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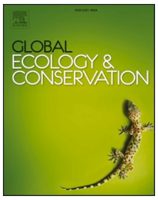

Original research article

Seasonal waterbird distribution patterns vary in response to current shellfish aquaculture and areas suitable for future development in Rhode Island USA

Dylan L. Bakner[a,*], Tori Mezebish Quinn[a], Martina S. Müller[a], Peter W. Paton[a], Jennifer E. Kilburn[b], Scott R. McWilliams[a]

[a] *Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA*
[b] *Rhode Island Department of Environmental Management Division of Fish and Wildlife, West Kingston, RI 02892, USA*

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ABSTRACT

Marine aquaculture is globally widespread and supplies most of the world's shellfish. In the United States, shellfish aquaculture spans all coastlines, with states like Rhode Island experiencing recent substantial increases in aquaculture. Rhode Island's marine ecosystem supports numerous migratory waterbird species, and the expansion of shellfish aquaculture has the potential to directly impact the distribution of these species. We used land-based survey data to assess whether and how distance to shellfish aquaculture affects seasonal waterbird distribution patterns and identify species most and least likely to be impacted by future aquaculture development. We conducted a total of 3698 surveys across 54 study sites from 2020—2023 and fit monthly generalized additive mixed models to predict waterbird distributions for 29 species. For most waterbird species, distance to aquaculture explained little to no spatial variation in their monthly distribution patterns; indicating other resource layers were more informative. Dabbling ducks often favored closer proximity to aquaculture, while sea ducks, mergansers, gulls, and terns showed species-specific preferences, and herons and egrets consistently favored shallower waters. Using model-derived distributions, we found that ~28 % of species preferred areas better suited for future aquaculture development, while ~10 % favored areas poorly suited. Our research provides valuable insights into the factors driving waterbird distributions, particularly in relation to their proximity to current shellfish aquaculture. Our findings suggest that although current aquaculture operations are not having substantial impacts on species distribution patterns, future development will likely conflict with species favoring shallow waters, as these areas are also most suitable for aquaculture expansion.

1. Introduction

Over the last three centuries, coastal marine landscapes worldwide have shifted from being predominantly wild to more anthropogenic, primarily due to food production and urbanization (Ellis et al., 2010; FAO, 2024). Landscape alteration has led to shifts in bird

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* Corresponding author.
E-mail addresses: dylan.bakner@uri.edu (D.L. Bakner), tmezebish@uri.edu (T.M. Quinn), martina@uri.edu (M.S. Müller), ppaton@uri.edu (P.W. Paton), jennifer.kilburn@dem.ri.gov (J.E. Kilburn), srmcwilliams@uri.edu (S.R. McWilliams).

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distributions which have caused major population declines or extinctions in some species (Dirzo et al., 2014; Singer et al., 2020; Wang et al., 2022), although populations of other species have remained stable or increased (Clavel et al., 2010; Ducatez et al., 2018; Barrett et al., 2019). Marine aquaculture (i.e., the farming of aquatic organisms) has rapidly grown since the 1950s, with commercial production now accounting for the majority of the world's supply of shellfish (Naylor et al., 2021; FAO, 2024). Assessing the effects of marine aquaculture on waterbird species is complex. For instance, aquaculture can increase local abundance and species diversity (Barrett et al., 2019); however, habitat generalists appear to benefit more as they are better adapted to use resources in landscapes dominated by aquaculture, while habitat specialists are less adaptable (Clavel et al., 2010; Ducatez et al., 2018). Therefore, it appears aquaculture provides habitat, or resources, to some species and populations while providing little to others.

In the United States, shellfish aquaculture extends across all coastlines, with oysters (*Crassostrea spp.*) being the most profitable crop, generating over $200 million annually in recent years (NOAA, 2022). The Atlantic coast is currently the most lucrative area (NOAA, 2022), where oysters were historically grown by either planting crop directly into the substrate or by placing them in mesh or rack bags positioned above the substrate (Botta et al., 2020). In more recent years, however, the shellfish aquaculture industry has used floating cages (i.e., cages float on water surface) to grow crops (Canty et al., 2020; Campbell and Gray, 2024) which may change how marine wildlife interacts with aquaculture.

