

COMPARING LOCAL AND REGIONAL DENSITY MODELS FOR MARINE BIRDS IN THE GULF OF MAINE

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ABSTRACT

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The Gulf of Maine has extensive potential for floating offshore wind energy development. However, to assess potential impacts, substantial spatiotemporal gaps exist in offshore wildlife data from standardized observational surveys in the region. Such data can support distribution and density modeling to inform marine spatial planning. In an effort to reduce these gaps, we modeled seasonal marine bird densities based on data from four digital aerial surveys conducted in 2023–2024 across a 6,700 km² area of the Gulf. We also compared these local models to existing regional density models for marine birds using spatial cross-correlation and center-of-gravity analyses to assess potential mismatches in predictions. Local and regional models were weakly spatially correlated for most taxon/season combinations (global spatial cross-correlation indices with negative exponential decay ranged from -0.21 to 0.23, mean = 0.07, median = 0.11), and local and regional centers of gravity did not consistently align (mean absolute difference = 11.7 km). We discuss several reasons for discrepancies between local and regional predictions of marine bird densities, including underlying differences in model structure and differences in spatiotemporal resolution of source data. Given the limitations of both models, we were unable to determine which model can best inform offshore planning and risk assessments. Further observational surveys are needed to refine models so they may be used reliably for management and conservation, particularly in winter, which is the least surveyed season in the Gulf. Future observational survey efforts should follow best available guidance for survey design to support effective consideration of marine birds in offshore planning and risk assessments.

Key words: density models, digital aerial survey, marine birds, offshore wind, risk assessment, spatial cross-correlation, seabird

INTRODUCTION

Understanding spatiotemporal variability in marine wildlife density and estimating population abundance in the offshore environment of the United States (US) Outer Continental Shelf (OCS) are critical for marine spatial planning, including the siting of offshore wind energy facilities, to minimize negative environmental effects. There are substantial spatial and temporal gaps in knowledge of marine biota occurrence in the Gulf of Maine, particularly due to the limited availability of standardized observational survey data. Data from such surveys can be used to develop spatial models of wildlife density to inform siting of offshore wind energy development and other activities (Winship et al., 2023). These data gaps are a concern because the Gulf of Maine exhibits the highest wind energy potential along the US Atlantic coast (Lopez et al., 2022).

Marine birds occur in the Gulf of Maine throughout the year, and many taxa migrate through the region annually in spring and autumn. Migrants from colonies both north and south are present in summer and winter and vastly outnumber breeding birds (Nisbet et al., 2013). This results in a complex ecosystem in which the composition of the avian community shifts regularly, and species distributions exhibit substantial spatiotemporal variability. Moreover, waters of the Gulf of Maine have warmed significantly (Pershing et al., 2015; Whitney et al., 2022), likely due to a

shift in the path and warming of the Gulf Stream (Gonçalves Neto et al., 2021; Seidov et al., 2021; Townsend et al., 2023). These oceanographic changes may affect avian prey populations, resulting in shifted avian species distributions. Consequently, it is challenging to collect sufficient data to accurately characterize and predict (with high precision and low bias) the spatiotemporal variability in wildlife densities in dynamic ecosystems such as the Gulf of Maine.

Regional spatial models of marine bird density generated by Winship et al. (2023; hereafter ‘regional models’) have been used to inform recent avian risk assessments for offshore wind permitting in US waters and to provide broader context where local, higher-resolution data exist (Bureau of Ocean Management [BOEM], 2024; Equinor, 2022; Ocean Wind, 2023). In Atlantic coastal waters of the US, these regional models were built using data from the Northwest Atlantic Seabird Catalog, a database of surveys conducted on the Atlantic OCS since the 1970s using a variety of field methods (O’Connell et al., 2009), as well as data from the Eastern Canada Seabirds at Sea database (Gjerdrum et al., 2024). The regional models incorporated survey data collected from the US Atlantic between 1998 and 2020. The models used relationships between environmental explanatory variables and seabird densities at surveyed locations to predict densities at both surveyed and unsurveyed locations. The models were designed to provide relative estimates of seasonal densities at the Atlantic

coast-wide scale (Winship et al., 2018; Winship et al., 2023) and are most informative at that scale, as noted by the authors (Winship et al., 2023), rather than at the scale of individual offshore wind lease areas. Also, the regional models included marine bird data only prior to 2021, which adds uncertainty when applying their predictions to current marine spatial planning in this area. Given ongoing oceanographic changes, standardized site-specific survey data are still recommended (BOEM, 2020) to effectively inform offshore wind risk assessments and complement the regional models. Properly conducted standardized local surveys can provide critical information at the appropriate spatial resolution for the characterization and risk assessment of individual lease areas (Avian Displacement Guidance Committee, 2023).

In 2024, BOEM approved the State of Maine's small lease (~40 km²) to develop the first floating offshore wind research site in federal waters, the Maine Research Array (Maine Offshore Wind Initiative, n.d.). BOEM funded four digital aerial wildlife surveys in 2023–2024, centered on an area surrounding the Maine Research Array. Digital aerial surveys obtain standardized wildlife and anthropogenic data via high-resolution imagery (Buckland et al., 2012) and are used at offshore wind farms worldwide (Collier et al., 2022; Harker et al., 2022). BOEM also funded analysis of these new Maine survey data to produce spatially explicit models (hereafter 'local models') that predict the absolute density of wildlife in the area.

In this study, we compared predicted spatial patterns of marine bird densities from regional and local models. Specifically, we examined how differences in the spatiotemporal scales (i.e., extent and resolution) and explanatory variables used in the regional and local models affected predictions of marine bird density in the Gulf.

Our overall goal was to evaluate the utility of predictions from the regional and local models for marine spatial planning and wildlife management in the Gulf of Maine. Our objectives were to: (1) compare the spatiotemporal patterns of marine bird density from large-scale, regional models (aggregating data over a vast area and an extended period of time) and finer-scale, local models (derived from a single year of localized digital aerial surveys) in the Gulf of Maine; and (2) identify research priorities to better understand existing use of the Gulf of Maine by avian communities and thereby improve risk assessments and inform spatial planning related to offshore wind development in the area.

METHODS

Study Site

The Gulf of Maine is semi-enclosed, spanning an area of over 93,000 km². It is bounded to the north by Cape Sable, Nova Scotia, Canada, and to the south by Cape Cod, Massachusetts, USA. Its complex bathymetry includes a series of three central basins reaching depths over 370 m, and two broad, shallow outer banks. Historically, the area has been fed by nutrient-rich, cold ocean currents from the north, which mix with fresh water from 60 rivers draining an enormous watershed (~180,000 km²). In recent decades, however, influxes of warmer Gulf Stream waters have warmed deep shelf waters in the region (Brickman et al., 2018). The Gulf of Maine supports a highly productive and dynamic ecosystem, and sustains numerous local communities and significant fishing, shipbuilding, and recreational industries.

Gulf of Maine Digital Aerial Surveys

Four seasonal digital aerial surveys were conducted within the designated survey area in 2023 and 2024 (spring: 05, 08 May 2023; summer: 19–20 August 2023; autumn: 24–25 October 2023; and winter: 03–04 January 2024). The survey area focused on and around a site identified in 2021 by the State of Maine's Department of Energy Resources as suitable for an offshore wind research lease. The Maine research lease (OCS-A 0553), located within this area, was granted to the State by BOEM in August 2024. Within the survey area, transects were oriented north-south, generally perpendicular to bathymetric, oceanographic, and ecological gradients. The same 22 transect lines were repeated on each survey, covering approximately 730 km², or > 10% of the designated survey area (6,673 km²; Fig. 1; Appendix, available on the website). Transects were spaced 2.5 and 5.0 km apart, with smaller gaps between transects in the center of the study area to increase coverage around the lease area (Fig. 1).

Each digital aerial survey took two days to complete and was conducted using four high-resolution digital video cameras specifically designed for high-quality wildlife surveys, mounted in the belly of a small, fixed-wing aircraft. Surveys were flown at ~400 m altitude at a ground speed of 220 km/h (~120 knots), capturing digital imagery at 1.5 cm ground sample distance (GSD) resolution. Each digital camera sampled a strip 104 m wide and was separated from the adjacent camera by ~17 m, providing a combined sampled width of 416 m within an overall strip width of 467 m. Survey flights were conducted predominantly in Beaufort sea states 2–4, with average conditions around sea state 3. Wind speeds ranged from 5–25 knots, with cloud cover consistently above the aircraft, typically exceeding ~900 m. Following completion of each survey, digital image review involved a multi-step process in which objects were first detected in the imagery and then identified to species or taxonomic group. Each step included a quality assurance review in accordance with best practices for the analysis of digital aerial survey data (Scott et al., 2023; Żydelis et al., 2019; Appendix).

