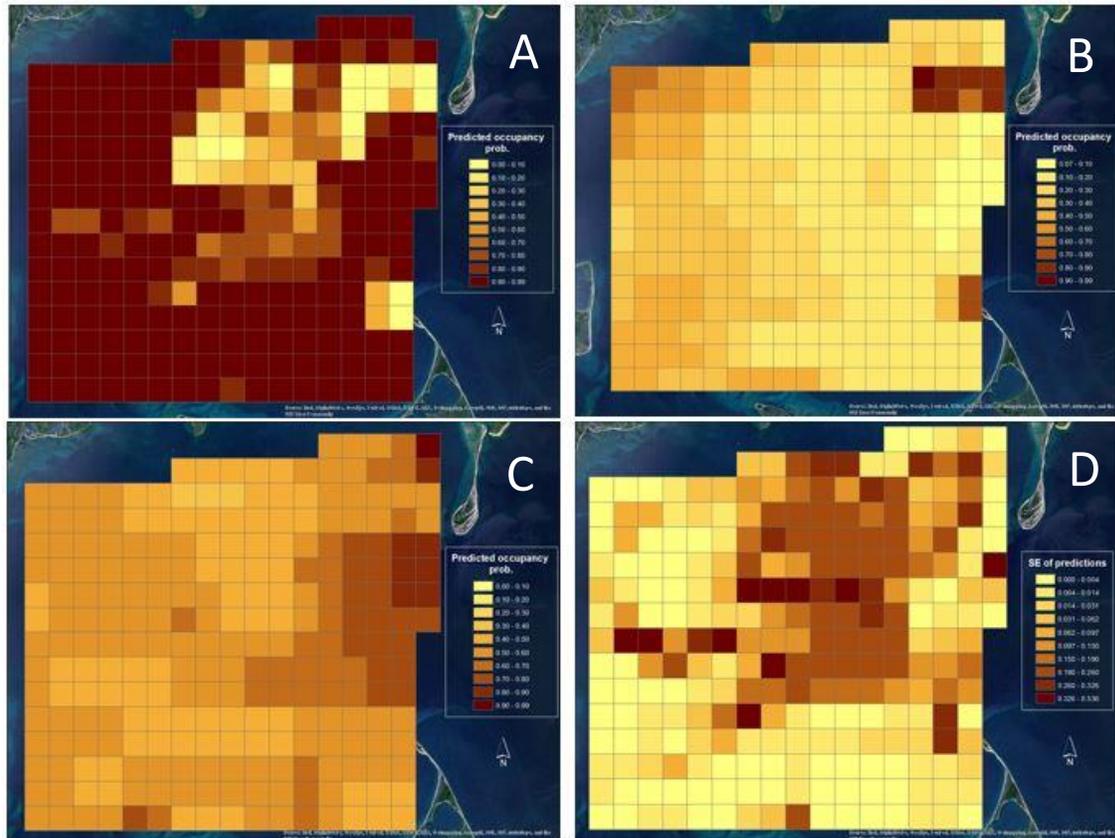


Figure 8. Black-legged kittiwake predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