Shellfish aquaculture has become an important industry in Rhode Island, USA, growing rapidly from just six farms in 1996 to 84 farms by 2022 (Goetsch, 2022). Much like the rest of the Atlantic coast, farms increasingly use floating gear, and oysters account for 99 % of total shellfish production, yielding an annual gate value exceeding $8 million. The coastal lagoons of Rhode Island are shallow water bodies separated from the Atlantic Ocean by beach barriers. Though they comprise a relatively small portion of the coastline, they provide the best conditions for shellfish aquaculture (Vinhateiro, 2024). Currently, regulations established by Rhode Island's Coastal Resources Management Council restrict aquaculture, regardless of crop type, to no more than 5 % of the total area within the coastal lagoons; a limit that has nearly been reached in some of the lagoons (Coastal Resources Management Council Working Group, unpublished report). Consequently, recent expansions in shellfish aquaculture have shifted to Narragansett Bay, the largest estuary in New England, where fewer restrictions apply.

Narragansett Bay and the coastal lagoons of Rhode Island are used by numerous migratory waterbird species especially during winter (McKinney et al., 2006, 2015), and the expansion of shellfish aquaculture in these areas has the potential to directly impact the distribution of these species (Barrett et al., 2019; Bath et al., 2023). For instance, some waterbird species are drawn to aquaculture, as these areas support high prey availability during specific times of the year (Cheng et al., 2022; Bath et al., 2023; Burr et al., 2023). Other waterbird species are attracted to the structures associated with aquaculture, especially cage floats, as they serve as convenient roosting sites (Comeau et al., 2009; Caron et al., 2023; Cunningham et al., 2023). Conversely, vessel activity and human presence

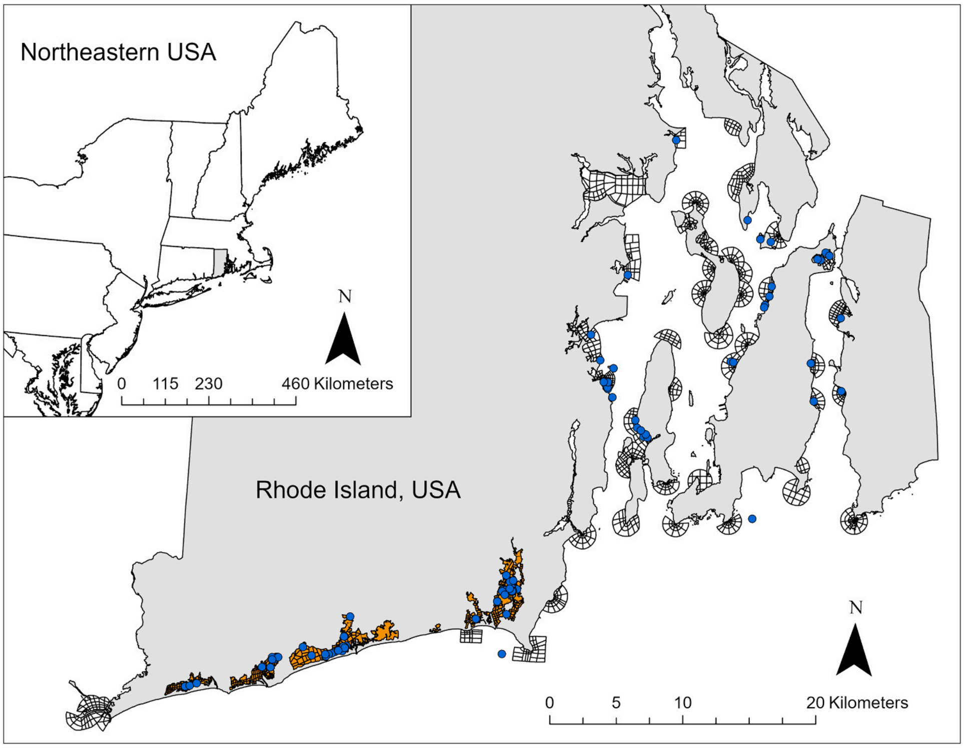

Fig. 1. Study area map of Rhode Island, USA showing the locations of 54 study sites where land-based waterbird surveys were conducted throughout Narragansett Bay and coastal lagoons (colored orange) from 2020–2023. Each study site was divided into different sized grid cells based off landmarks that could be used to delineate grid cell boundaries. Blue points show locations of active aquaculture farms during the study period.

associated with shellfish aquaculture can displace certain waterbird species from their preferred areas (Pease et al., 2005; Schwemmer et al., 2011). Therefore, shellfish aquaculture can both negatively and positively affect waterbirds and thus change their distributions (Ji et al., 2024; Xu et al., 2020). However, the extent to which the distributions of certain species are affected remains unclear.

Understanding the relationships between waterbird distributions and shellfish aquaculture farms is essential for effective spatial planning that considers wildlife impacts and for determining appropriate solutions to mitigate bird conflict at shellfish aquaculture facilities (Glahn et al., 1999; Burr et al., 2020; Montevecchi, 2023).