Regional Surveys

At-sea survey data used to construct the regional models spanned the US Atlantic OCS nearshore and offshore waters from Maine to Florida (Winship et al., 2023). Data were collected from a variety of survey platforms, including boats and aircraft, using a variety of survey methods, including visual observations and digital imagery. The at-sea data used to build the regional models were collected over a two-decade period (1998–2020) and throughout the year, although sampling effort varied among months and years. In the Gulf of Maine, the regional models were informed by data from both boat and aerial visual surveys, with boat-based surveys extending farther offshore (see Fig. 6 in Winship et al., 2023). Survey coverage in the Gulf of Maine contained large spatiotemporal gaps, particularly in areas farther from shore, and some months had very few or no observations (e.g., December and January; see Fig. 5 in Winship et al., 2023).

Gulf of Maine Surveys: Local Spatial Modeling

We developed single-season density surface models (hereafter referred to as "seasonal DSMs") for species and species groups using sightings data from the 2023–2024 Gulf of Maine digital aerial surveys. Surveys were conducted in only one month per

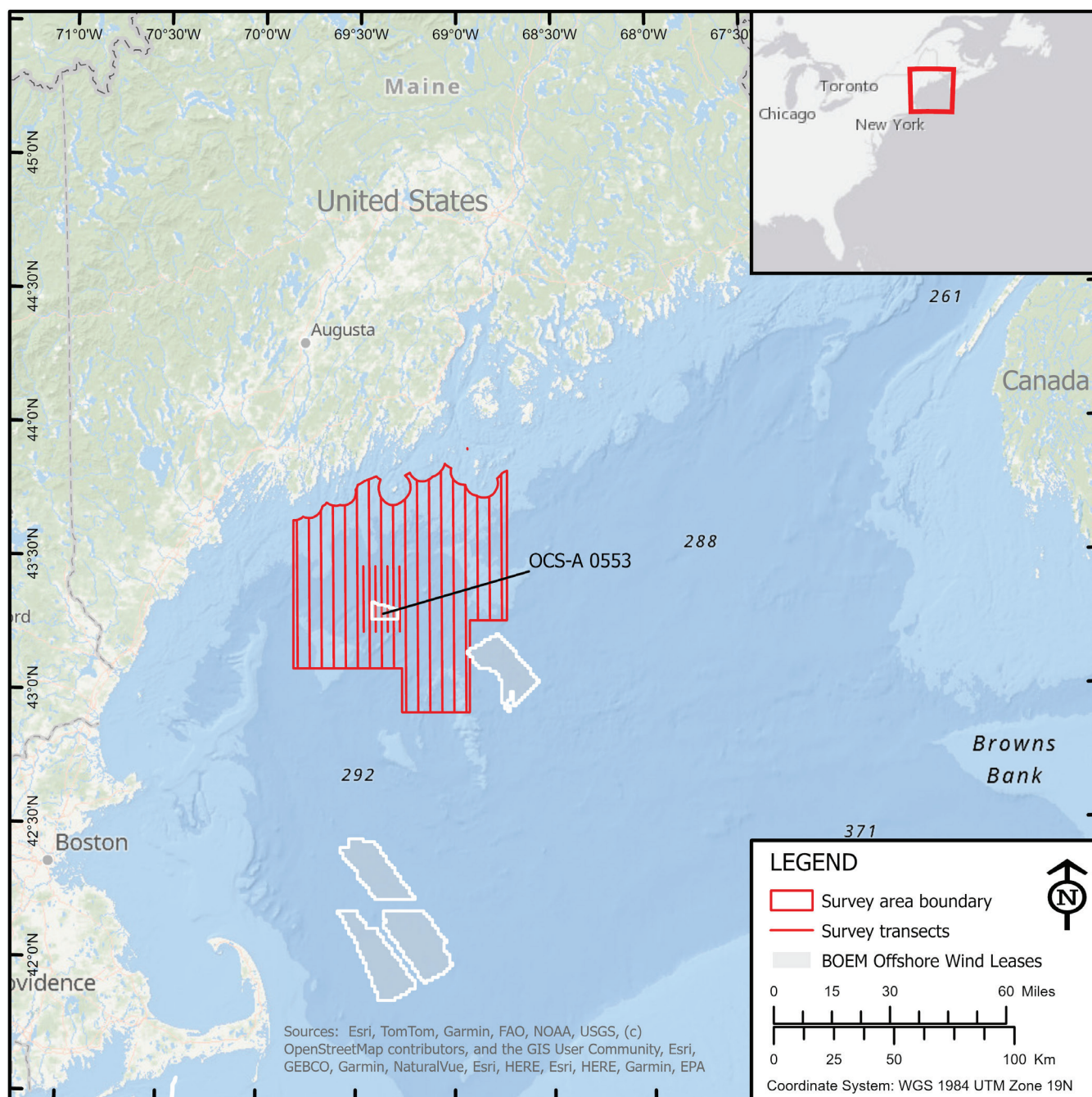


Fig. 1. Survey area for four digital aerial surveys in the Gulf of Maine, USA, in 2023–2024, centered on the State of Maine’s research lease area (OCS-A 0553). Current nearby US federal offshore wind lease areas are shown in gray.

season (defined above). We attempted to build a seasonal DSM for each species with at least 30 sightings in that season. Whenever possible, each seasonal DSM was based on data from only a single species. However, in a few instances, we pooled sightings of species or species groups with small sample sizes but similar ecological characteristics. To provide insight into spatiotemporal variability in the density of the entire bird community, we created seasonal DSMs for all bird sightings combined, including sightings that were not identified to species.

In the following sections, we provide an overview of the mathematical structure of the DSMs, model evaluation methods, and abundance

prediction methods; see the Appendix for additional details. All analyses were conducted using R version 4.4.2 (R Core Team, 2024). DSMs were constructed using the “sdmTMB” and “sdmTMBextra” packages in R (Anderson et al., 2024; Anderson, 2025).

Gulf of Maine Surveys: Density Surface Model Structure and Evaluation

To construct each seasonal DSM, we related the number of birds sighted on a 4-km (2.16-nautical miles) transect segment to three types of explanatory variables: (1) spatial coordinates; (2) dynamic environmental variables; and (3) static environmental variables.

The spatial component of each DSM was defined as one of two types of random effects: either (i) a stochastic partial differential equation (SPDE) approximation to model the precision matrix associated with the Matérn covariance function (i.e., an “SPDE Matérn model”; Lindgren et al. 2011); or (ii) an SPDE Matérn model that accounts for barriers (i.e., an “SPDE Matérn with barriers”). The SPDE Matérn with barriers is often useful for modeling coastal species in areas with complex coastlines (such as the Gulf of Maine) that have islands, bays, peninsulas, or points, because the model’s barriers ensure that correlations between two locations are calculated based on the distance over water between the locations (Bakka et al., 2019).

The full suite of environmental variables that were considered as potential predictor variables included eight dynamic and four static variables (Table A1, Appendix). Correlation tests (Kendall’s Tau and Spearman’s Rho) were used to identify potential dynamic and static environmental variables with statistically significant correlations ($p = .05$). When significant correlations existed, only one variable was retained for model-building based on ecological understanding of the ecosystem. The five environmental variables retained for model-building were sea surface temperature, current velocity, depth, rugosity, and sediment class.

For each combination of season and taxon, we evaluated purely spatial DSMs and DSMs with both spatial and environmental variables. The DSMs with both spatial and environmental terms included all five environmental variables in the linear predictor as univariate thin-plate regression splines with shrinkage, allowing each term to shrink to zero during model fitting if the term was not important for describing the spatial pattern of the observations (Wood, 2003).

The basic DSM structure for taxon i in season j at location k may be represented as (Bravington et al., 2021):

$$E[Y_{i,j,k} | \beta_{i,j}] = a_{j,k} \exp \left[\beta_{i,j,0} + \sum_q f_{i,j,q}(u_{i,j,k,q}) \right] \quad [1]$$

where,

$a_{j,k}$ = area corresponding to season j and location k , which equals the total area within the imagery located in each transect segment for model-building and the cell area for predicting (see “Gulf of Maine Surveys: Abundance Estimation”);

$Y_{i,j,k}$ = random variable for the number of birds from taxon i in season j at location k ;

$u_{i,j,k,q}$ = covariates (indexed by q) that influence bird density (in this case, projected latitude and longitude, and possibly the environmental covariates listed above);

$f_{i,j,q}$ = smooth function for the i th species, j th season, and q th covariate;

$\beta_{i,j}$ = vector of parameters in the smooth functions for taxon i in season j ; for simplicity, we include in this vector the intercept parameter $\beta_{i,j,0}$.