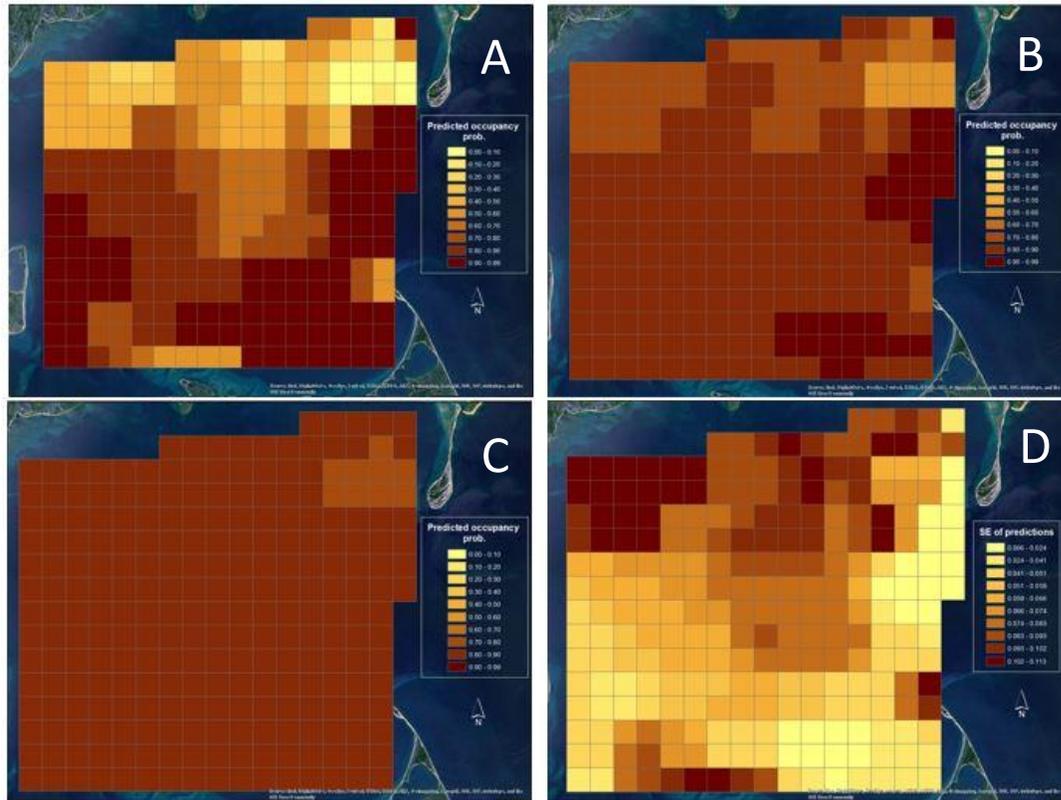


Figure 9. Herring gull predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

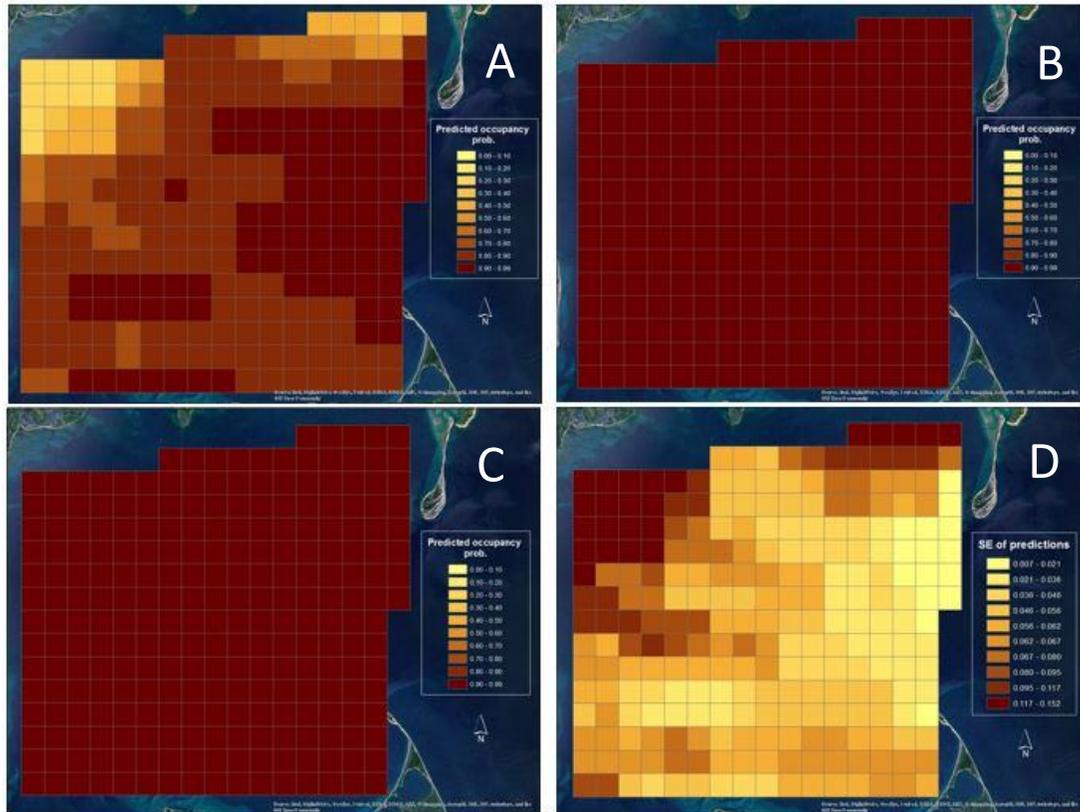


Figure 10. Great black-backed gull predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