Here, our goal was to evaluate the influence of shellfish aquaculture on seasonal waterbird distribution patterns in Narragansett Bay and coastal lagoons by estimating occurrence probabilities across the landscape for each species as well as taxonomic groups (e.g., geese, dabbling ducks, gulls and terns). Our research objectives were to 1) assess whether and how shellfish aquaculture farms affect seasonal occurrence probabilities of different waterbird species in southern New England, and 2) use model-derived species distributions to identify waterbird species most and least likely to be affected by future shellfish aquaculture development. To meet our objectives, we conducted weekly land-based waterbird surveys over three years at 54 sites across coastal Rhode Island that varied in their proximity to shellfish aquaculture operations. We predict that waterbird distribution patterns will vary in response to shellfish aquaculture farms, both at the species and group levels. However, we predict the potential impacts of future shellfish aquaculture development on waterbirds will be primarily species-specific because waterbird species respond differently to disturbance, (Pease et al., 2005; Schwemmer et al., 2011). Additionally, shellfish aquaculture may create novel foraging opportunities for certain species, leading to distribution patterns that favor areas near aquaculture sites (Cheng et al., 2022; Bath et al., 2023; Burr et al., 2023). At the group level, waterbirds differ in how they use our study area and so the extent to which they encounter aquaculture farms. For example, sea ducks typically forage in deeper offshore waters (Baldassarre, 2014), whereas egrets feed in shallow nearshore areas (Trocki and Paton, 2006). Consequently, waterbird groups that depend on shallow coastal area are more likely to spatially overlap with aquaculture operations, increasing the likelihood of interaction and potentially influencing their distribution patterns.

2. Methods

2.1. Study area

Our study area was located in Narragansett Bay, situated in the central part of Rhode Island, and in the coastal lagoons, which are found along the southwestern coastline (Vinhateiro, 2024; Fig. 1). Narragansett Bay is a ~35,000-hectare urban estuary that extends ~40 km in length from north to south (McKinney et al., 2015). Our 54 study sites were strategically placed to encompass the diverse habitats and landscape features across the state, which are known to influence species distributions (McKinney et al., 2006, 2015). Each study site was divided into different sampling units (hereafter, grid cells; Fig. 1) based on the number of available landmark features that could be used to define grid cell boundaries. Grid cells averaged 6.2 ± 6.6 ha in size, and the delineation of these grid cells allowed us to match waterbird presence-absence data to resource layers (see methods below) to predict species distribution patterns across the entire study area.

2.2. Waterbird data

We conducted land-based waterbird surveys roughly once per week from January 2021 — April 2023, at 54 study sites in total (Fig. 1). In addition, in December 2020, initial surveys were conducted as part of a pilot study across 21 study sites, each surveyed an average of 4 ± 1.3 times during that month. In 2021, surveys were conducted throughout the entire year, at all 54 study sites, with each being surveyed an average of 45 ± 18.7 times that year. The notable variation in survey replicates for 2021 reflects reduced sampling effort occurring at 9 sites located around Prudence Island (Bristol, Rhode Island), which were surveyed monthly. In 2022, surveys were conducted at 53 study sites from January — May, with each site being surveyed on average 20.5 ± 12.5 times. Sampling efforts were reduced during the summer months because most of the waterbird species in our study area were migratory and had departed for their breeding grounds. Like 2021, the large variation in survey replicates in 2022 was due to monthly sampling occurring around Prudence Island. In 2023, surveys were conducted from January — April at 4 study sites as part of a separate research project. We surveyed each of these study sites an average of 21.8 ± 1.5 times during these four months.

During each survey, observers used 20–60x powered Swarovski ATS 80 spotting scopes to document the presence of waterbird species within each grid cell. Each survey was conducted from the same fixed location on the shoreline. Birds standing, sitting, or swimming within grid cells were recorded as present, while birds observed flying were not included in our analyses. Surveyors used as much time as needed to identify all species present within grid cells, and surveys averaged 28 min (range = 2—244 min). All surveys were conducted at open-water sites; therefore, we assumed perfect detection.