As is typical for analyses of digital aerial survey data (e.g., Buckland et al., 2012), we assumed that all birds located at the surface of the

water and available to be seen in the imagery were detected. Hence, $\hat{Y}_{i,j,k}$ is more precisely defined as the number of available birds of taxon i in season j and location k .

We formulated each DSM using a logarithmic link function. We evaluated seven different probability distributions for the likelihood: Tweedie, Poisson, delta gamma, delta lognormal, Poisson delta gamma, Poisson delta lognormal (Thorson, 2018), and negative binomial.

Each seasonal DSM was evaluated based on the following metrics: conditional Akaike Information Criterion (cAIC; Zheng et al. 2024); model evaluation criteria flagged by the “sdmTMB” *sanity* function (Anderson et al. 2024), including model convergence and relative magnitudes of key parameters; the number of segments with sightings; residual analyses (PIT residuals via R package “DHARMa”; Hartig, 2024); and visual inspections of maps showing model predictions with the sightings overlaid. Models were excluded from further evaluation if they exhibited one or more of the following problems: at least one flag returned by the *sanity* function; $\leq$ six segments with sightings; poor fit to the data based on residual analyses or visual inspection of prediction maps. For each taxon and season, we chose the single best model with the lowest cAIC.

Gulf of Maine Surveys: Availability Bias

Diving birds spend a proportion of their time underwater, at which time they are not visible in imagery from aerial surveys. If abundance estimates are not corrected for the probability that birds are available for detection during data collection, they will be subject to availability bias (Marsh & Sinclair, 1989). Birds that spend a low proportion of time at the surface, where observers can detect them (i.e., low availability), will be detected infrequently relative to their true density (i.e., raw counts will have considerable bias relative to true abundance). Availability probability is the inverse of the availability bias correction factor; it is a function of the bird’s respiratory and/or foraging behavior, and the duration for which the bird remains within the observer’s field of view. Availability probability ($\hat{p}_{a,i}$) can vary by species, age or life stage, season, location, activity state, and other factors. We estimated species-specific availability probabilities ($\hat{p}_{a,i}$). The species that commonly dive and for which there were sufficient sample sizes to build DSMs were the Common Murre *Uria aalge*, Atlantic Puffin *Fratercula arctica*, and Little Auk *Alle alle*. Because there were no estimates of availability specific to the Gulf of Maine for these species, we conducted a literature review and based our estimates of availability probability on the best available information (see Appendix).

Gulf of Maine Surveys: Abundance Estimation

Abundance estimates from each seasonal DSM were based on a hexagonal grid (the prediction surface) with cell centroids located 4 km (2.16 nautical miles) apart. The predicted number of birds in each hexagon in each season, $\hat{Y}_{i,j,k}$, was based on the relationships defined in Eq. [1], where a_k is the total area of the hexagon, which was constant across seasons. For each seasonal DSM, we used the *sdmTMB* function *simulate.sdmTMB* to simulate 1,000 samples of abundance for each cell ($\hat{Y}_{i,j,k}$). A Horvitz-Thompson estimate was used to predict the number of birds in the study area in each season for each simulation, based on the sum of cell-specific abundance

estimates ($\hat{Y}_{i,j,k}$), divided by the estimated availability probability ($\hat{p}_{a,i}$):

$$\hat{N}_{i,j} = \frac{\sum_k \hat{Y}_{i,j,k}}{\hat{p}_{a,i}} \quad [2]$$

Then, we computed the abundance estimate for each seasonal DSM as the median value of $\hat{N}_{i,j}$ among all simulations. The lower and upper 95% confidence intervals on $\hat{N}_{i,j}$ were computed from the 2.5th and 97.5th quantiles of the simulated distribution of $\hat{N}_{i,j}$.

Gulf of Maine Surveys: Species Richness

We examined spatial and seasonal variability in species richness using a simple index. For each season, species richness was calculated for each hexagonal cell and season as the number of unique species identified in the digital aerial survey (DAS) imagery.

Regional Models

The regional models were statistical species distribution models of observed bird counts (from the regional survey data described above) as a function of survey, temporal, and contemporaneous spatial environmental covariates (Winship et al., 2023). The models were constructed for the period 1998–2020, when both at-sea bird survey data and contemporaneous spatial environmental covariates were available. The models predicted the density of each of 49 species of marine birds across the US Atlantic OCS for each month in each year, 1993–2019, corresponding to the period in which environmental covariate data were available for every month. The regional model predictions were made on a rectangular grid with a spatial resolution of 10 km (Winship et al., 2023). Monthly predictions for each cell in the prediction surface were averaged across years to produce estimates of the long-term average density for each cell in each month. Bootstrapping was used to derive estimates of uncertainty in the model predictions for each cell, including the coefficient of variation (CV). Because these models did not account for availability or detection bias, it was not advised to compare the predicted densities between species. It was also not appropriate to directly compare the predictions from the regional models to those from the local seasonal DSMs described above. Nevertheless, the regional model predictions were expected to be proportional to the estimated number of birds per unit area, and thus the *relative* spatial patterns could be compared among taxa within the regional models and between the regional and local density models.

Model Comparison: Spatial Cross-Correlation

We used spatial cross-correlation (SCC) analysis (Chen, 2015) to make two types of comparisons between the regional and BOEM Gulf of Maine (local) models for all 14 species or species groups for which local models could be developed, including Atlantic Puffin, Little Auk, murre spp. (almost entirely made up of Common Murres), Black-Legged Kittiwake *Rissa tridactyla*, Bonaparte's Gull *Chroicocephalus philadelphia*, Laughing Gull *Leucophaeus atricilla*, Ring-billed Gull *Larus delawarensis*, American Herring Gull *L. smithsonianus*, Great Black-backed Gull *L. marinus*, Common Tern *Sterna hirundo*, tern spp. *Sterna* spp., Wilson's Storm Petrel *Oceanites oceanicus*, Northern Fulmar *Fulmarus glacialis*, and Northern Gannet *Morus bassanus*. The first comparison examined the relationships between the scaled estimates of the

relative density (regional) and absolute abundance (local) of birds by season, using the monthly estimates from the regional models to compare to the same months in the local models. Twenty-four taxon-season pairs were modeled at the local scale and examined in the SCC analysis. The second comparison was between the scaled estimates of the respective coefficients of variation (CVs) for these same models. The comparison of CVs was conducted as a supplementary analysis to explore potential causes of differences in the spatial patterns between the regional and local models. To compute the SCC statistics and generate figures, we used a combination of customized code based on the methods of Chen (2015) and the *crossCorrelation* function from the “spatialEco” package in R (Evans & Murphy, 2023).

Estimates of local abundance for the SCC analysis were derived by projecting the local models onto the $n = 70$ centroids of the raster cells from the regional model predictions that were located within the Gulf of Maine study area. The local CV estimates were generated for the same cell centroids using the methods described above to estimate the CV for each cell in the original Gulf of Maine hexagonal prediction grid.

Local DSMs were created for murre spp. and tern spp. To generate analogous relative density estimates for these groups from the regional prediction rasters, we computed cellwise sums of Common Murre and Thick-billed Murre *U. lomvia* densities to represent the murre spp. group, and we summed cellwise density estimates of Arctic Terns *S. paradisaea*, Common Terns, Forster's Terns *S. forsteri*, and Roseate Terns *S. dougallii* to represent the tern spp. group. Although availability and detection biases were not accounted for in the regional models, we considered it reasonable to sum model predictions across species within these species groups, assuming that these biases would be relatively similar for related species. We did not estimate CVs for the density estimates from the regional models for these pooled species groups.

We used Chen's (2015) methods to scale the cellwise values of the estimated parameters (density or abundance, and CV) for each taxon. Scaling was done independently for each combination of taxon (i.e., species or species group; indexed by i), season (j), and model (i.e., regional or local; indexed by m). The scaling process required computing standard scores based on the mean and population variance of the estimated parameters for locations in the Gulf of Maine study area (see Appendix for details).