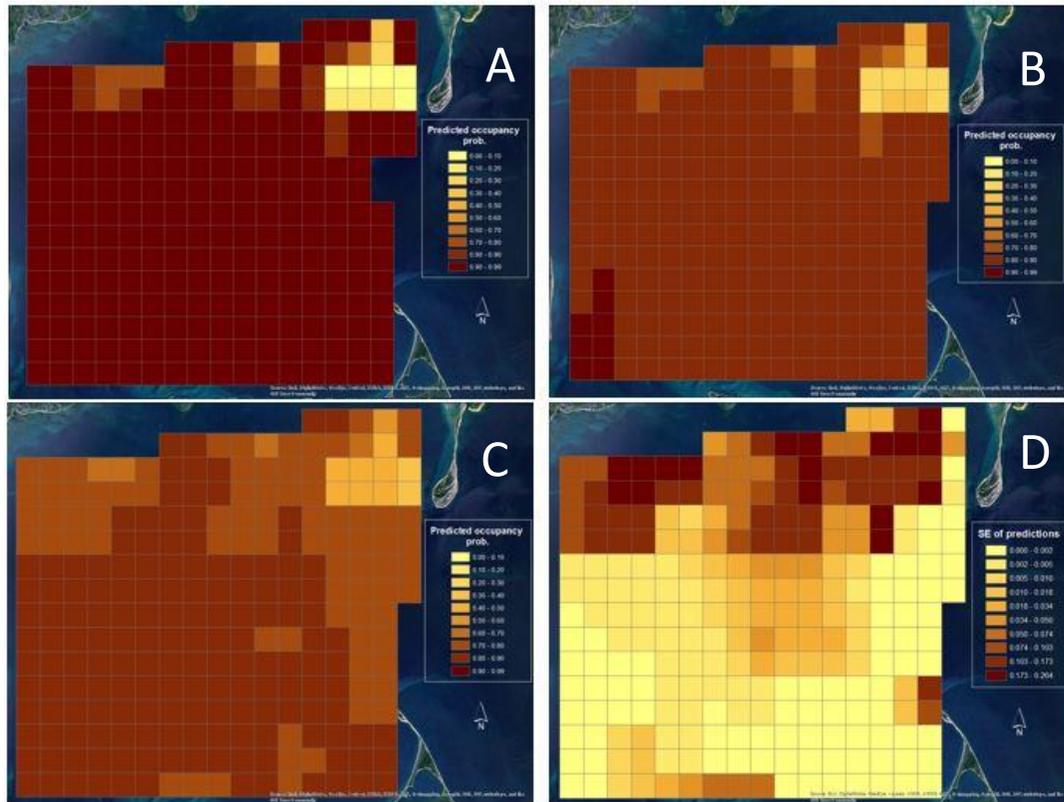


Figure 11. Razorbill predicted initial occupancy (winter 2003-2004, A), predicted occupancy in winter 2004-2005 (B), predicted occupancy in winter 2005-2006 (C), and standard errors of initial occupancy predictions (D).