2.3. Resource layers

We considered a suite of resource layers which we expected a priori to influence the distribution patterns of waterbirds and included these layers as covariates in models outlined below. Resource layers were provided by the Rhode Island Geographic Information System (hereafter, RIGIS; Rhode Island Geographic Information System, 2024) and the Nature Conservancy (The Nature Conservancy, 2020). From RIGIS, we obtained a raster data layer containing water depth and shapefiles that outlined boundaries for different sediment types (i.e., mud, sand, or gravel bottom), submerged aquatic vegetation beds (i.e., eel grass [*Zostera spp.*] and widgeon grass beds [*Ruppia maritima*]), shorelines, and active aquaculture farms. The aquaculture shapefile primarily represented oyster farms (99 %), with a small portion of farms cultivating other species, such as blue mussels (*Mytilus edulis*), clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and sugar kelp (*Saccharina latissimi*; Goetsch, 2022). Consequently, this resource layer predominantly reflects floating oyster farms. The sediment type shapefile provided by RIGIS did not include data for Narragansett Bay. To address this, we utilized a second sediment type shapefile from the Nature Conservancy for these areas and merged the two shapefiles together. We used the Calculate Geometry tool in ArcGIS Pro version 3.2.0 (Esri, Redlands, CA, USA) to determine the centroid of each grid cell. We then used the Euclidean Distance tool to create raster layers that indicated the distance between centroids and shapefile (i.e., resource) boundaries. All raster layers considered in our analyses were scaled to 30-m resolution.

2.4. Distribution model

We modeled probability of occurrence across our study area for each species in our dataset by fitting Bayesian generalized additive mixed models in R (R Core Team, 2024) version 4.1.1. We fit models using the ‘brms’ package (Bürkner, 2017) which interfaces with the ‘mgcv’ package (Wood et al., 2016) to fit smoothing terms (i.e., nonlinear effects). We employed the Bernoulli family to model our presence-absence data where each species had the potential to be detected in each grid cell during each survey. We used the logit link function to evaluate the relationship between probability of occurrence and resource layers. We considered the distance from grid cell centroids to mud bottom, sand bottom, gravel bottom, submerged aquatic vegetation beds, shoreline, and aquaculture farms as fixed effects in our models. Additional fixed effects included in each model were the latitudinal positioning and water depth of grid cell centroids, and grid cell size. We specified smoothing terms for all fixed effects except grid cell size which we held as a linear effect. We used a Pearson correlation coefficient to test for correlation among covariates. Distances to submerged aquatic vegetation beds and mud bottom were highly correlated with other covariates ($|r| > 0.7$); hence, we excluded these two resource layers from the distribution models (Dormann et al., 2013). In addition to fixed effects, we considered grid cell identity (hereafter, ID) as a random effect in all models.

To evaluate whether aquaculture was an important predictor of waterbird distributions, we fit one global model for each species, followed by a reduced model that contained all the same fixed and random effects except distance to aquaculture (hereafter, reduced model). We also fit a null model that contained only the random effect of grid cell ID, which was used to calculate the variance explained by fixed effects for global and reduced models (Grosbois et al., 2008). We then calculated the variance attributed to distance to aquaculture by subtracting the variance explained by the reduced model from that of the global model. Because waterbird species composition and distributions in our north-temperate study area include mostly migratory species that are resident during either breeding (i.e., May—August), wintering (i.e., November— March), or migrating periods (i.e., spring migration: April— May; autumn migration September— November) of the annual cycle, we fit separate sets of models for each month for each waterbird species. To ensure an adequate sample size for models to converge, we only fit monthly models for a given species when there were > 50 detections of that species within a given month. Prior to running our models, we scaled all covariates to have a mean of 0 and a standard deviation of 1. After executing the models, we used the ‘predict’ function within the ‘raster’ package to produce monthly raster files that contained probability of occurrence values across our study area for each species (Hijmans, 2024). All predicted raster files were scaled to 30-m resolution.

2.5. Aquaculture suitability model

In order to relate predicted waterbird occurrence probabilities to areas with varying suitability for aquaculture development, we fit an aquaculture suitability model. We used a presence-absence approach to identify the areas of coastal Rhode Island that were most suitable for aquaculture relative to key resources (hereafter, aquaculture suitability index; Guillera-Arroita et al., 2015). Although the establishment of aquaculture farms is highly restricted in some areas of Rhode Island, this portion of the analysis provided insights into the areas that are and would be preferred by the aquaculture industry regardless of these restrictions. We determined the centroid locations of the polygons within the aquaculture shapefiles provided by RIGIS (Fig. 1), resulting in a set of aquaculture presence points for 2020, 2021, and 2023. Since no aquaculture shapefile was available through RIGIS for 2022, we used the 2021 data for 2022, as the locations of active farms did not change much between these years (Goetsch, 2022). For each year, we generated a set of 500 true aquaculture absence points within our study area using the Create Random Points tool in ArcGIS Pro, which served as locations where aquaculture farms were not present in that year.