SCC compares the spatial pattern of the values from two measures (e.g., variables, parameters, indices). The local spatial cross-correlation index (LSCI) quantifies the cross-correlation between the value from one measure at a given location and the values of the second measure at all other locations in a geographical system. Our SCC analysis that treated local abundance as the independent variable and regional density as the dependent variable produced 70 LSCI indices. Each index represented the cross-correlation between the scaled estimate from the local model at one centroid and the scaled estimate from the regional model at all other centroids in the study area. Analogously, the SCC analysis that treated the regional density as the independent variable and local abundance as the dependent variable also produced 70 LSCI indices. In this case, each LSCI represented the cross-correlation between the scaled estimate from the regional model at one centroid and the scaled estimates from the local model at all other centroids in the study area.

The weights assigned to the values of neighboring cells in the LSCI computation were a function of the distance between centroids. Distance effects were defined using either an inverse-distance or a negative-exponential weighting function. Compared with negative-exponential weighting, inverse-distance weighting assigned relatively more weight to distant neighbors.

The global spatial cross-correlation index (GSCI) is a single value that is computed as the sum of the LSCIs. It quantifies the broadscale spatial cross-correlation between the two measures across the entire study area. GSCI values range from -1.0 to 1.0, with larger absolute values indicating stronger correlations. Positive GSCI values indicate that areas with high scaled values in one measure generally align with areas of high scaled values in the second measure, and areas with low values also tend to coincide (i.e., positive spatial correlation). In contrast, negative GSCI values indicate a spatial mismatch between the measures, such that areas with high values in one measure tend to correspond to areas with low values in the other (i.e., negative spatial correlation). The goodness-of-fit in the relationship between the LSCIs and the GSCI was evaluated separately using the coefficient of determination (R^2). Although our objective was not to assess whether spatial patterns in the regional models influenced those in the local models (or vice versa), R^2 provided an indication of the degree to which the two models produced complementary spatial predictions.

Model Comparison: Center of Gravity

Because the spatial extent of the regional models was larger than the local models, and the resolution of the regional analysis was coarser than that of the local models, we computed the center of gravity (COG) statistic from Thorson et al. (2016). This statistic provides a simple way to show the center of a species predicted distribution on a map, and it can account for spatially variable survey effort. The COG weighted spatial coordinates of the centroid of each cell by the estimated abundance or relative density of birds at each location:

$$C_x = \frac{\sum_{c=1}^{n_c} \hat{N}_c x_c}{\sum_{c=1}^{n_c} \hat{N}_c} \quad [3]$$

$$C_y = \frac{\sum_{c=1}^{n_c} \hat{N}_c y_c}{\sum_{c=1}^{n_c} \hat{N}_c}$$

where C_x is the COG for the x-coordinate, C_y is the COG for the y-coordinate, $\hat{N}_c$ is the estimated abundance (local model) or relative density (regional model) at centroid c , and the denominator equals the total estimated abundance or relative abundance in the study area. We based the COG analysis on the raw model output (i.e., the relative density estimates from the regional models, and absolute abundance estimates from the local models).

RESULTS

Gulf of Maine Local Surveys

The Gulf of Maine digital aerial surveys in 2023–2024 recorded a total of 7,659 birds, with an overall identification rate to species of 94% (Table A4, Appendix). Thirty-three species were identified from the footage; 413 individual birds could not be assigned to a species and were instead assigned to a species group (e.g., tern spp.). More than 68% of birds were observed in the winter survey, with

15% observed in autumn and the remaining 17% occurring between spring and summer. Bird densities were an order of magnitude higher in winter than in any other season (Fig. 2). Several bird species were present in the survey area year-round (e.g., American Herring Gull and Great Black-backed Gull), whereas some species were only present during one or two seasons (e.g., Common Tern and Wilson's Storm Petrel). The most frequently observed species was the Common Murre (> 45% of all observations, almost all in winter).

Several taxa had the minimum required number of observations per season to be candidates for density modeling ($n = 30$ observations) but were highly clustered in space such that seasonal density surface models could not be constructed (e.g., the scoters *Melanitta* spp. and Leach's Storm Petrel *Hydrobates leucorhous*). For the remaining 24 taxon-season combinations, the purely spatial model was selected over the model with environmental covariates in all cases (Fig. A1, Appendix).

Across all species, predicted densities of birds in the study area tended to be highest nearshore in spring and summer and highest offshore in autumn and winter (Fig. 2). On average, overall predicted densities were ~5–7 times greater in winter (mean = 7.07 individuals per km², standard error [SE] = 0.21) than in any other season and lowest in summer (mean = 0.72 individuals per km², SE = 0.02).

Similarly, observed species richness tended to be higher offshore during autumn and winter relative to spring and summer (Fig. 3), indicating that offshore areas became more species-diverse in winter along with the general increase in predicted bird densities. In spring and summer, species richness tended to be highest nearshore.

Local and Regional Model Comparison

SCC and COG analyses were used to assess the spatial relationships between the local absolute abundance predictions and Winship et al. (2023) regional relative density predictions. We also conducted SCC analyses to compare the spatially-explicit CV estimates from each model type. However, because the results of the CV analyses provided limited additional insight, they are presented only in the Appendix (Fig. A5) and are not discussed further.

While most taxa showed positive correlations in seasonal densities, relationships varied and correlations overall were generally weak (magnitudes < 0.25; Table 1). GSCI values were relatively low for many taxa even when they were positively correlated, and some taxa were negatively correlated (Fig. 4; Table 1). Maximum, mean, and median GSCI values based on negative exponential weighting were higher than GSCI values based on inverse distance weighting (Table 1). Explanatory power (measured by R^2) varied across SCC-based comparisons and tended to increase with GSCI magnitude (Table 1). While SCC indicated general agreement between the local and regional models, negative correlations highlighted notable differences in predicted spatial patterns of marine bird density for certain combinations of taxon and season. Likewise, centers of gravity for local and regional model predictions showed some consistency; however, results varied considerably across taxa (Fig. 5). Overall, center of gravity estimates showed an average absolute displacement of 11.7 km (min = 1.4; max = 35.3) between the local and regional models. Local models tended to predict centers of bird distributions more towards the east of the regional models (mean = 2.8 km ± 8.5; Fig. 5). In addition, SCC results did not always align with center