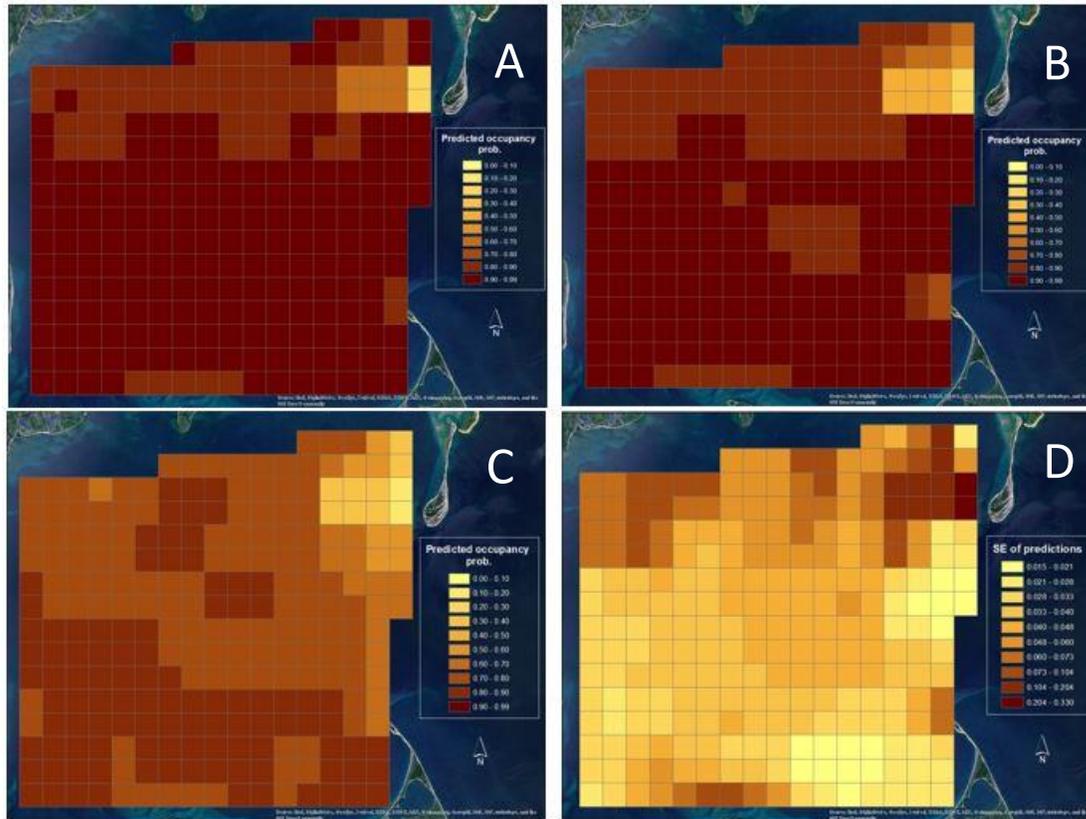


Figure 12. Year-specific detection probability intercept estimates for winter 2003-2004, winter 2004-2005, and winter 2005-2006 for eight diving species.

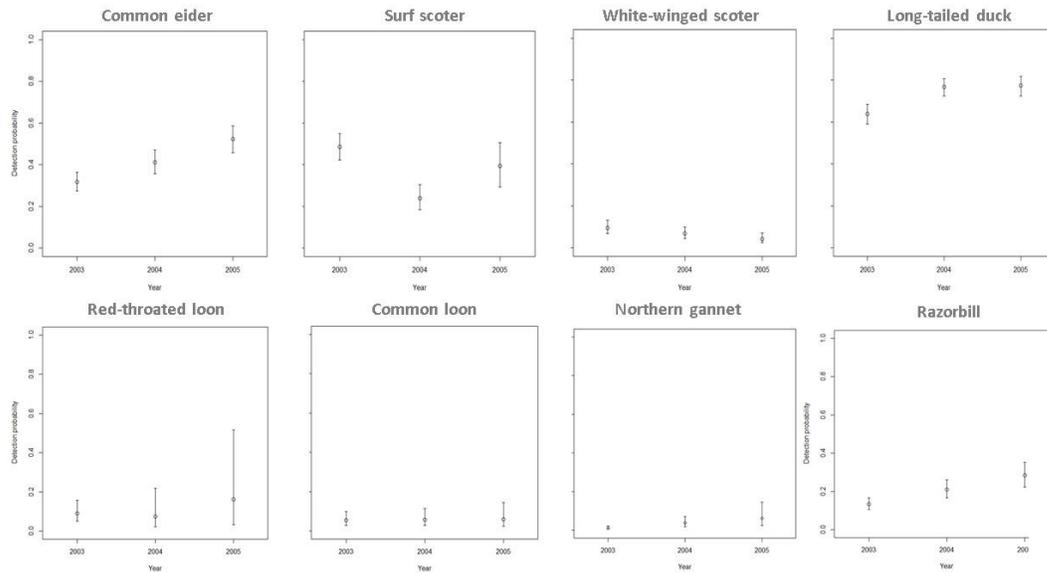


Figure 13. Year-specific detection probability intercept estimates for winter 2003-2004, winter 2004-2005, and winter 2005-2006 for three surface-feeding species.