We pooled the presence and absence points across years to model aquaculture suitability indices. We employed the Bernoulli family to fit a Bayesian generalized linear model in the ‘brms’ package (Bürkner, 2017). We used the logit link function to model the linear effects of water depth, distance to sand bottom, distance to gravel bottom, and distance to shoreline. Additionally, we obtained a shapefile delineating boat launch locations across the entire study area. Using the methods described above, we converted this shapefile into a distance-to raster file and considered it as a fixed effect in the model. Prior to running our models, we scaled all covariates to have a mean of 0 and a standard deviation of 1. We considered model coefficients significant when the 95 % credible intervals did not overlap zero (hereafter, CrI; 95 % CrI indicates a significant level at the 0.05 alpha level). After fitting the model, we used the predict function within the ‘raster’ package to produce a raster file that documented aquaculture suitability index values across our study area (Hijmans, 2024). The predicted raster file was scaled to 30-m resolution.

2.6. Model execution and evaluation

We fit all models for 3 chains of 5000 iterations, considered 1000 as burn-in, and saved each iteration. We assessed model convergence using the Gelman Rubin statistic where $\widehat{R}$ values < 1.05 indicated a model converged. We utilized the default uninformative priors provided by the brms package for both the fixed and random effects in our models.

We evaluated the performance of our distribution models by calculating area under the curve (hereafter, AUC) values using the 'ROCR' package (Sing et al., 2005). Any AUC values < 0.5 indicate the model provides predictions that are no better than random (i.e., unreliable estimates) whereas values of 1.0 indicate perfect predictions (Zipkin et al., 2012); values > 0.7 are generally accepted as being informative by the research community (Lemeshow and Hosmer, 1982). For each species, we calculated the AUC value for each monthly model and then determined the frequentist mean (hereafter, $\bar{x}$) ± standard deviation of these values. This approach enabled us to evaluate the overall performance of the models. While we report on all AUC values for each species considered in distribution models, we did not describe the relationships between occurrence probabilities and distance to aquaculture when a species' mean monthly AUC value was < 0.7.

Like distribution models, we evaluated the performance of our aquaculture suitability model using AUC (Lemeshow and Hosmer, 1982, Zipkin et al., 2012). To do so, we fit a model using a training dataset comprising 80 % of the data (hereafter, training model), selected at random, leaving out the remaining 20 % (hereafter, validation data; Hastie et al., 2009; Kuhn and Johnson, 2013). After executing the training model, we used the prediction function within the ROCR package to predict an AUC value for both the training and validation data (Sing et al., 2005). We ensured AUC values closely resembled one another, which indicated the performance of our aquaculture suitability model was consistent.

2.7. Connecting occurrence probabilities and aquaculture suitability indices

We assessed the relationship between occurrence probabilities and aquaculture suitability indices using one-way ANOVAs. First, we used the global models to calculate the mean probability of occurrence for each raster pixel, across months, for each species. This resulted in a single new raster file containing 562,901 pixels for each species. We then divided the aquaculture suitability index raster into five distinct range bins: 0.00–0.20, 0.21–0.40, 0.41–0.60, 0.61–0.80, and 0.81–1.00. Finally, for each range bin, we extracted the corresponding data from the mean probability of occurrence raster layer for each species. We considered mean probability of occurrence as the dependent variable and range bin as the independent variable in our ANOVAs. Due to the large size of this data set, p-values alone were poor indicators of significance (Greenland et al., 2016); therefore, we used Cohen's f statistic to determine which species occurrence probabilities were significantly different across aquaculture suitability index range bins (Cohen, 1988). We considered all ANOVAs with moderate to large effect sizes (i.e., > 0.5) to be significant; all others were deemed insignificant (Cohen, 1988).

Table 1
Total number of presence observations for 29 waterbird species surveyed in Narragansett Bay and the coastal lagoons of Rhode Island, USA, from 2020–2023.