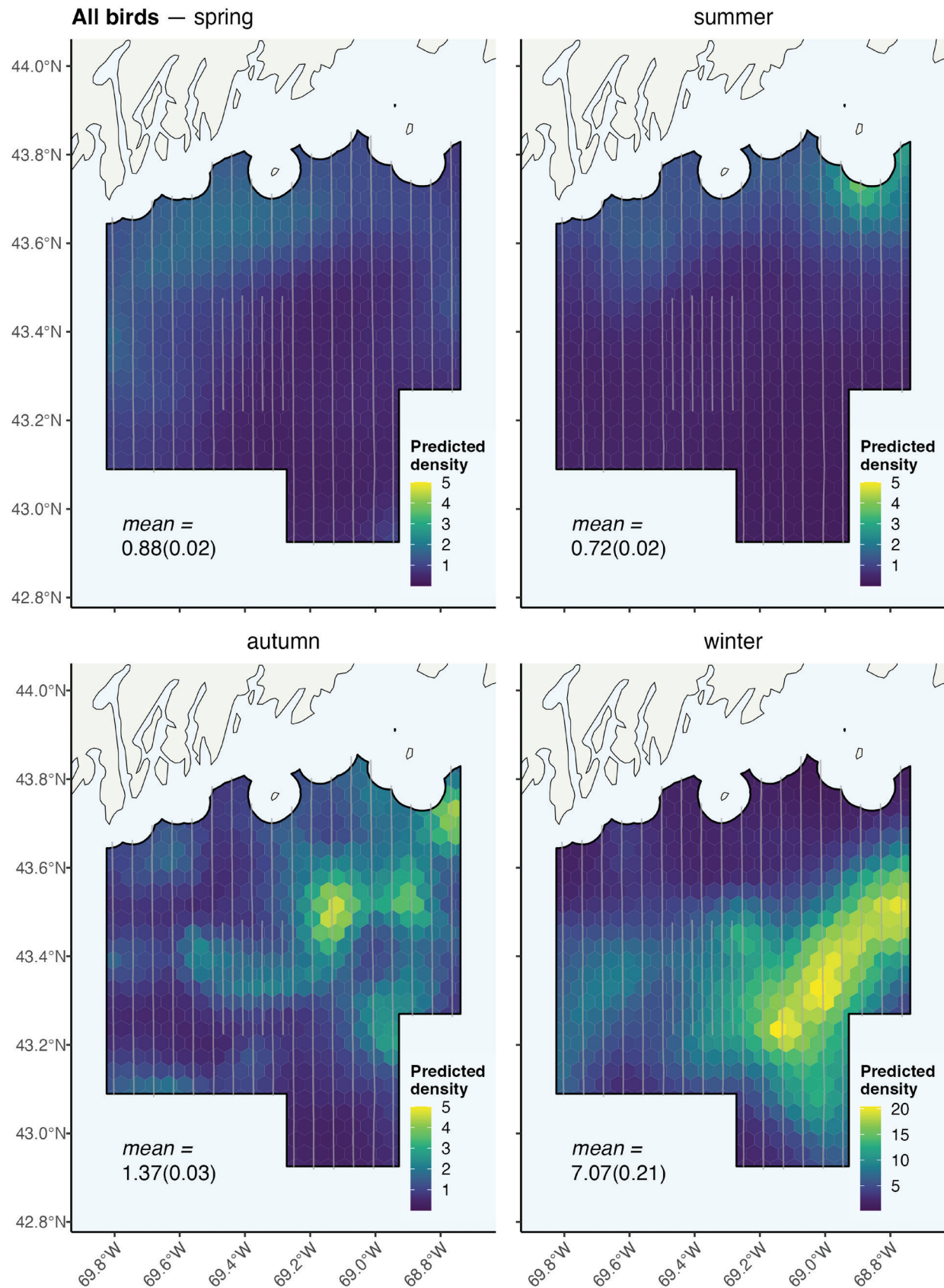


Fig. 2. Median bird densities (birds per km²) predicted by the local density models (not corrected for availability). All predicted values are greater than zero. Text annotations in the lower left of each panel indicate the mean seasonal bird density (birds per km²) and standard error for the 2023–2024 Gulf of Maine survey area. Note that the color scale for the winter panel has been adjusted to accommodate higher maximum density values. Survey transects are shown as gray vertical lines.

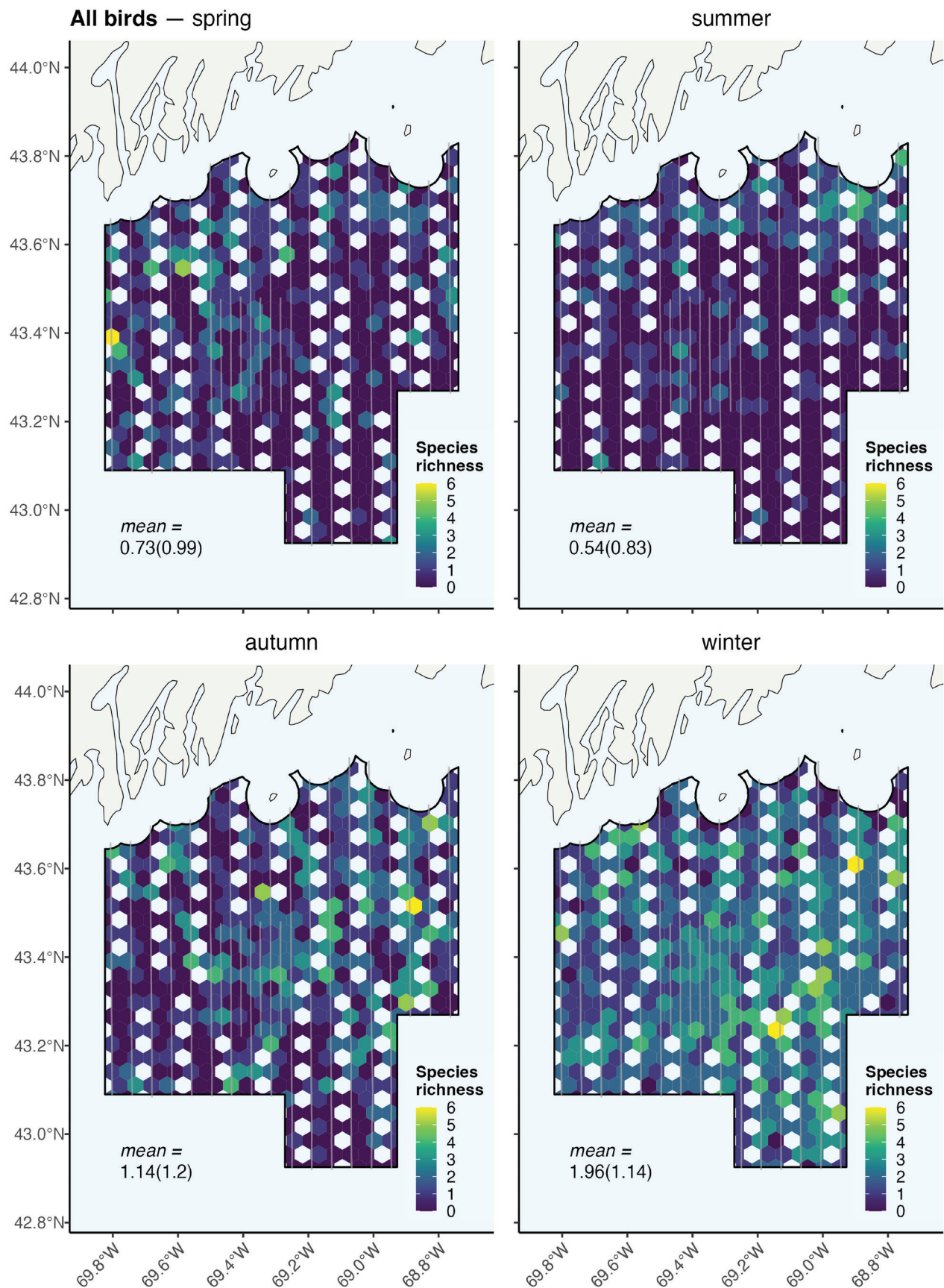


Fig. 3. Observed species richness across the hexagonal grid (4 km between cell centroids) used for the Gulf of Maine local digital aerial survey data. Text annotations indicate mean observed species richness per grid cell with standard deviation for the entire surveyed area. Empty cells were not surveyed. Survey transects are shown as gray vertical lines.

TABLE 1
Global spatial cross-correlation indices (GSCI) of scaled local and regional density estimates
and of their respective coefficient of variation (CV) estimates for all taxon/season combinations ($n = 24$)^a

Species	Season	Density				CV (Density)			
		GSCI		R^2		GSCI		R^2	
		Inverse Distance	Negative Exponential	Inverse Distance	Negative Exponential	Inverse Distance	Negative Exponential	Inverse Distance	Negative Exponential
Atlantic Puffin	spring	0.17	0.22	0.41	0.4	-0.1	-0.14	0.19	0.18
	autumn	0	0	0	0	0	0.01	0	0
Black-legged Kittiwake	autumn	0.13	0.18	0.19	0.2	0.04	0.06	0.25	0.28
	winter	0.15	0.2	0.34	0.34	0.04	0.05	0.03	0.03
Bonaparte's Gull	autumn	-0.05	-0.06	0.04	0.03	-0.02	-0.02	0.01	0.01
Common Murre/murre spp.	autumn	-0.03	-0.03	0.02	0.02	—	—	—	—
	winter	-0.15	-0.21	0.39	0.37	—	—	—	—
Common Tern/tern spp.	spring	0.14	0.2	0.26	0.26	—	—	—	—
Common Tern	summer	0.01	0.02	0	0	0.1	0.13	0.29	0.27
Little Auk	winter	-0.05	-0.06	0.04	0.03	-0.07	-0.09	0.07	0.07
Great Black-backed Gull	spring	0.06	0.08	0.05	0.05	0.04	0.05	0.03	0.03
	summer	0.11	0.15	0.19	0.19	-0.05	-0.07	0.11	0.12
	autumn	0.1	0.14	0.2	0.19	-0.12	-0.18	0.29	0.32
	winter	-0.01	-0.01	0	0	-0.02	-0.03	0.01	0
American Herring Gull	spring	0.17	0.23	0.59	0.58	0	0	0	0
	summer	0.1	0.14	0.21	0.21	-0.03	-0.04	0.04	0.05
	autumn	0.08	0.11	0.18	0.17	-0.02	-0.02	0.01	0.01
	winter	0.09	0.11	0.19	0.18	0	0	0	0
Laughing Gull	spring	0.12	0.16	0.41	0.37	-0.06	-0.09	0.1	0.11
Northern Fulmar	autumn	0.03	0.04	0.06	0.06	0.11	0.15	0.2	0.2
Northern Gannet	spring	0.08	0.12	0.14	0.16	0.07	0.1	0.12	0.13
	autumn	0.1	0.12	0.19	0.16	-0.01	-0.01	0	0
Ring-billed Gull	winter	-0.07	-0.11	0.12	0.15	0.08	0.11	0.11	0.12
Wilson's Storm Petrel	summer	-0.09	-0.13	0.29	0.29	-0.05	-0.06	0.04	0.04

^a GSCI values can range -1 to 1. Coefficients of determination (R^2) indicate goodness-of-fit in the relationship between local spatial cross-correlation indices and the GSCI for the analysis in which the local scaled predictions are treated as the independent variable (see Appendix, available on the website, for more details). CVs for pooled taxa groups were not compared. Results from both weighting methods are provided.

of gravity calculations for the same taxon/season combinations. For example, local and regional centers of gravity were similar for Common Terns in summer (Figs. 5–6), but SCC-based comparisons indicated a lack of correlation between local and regional estimates (GSCI = 0.02 with negative exponential weighting; Fig. 4).

Species distributions and correlations across surveys

Local and regional models were weakly correlated for most taxa and seasons, but patterns varied substantially (Fig. 4). In general, taxon/season combinations fell into three main categories: (1) local and regional models were spatially correlated; (2) regional models suggested a more offshore distribution than local models; and (3) regional models suggested a more nearshore distribution than

local models. Selected examples of each category are discussed below. The terms “nearshore”, “inshore”, and “offshore” are used to describe patterns relative to distance from the mainland. The distinction between offshore and nearshore/inshore varies across taxa and seasons; we did not define strict geographic strata based on proximity to the mainland because the DSMs provide predictions at a relatively fine resolution compared to the size of the study area.

For Atlantic Puffins in spring, local and regional models were positively correlated (GSCI = 0.22; Fig. 4) and modeled distributions had similar centers of gravity (Fig. 6A). However, the regional model indicated a distribution that extended farther offshore and was less patchy than the local model (Figs. 6D and 6G), the latter of which was based on $n = 36$ sightings (Table A2, Appendix).



Fig. 4. Global spatial cross-correlation indices (GSCI) comparing scaled local and regional density estimates for all taxon-season combinations ($n = 24$), calculated using negative exponential weighting for the distance between locations. The GSCI quantifies the broadscale spatial cross-correlation between the two model estimates across the entire Gulf of Maine study area. Index values can vary from -1 to 1 ; blue indicates values < 0 (negative correlations), yellow indicates values > 0 (positive correlations), and gray indicates no correlation (values of 0). Common names and alpha codes are shown on the vertical axis.

Common Tern distributions in summer were not strongly correlated between the two models (GSCI = 0.02 ; Fig. 4), due to a more widespread distribution in the regional model (Fig. 6H), but they had similar centers of gravity (Fig. 6B). Predicted densities from the local model were spatially patchy (based on $n = 95$ sightings;

Fig. 6E, Table A2), while the regional model predicted more uniform densities across the study area.

Where local and regional models were not well correlated spatially, regional models tended to predict higher densities nearer shore

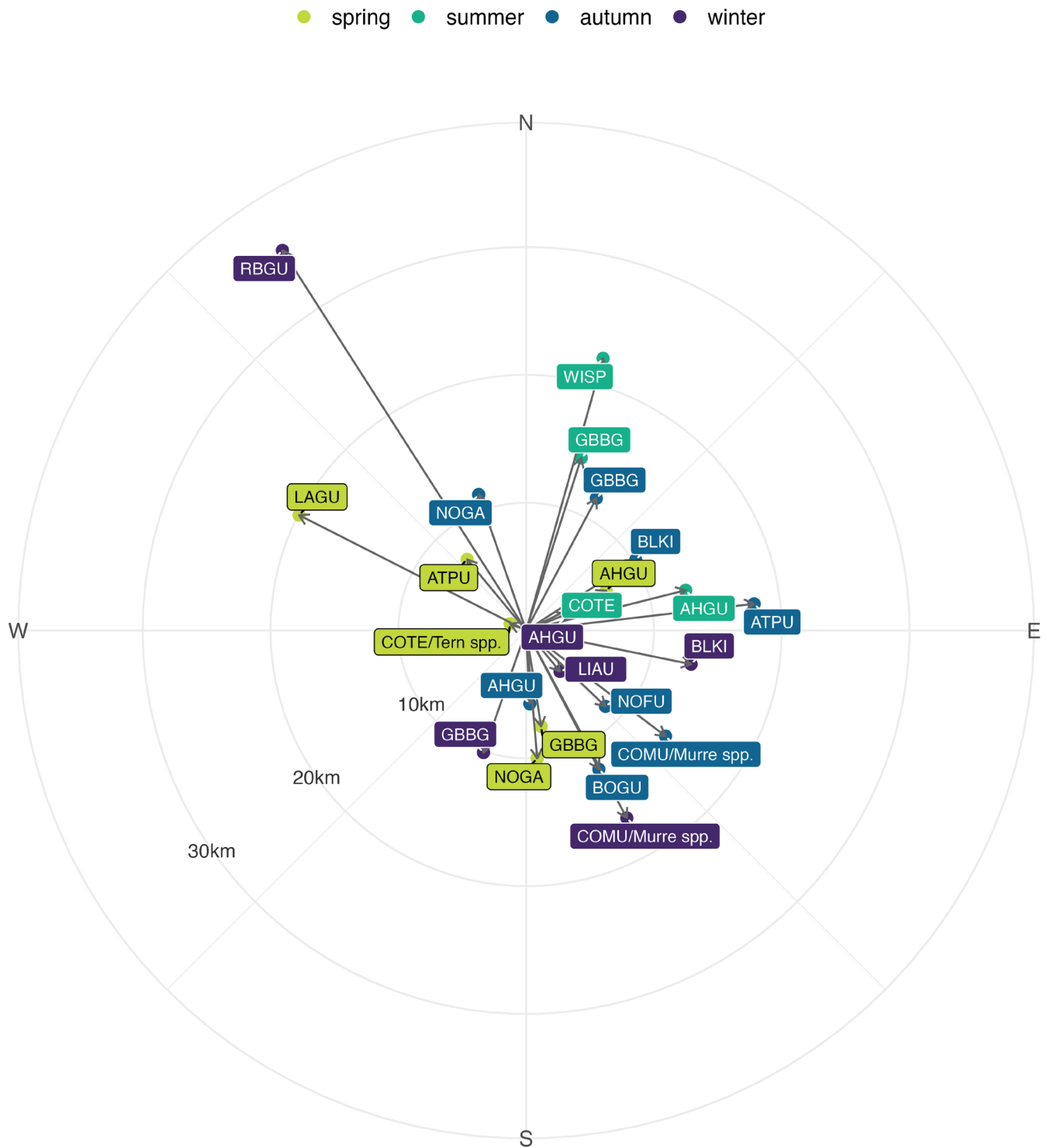


Fig. 5. Direction and magnitude of shifts in centers of gravity (COGs) of the local density model predictions relative to the COGs of the regional model predictions. The radial plot shows a compass direction of the local COG relative to the regional COG. The concentric circles show the magnitude of the distance (km) between the COGs. Colors indicate season of model comparison, and text labels indicate species/taxonomic group via alpha code (defined in Fig. 4). For example, the predicted COG for winter Ring-billed Gull (RBGU) from the local model was ~35 km north-northwest of the predicted center of gravity from the regional model. Points near the center of the plot indicate that local and regional models had similar centers of gravity (e.g., spring COTE/tern spp.).

than the local models. For example, the most commonly observed species group in local models was murre during the winter survey. For Common Murre and murre spp. in winter, the two

modeled distributions were negatively correlated (GSCI = -0.21; Fig. 4), with a clear difference in distributions tending nearshore in regional models (Fig. 6I) and offshore in local models (Fig. 6F).