Group	Common name	Scientific name	Observations
Geese	Atlantic brant	*Branta bernicla*	1328
Geese	Canada goose	*Branta canadensis*	2205
Dabbling ducks	Gadwall	*Mareca strepera*	303
Dabbling ducks	American wigeon	*Mareca americana*	247
Dabbling ducks	Mallard	*Anas platyrhynchos*	973
Dabbling ducks	American black duck	*Anas rubripes*	1818
Sea ducks	Greater scaup	*Aythya marila*	910
Sea ducks	Common eider	*Somateria mollissima*	3489
Sea ducks	Harlequin duck	*Histrionicus histrionicus*	502
Sea ducks	Surf scoter	*Melanitta perspicillata*	1004
Sea ducks	White-winged scoter	*Melanitta deglandi*	786
Sea ducks	Black scoter	*Melanitta americana*	1433
Sea ducks	Long-tailed duck	*Clangula hyemalis*	359
Sea ducks	Bufflehead	*Bucephala albeola*	5124
Sea ducks	Common goldeneye	*Bucephala clangula*	2646
Mergansers	Hooded merganser	*Lophodytes cucullatus*	5233
Mergansers	Red-breasted merganser	*Mergus serrator*	427
Gulls and terns	Laughing gull	*Leucophaeus atricilla*	1029
Gulls and terns	Ring-billed gull	*Larus delawarensis*	2822
Gulls and terns	Herring gull	*Larus argentatus*	11,546
Gulls and terns	Great black-backed gull	*Larus marinus*	4096
Gulls and terns	Common tern	*Sterna hirundo*	451
Loons	Red-throated loon	*Gavia stellata*	744
Loons	Common loon	*Gavia immer*	3767
Cormorants	Great cormorant	*Phalacrocorax carbo*	309
Cormorants	Double-crested cormorant	*Phalacrocorax auritus*	4760
Herons and egrets	Snowy egret	*Egretta thula*	238
Herons and egrets	Great egret	*Ardea alba*	761
Herons and egrets	Great blue heron	*Ardea herodias*	878