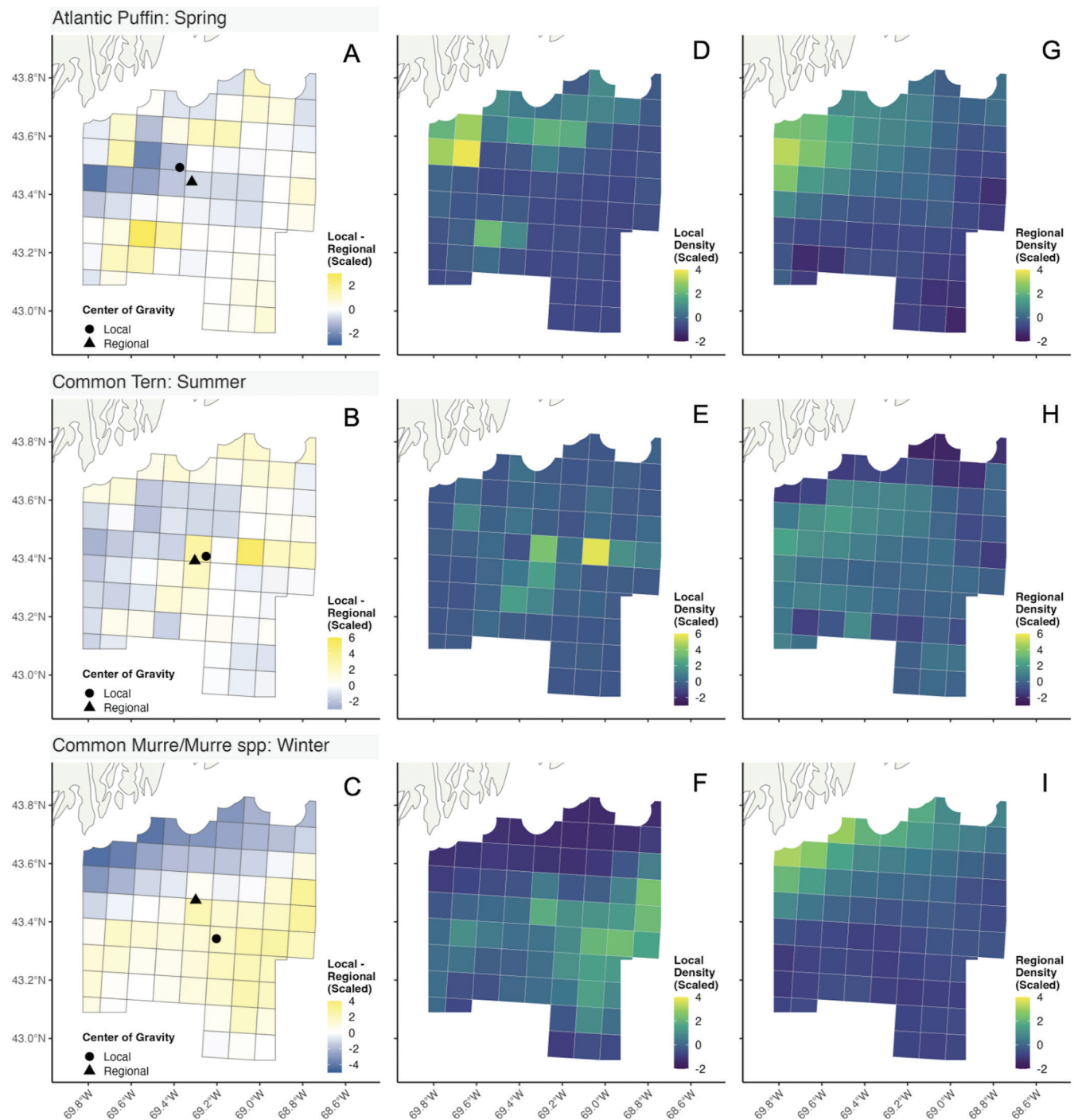


Fig. 6. Scaled density maps for Atlantic Puffins *Fratercula arctica* in spring (top row), Common Terns *Sterna hirundo* in summer (middle row), and Common Murres *Uria aalge*/murre spp. in winter (bottom row). Panels A–C show the absolute differences in scaled density values between the local and regional models, as well as the center of gravity (COG) for each model (white: no difference between model values; yellow: local > regional value; blue: regional > local value). Panels D–F show the scaled values from the local model, and panels G–I show the scaled values from the regional model. The remaining 21 sets of taxon-season scaled density maps are presented in the Appendix, available on the website (Fig. A4, Appendix).

Centers of gravity also differed distinctly between the two modeled distributions (Fig. 6C). In this case, the number of sightings used to build the local model was high ($n = 3,315$) and CVs for both models were higher nearshore, suggesting that local models likely represent the true distribution of birds, at least for the narrow time window within which survey data were collected.

A similar pattern was observed for other species, such as Northern Gannets in spring, where the local model suggested a more offshore distribution than the regional model (Fig. A4), though unlike for murre, the two models were mildly positively correlated ($GSCI = 0.12$; Fig. 4). There were also a few notable taxon/season combinations for which regional models predicted a more offshore

distribution than the local models, such as Ring-billed Gulls in winter and Wilson's Storm Petrels in summer (Fig. 5; also see scaled density maps in Appendix, Fig. A4).

DISCUSSION

We applied rigorous statistical methods to compare marine bird density predictions from local and regional models within a portion of the Gulf of Maine. The Gulf of Maine supports a diverse and productive marine ecosystem, yet key taxa such as marine birds have been understudied in recent decades. This lack of ecological information and understanding may hinder effective management as interest in offshore wind energy development continues to grow. The local, fine-scale digital aerial surveys conducted in this study address a critical information gap by providing updated estimates of marine bird densities in the Gulf of Maine.

Predicted densities based on spatially explicit analysis of local digital aerial survey data indicated that spatial patterns in marine bird densities changed considerably across seasons; highest densities were predicted closer to the coast (i.e., within ~20 km) in the spring and summer and farther from the coast (> ~20 km) in autumn and winter (Fig. 2). Bird species richness was highest nearshore (< ~20 km from shore) during spring and summer but shifted offshore (> ~15 km from shore) during autumn and winter (Fig. 3). Species composition in the winter primarily consisted of auks and gulls, while the summer community mostly comprised shearwaters *Procellariidae* and terns. American Herring Gulls and Great Black-backed Gulls were observed year-round. Spatial patterns in densities varied considerably across taxonomic groups, although hotspots of high density and diversity were found along the coast in summer and offshore to the southeast of the survey area in winter. These patterns were likely due to breeding birds foraging near coastal or island colonies (Boyd et al., 2014; Gutowsky et al., 2021) and a large annual influx of overwintering migrants (Baran et al., 2022).

In the spatial cross-correlation analysis of density predictions from the local and regional models, weak positive correlations were the most common outcome, although spatial patterns were not well matched for several taxon-season combinations. Of the 24 combinations evaluated under each weighting scheme, 14 produced GSCI values > 0.05 in both inverse distance and negative exponential analyses. The maximum correlation was 0.17 for inverse distance weighting and 0.23 for negative exponential weighting, suggesting stronger agreement between the models over shorter distances. This finding was likely due to the increased patchiness of the predicted densities from the local models compared to the broader gradients in predicted densities from the regional models.

Interpretation of the COG analysis requires caution because this metric is a simplification of the information in the spatial density predictions. We found minimal differences in COGs for 12 taxon-season combinations (< 10 km between local and regional centers). However, this sometimes provided a misleading impression of how well the predicted densities aligned. For example, the COGs for Black-legged Kittiwakes in winter were relatively close. However, the local model predicted a long, narrow band of high density along a northeast-southwest axis located offshore, whereas the regional model predicted a more uniform distribution throughout the study area, with slightly higher densities offshore. The summer models for Common Terns provided another example of similar COGs, yet

the local model predictions were patchy and the regional model predictions were more uniform (Figs. 6B, 4E, 4H). The greatest difference in COGs between models was seen in Ring-billed Gulls, where the local model predicted higher densities much farther inshore than the regional model. In our experience, this species is observed relatively rarely offshore in the Gulf of Maine, and indeed the regional model predictions for January were highest along the coast, farther inshore than the current study area, especially to the northeast (see Fig. D-23 in Winship et al., 2023). In general, different COGs provided a reliable signal of real differences in spatial density predictions between the models, while interpretation of comparisons resulting from similar COGs should draw on additional information from the spatial cross-correlation analysis and visual inspection of the scaled density maps.

Causes of Mismatched Spatial Patterns in Density

Although the results of local and regional density models may differ for many reasons, three overarching factors are likely to underlie these differences: variation in sampling scope, differences in analytical methods, and environmental changes across multiple temporal scales. Understanding the contributions of these factors can help prioritize future data collection and modeling efforts.

The data used to build the local and regional models of marine bird densities in the Gulf of Maine study area had different spatial and temporal scopes. The local survey included only four surveys over a one-year period from a relatively small study area. Marine bird distributions are spatially dynamic over multiple temporal scales (Certain et al., 2007; Ouled-Cheikh et al., 2020). The lack of surveys across multiple months within a season or over multiple years makes it impossible to distinguish intraseasonal trends from temporal variability over shorter periods (e.g., monthly, weekly, daily, or hourly). In contrast, the regional models integrated data collected over a 20-year period across the Gulf of Maine to the Florida Straits. Survey effort used in the regional models was unevenly distributed in both space and time, and limited data from the Gulf of Maine were available for inclusion.