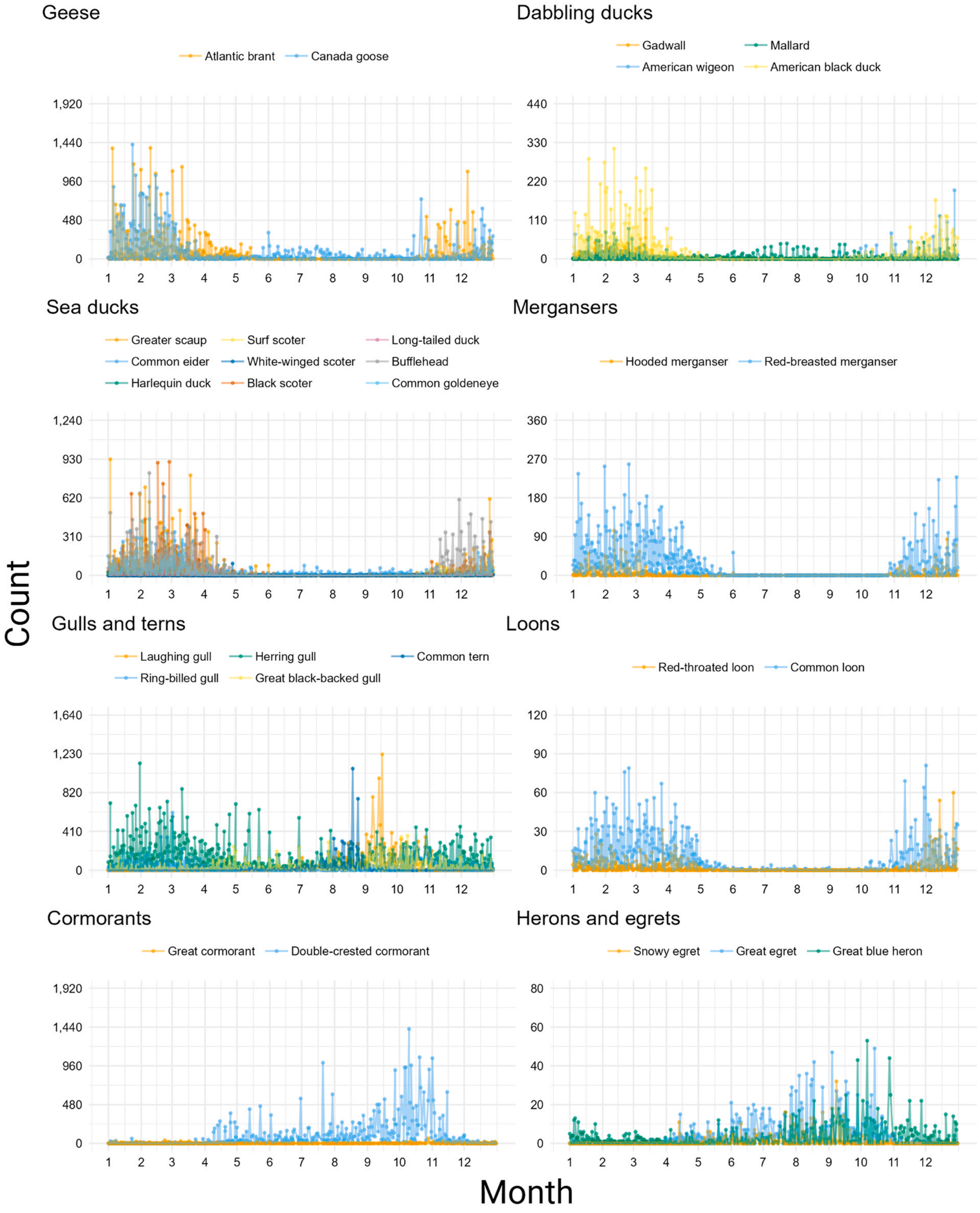

Fig. 2. Count data for different waterbird groups observed in Rhode Island, USA, from December 2020 — April 2023. The x-axis represents calendar dates of weekly surveys with labels showing month for simplicity. Using count data, waterbird occurrence data were derived and used to fit monthly generalized additive mixed models to estimate species occurrence probabilities across coastal lagoons and Narragansett Bay.

3. Results

3.1. Waterbird dataset

We conducted a total of 3698 surveys across the 54 study sites from 2020–2023, totaling 37,443 grid cell-level surveys. We observed 29 waterbird species (hereafter, focal species; Table 1) during these surveys that had sufficient data to fit distribution models. Our focal species were from the following groups: geese, dabbling ducks, sea ducks, mergansers, gulls and terns, loons, cormorants, and herons and egrets. Both group- and species-level abundance varied seasonally within our study area (Fig. 2). Most waterfowl and loons departed the study area between May–October, whereas the remaining waterbird groups were present year-round. Across all surveys, we documented a total of 60,188 presences of focal species. Gulls and terns made up most of these observations (n = 19,944 occurrences) followed by sea ducks (n = 16,253 occurrences), mergansers (n = 5660 occurrences), cormorants (n = 5069 occurrences), loons (n = 4511 occurrences), geese (n = 3533 occurrences), dabbling ducks (n = 3341 occurrences), and herons and egrets (n = 1877 occurrences). Regulated hunting is permitted for species within the goose, dabbling duck, sea duck (excluding harlequin duck; *Histrionicus histrionicus*), and merganser guilds. All species within the gull and tern, loon, cormorant, and heron and egret guilds are protected at either the state or federal level. None of our focal species are considered rare within our study area, and no species are currently listed as threatened or endangered by the IUCN. Below, we frequently present our results at the group level, as these taxonomic groups reflect similarities in resource use among the focal species.

3.2. Distribution model performance

Mean monthly AUC values were all > 0.7 (Fig. 3), except for the models of red-breasted merganser (*Mergus serrator*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), common loon (*Gavia immer*), and double-crested cormorant (*Phalacrocorax auritus*). Additionally, we only had one month of sufficient data for great cormorant (*Phalacrocorax carbo*) which prevented us from assessing mean monthly AUC values for this species. We excluded this species, as well as those with mean monthly AUC values < 0.7 from the model interpretations and ANOVAs discussed below.