The differences in analytical methods are particularly complex because the datasets and analytical objectives were different between the two modeling endeavors. The local models were designed to assess the observed spatial patterns in marine bird absolute density in the Gulf of Maine during four distinct seasons, with each season surveyed only once. Because the survey area was uniformly sampled with standardized transect spacing and each season was modeled independently for each taxon, a purely spatial model provided the best fit to the data. Given data spanning additional years of surveys, models would likely require environmental covariates to explain inter-annual variability in the spatial patterns. Due to their strict reliance on spatial random effects, the local models cannot be used to predict future states subject to environmental changes.

In contrast, the regional models, which were based on multi-year observations, relied on relationships with environmental covariates, but those relationships were inferred from data collected across the entire Atlantic OCS (Winship et al., 2023). Due to unreconciled differences in the data collection methods across the datasets incorporated into the regional models, the predictions were of relative density. The spatial cross-correlation analysis relied on centered and scaled estimates of density because of the differences

in the scale of the predicted density estimates from the two model types. For taxon-season combinations that had relatively low predicted densities in the study area relative to other areas and seasons in the regional models, the transformed density predictions used in the SCC analysis may produce misleading results by amplifying minor variations in spatial patterns that were relatively uniform overall (Winship et al., 2023; e.g., murre and Atlantic Puffin in October, Ring-Billed Gull in January). In addition, although the regional models were built using environmental data collected during the same period as the sighting surveys, and the environmental data used to extrapolate the model results to the prediction rasters were based on the same contemporaneous data, those contemporaneous predictions were averaged to generate the rasters of long-term average predicted densities that we used in our spatial cross-correlation analyses. We should not expect the long-term average of predicted species densities to tightly reflect actual densities at any single point in time.

These analytical differences also emphasize the differing structures of the models, which affect how uncertainty is estimated and propagates to the estimates of uncertainty in predicted densities. Uncertainty in the local models depended on statistical boundary conditions and the estimated uncertainty in the spatial correlation function parameters for the precision and the inverse geostatistical range. In contrast, uncertainty in the regional models was partially a function of the estimated uncertainty in the covariate relationships across the Atlantic OCS. The Gulf of Maine is at the extreme end of some oceanographic variables on the US Atlantic coast, so this could translate into additional uncertainty in the regional model predictions at this location.

Finally, recent environmental changes appear to be affecting distributions of marine predators in the North Atlantic (Braun et al., 2023). The Gulf of Maine is currently undergoing significant ecosystem changes that are expected to continue. Over the last 20 years, these changes include an overall rapid rise in ocean temperature at multiple depths (Seidov et al., 2021), several marine heatwaves (Townsend et al., 2023), and phenological shifts (Staudinger et al., 2019; Thomas et al., 2017). Under high emissions scenarios, average sea surface temperatures are expected to increase by 1.1–2.4 °C by 2050, in addition to salinity and stratification changes (Pershing et al., 2021). Climate change modeling also predicts drastic declines in key prey species, such as the copepod *Calanus finmarchicus*, in the Gulf of Maine over the next several decades (Grieve et al., 2017), as well as impacts to forage fish, such as sand lance *Ammodytes* spp. (Suca, 2021), and commercially important species, like Atlantic cod *Gadus morhua* and American lobster *Homarus americanus* (Pershing et al., 2021).

The effects of ocean climate change on higher trophic levels, including marine birds, have already been documented and may be more extensive than current observations suggest. For several auk species, breeding phenology and diet have changed in recent decades in response to ecosystem changes in the Gulf of Maine (Major et al., 2021; Scopel et al., 2019). Additional studies highlight warming-related effects on reproductive success, nestling diet, and growth rates in Northern Gannets and Common Terns (d'Entremont et al., 2022; Smith & Craig, 2023). Environmental covariates such as sea surface temperature, freshwater input, and stratification strongly influence forage fish distributions (Goetsch et al., 2023), and these relationships, in turn, affect marine bird movement behaviors (Gulka et al., 2023). Marine birds are highly mobile

and responsive to environmental change, so sudden shifts in their distributions that reflect inter-annual variability or climate-related trends should be expected in rapidly changing ecosystems (Grémillet & Boulinier, 2009; Sydeman et al., 2012). Climate change scenarios predict marine species distribution shifts to the northeast on the northeastern US continental shelf (Morley et al., 2018), and a recent study documented significant northeast shifts for some species in the southern Gulf of Maine (Mills et al., 2024). In our study, COGs derived from local models were displaced northeast relative to those derived from the regional models. This pattern suggests that climate is a contributing factor to differences between the models. However, because variation in COG location among species was high, this result should be considered exploratory.

Currently, insufficient information exists to attribute the observed differences between the model types to one or more of these causative factors. Thus, we were unable to determine which model type provides the ‘best’ predictions of marine bird densities in the study area under the present conditions. Measured model uncertainty was high in many cases, and there was unmeasured uncertainty regarding the extent to which the observations approximate long-term stationary distributions for these taxa. Additional data are needed to determine the degree to which the local model predictions primarily reflect short-term (e.g., daily or inter-annual) variability in distributions versus more substantial changes in marine bird distributions relative to the recent past.

RECOMMENDATIONS

Quantifying risk to marine birds from offshore wind energy development and other human activities requires more than four surveys of the area of interest over a one-year period. Likewise, regional models are not designed to inform site-specific decisions on their own. Integrated density models could be a useful approach to determine how the new local data presented here could be used to update assessments of habitat use or habitat change over time (Matthiopoulos et al., 2022).

Offshore wind risk assessments should consider the information from regional models as providing context for interpreting the results of local studies (Avian Displacement Guidance Committee, 2023; Winship et al., 2023). Limitations of our two modeled data products for site characterization purposes became clear when they were compared. For many species and seasons, the local and regional models were not well correlated, and it was difficult from existing information to assess which model was ‘better’ for informing risk assessments. Overall, we recommend following existing guidance for site characterization surveys (Avian Displacement Guidance Committee, 2023; BOEM, 2020), including increasing survey frequency over a considerably longer study period. We also recommend adhering to guidelines for pre- and post-construction surveys designed to assess the effects of offshore wind energy development on marine birds (Avian Displacement Guidance Committee, 2024), including ensuring surveys are of a suitable scale and resolution to determine displacement of marine birds, if it occurs.

Additional survey data are needed to inform our understanding of marine bird distributions in the Gulf of Maine, including in and around commercial leases for offshore wind energy development. While some local bird surveys have occurred in recent years, these surveys have had highly variable effort and are typically not located

in areas of planned commercial-scale offshore wind development (Fig. 1). In addition, weather-related limitations have historically meant that few surveys are conducted in winter (Winship et al. 2023). Marine bird densities were an order of magnitude higher in winter than in any other season in the local surveys, suggesting that this is an important data gap for understanding the potential risk of offshore wind energy development and other offshore activities to the marine bird community in the Gulf of Maine.

Large numbers of auks, particularly murre, were observed in the study area in winter during local surveys. These taxa could be a fruitful target for further research in the Gulf of Maine given: (1) their seasonal abundance; (2) the lack of spatial correlation between the local and regional surveys, suggesting that further work is required to understand their winter distributions; and (3) their known behavioral responses to offshore wind energy development (Grundlehner et al., 2025; Lamb et al., 2024).

CONCLUSIONS

As offshore wind energy development proceeds in the Gulf of Maine and elsewhere in the US, site-specific observational survey data are needed to understand local species occurrence and density and to inform decision-making related to offshore wind energy development and other human activities (e.g., Wallach et al. 2025). Region-scale models are not designed to inform such fine-scale risk assessments and decision-making. Likewise, local surveys with limited spatiotemporal scope (e.g., four surveys conducted over a single year, as in this study) cannot adequately characterize marine bird distributions to address the questions that decision makers have regarding the potential impacts of alternative development scenarios on marine bird populations. The results of this study suggest that predictions from local and regional models may lead to different conclusions about the potential effects of offshore wind energy developments on marine birds in the Gulf of Maine, as well as optimal siting of such developments to mitigate impacts. Available guidance on the design and spatiotemporal scope of local surveys (e.g., Avian Displacement Guidance Committee, 2024; BOEM, 2020) should be followed during offshore wind energy siting and permitting to ensure that sufficient data are available to inform decision-making.

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AUTHOR CONTRIBUTIONS

Conceptualization: MCF, EMA, MEM, IJS, ATG, AJW, KAW. Funding acquisition: KAW, EMA, IJS, ATG. Formal analysis: MCF, EMA, MEM. Writing: MCF, EMA, MEM, IJS, ATG, AJW, KAW.

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