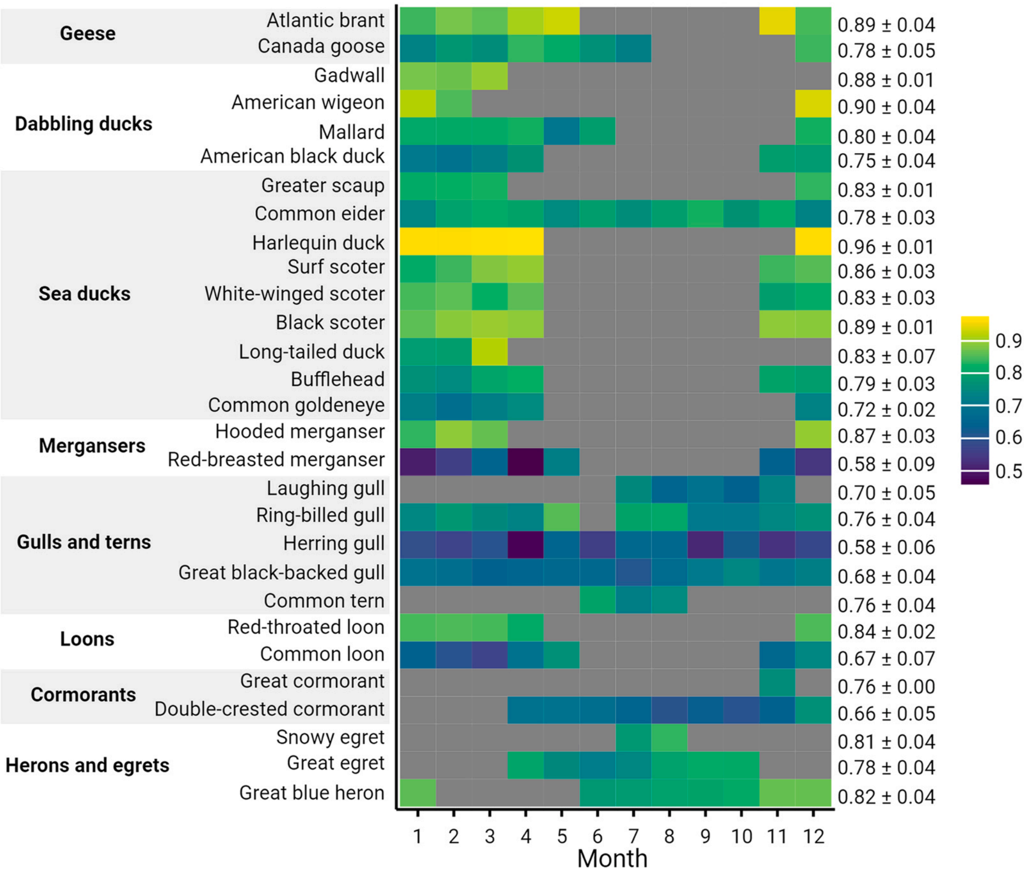

Fig. 3. Area under the curve (hereafter, AUC) values used to evaluate the performance of monthly (e.g., 1 = January 2 = February, etc.) species distribution models for waterbirds in Rhode Island, USA, from 2020–2023. The column of values on the right side of the figure are frequentist monthly AUC mean ± standard deviation values and were used to evaluate the overall performance of each species models.

For the waterfowl species groups (i.e., geese, dabbling ducks, sea ducks, and mergansers), model performance varied across months, with higher AUC values occurring at the beginning (November–December) and end of migration (April– May) for these mostly higher-latitude breeding species. Waterfowl species such as Atlantic brant (*Branta bernicla*), gadwall (*Mareca strepera*), American wigeon (*Mareca americana*), harlequin duck, and black scoter (*Melanitta americana*) exhibited the highest mean monthly AUC scores (range = 0.89—0.96). In contrast, Canada goose (*Branta canadensis*), American black duck (*Anas rubripes*), common eider (*Somateria mollissima*), bufflehead (*Bucephala albeola*), and common goldeneye (*Bucephala clangula*) had lower mean monthly AUC scores (range = 0.72—0.79). The models for gulls, terns, loons, and cormorants showed poorer performance compared to waterfowl based on mean monthly AUC values (range = 0.58—0.84), while the performance for herons and egrets was comparable (range = 0.78—82). For gull species, monthly AUC scores were lowest in herring gull ($\bar{x}$ = 0.58) and great black-backed gull ($\bar{x}$ = 0.68), and highest in laughing gull (*Leucophaeus atricilla*; $\bar{x}$ = 0.70) and ring-billed gull (*Larus delawarensis*; $\bar{x}$ = 0.76). Likewise, the performance of the common tern (*Sterna hirundo*) models was acceptable across the three months when they were sufficiently abundant in our study area (AUC > 0.70).

3.3. *Distribution model results*

The fixed effects in our global model explained on average 44.1 % (median = 44.6 %) of the monthly variation in occurrence probabilities observed across grid cells. Variance explained values were higher for waterfowl groups ($\bar{x}$ = 50.2 %, median = 53.3 %; Fig. 4a), and slightly lower ($\bar{x}$ = 30.6 %, median = 32.2 %) for the remaining groups. Variance explained was higher for most species during November–April ($\bar{x}$ = 53.4 %, median = 53.3 %), coinciding with increased overall survey counts for many species wintering in our study area. In contrast, variance explained was lower during May–October ($\bar{x}$ = 20.2 %, median = 20.9 %) when overall survey counts declined as species migrated out of our study area to breed.

The comparison of the global model to the reduced model (i.e., model that excluded distance to aquaculture as a fixed effect) revealed that distance to aquaculture did not account for much of the monthly variation observed across grid cells ($\bar{x}$ = 3.0 %, median = 1.1 %; Fig. 4b). This suggests that the remaining covariates (e.g., distance to shoreline, water depth, etc.) explained 41.1 % of the monthly variation in occurrence probabilities observed across grid cells. Distance to aquaculture explained less variation for waterfowl groups ($\bar{x}$ = 2.7 %, median = 1.0 %) when compared to the remaining groups ($\bar{x}$ = 3.7 %, median = 2.0 %). In addition, and unlike

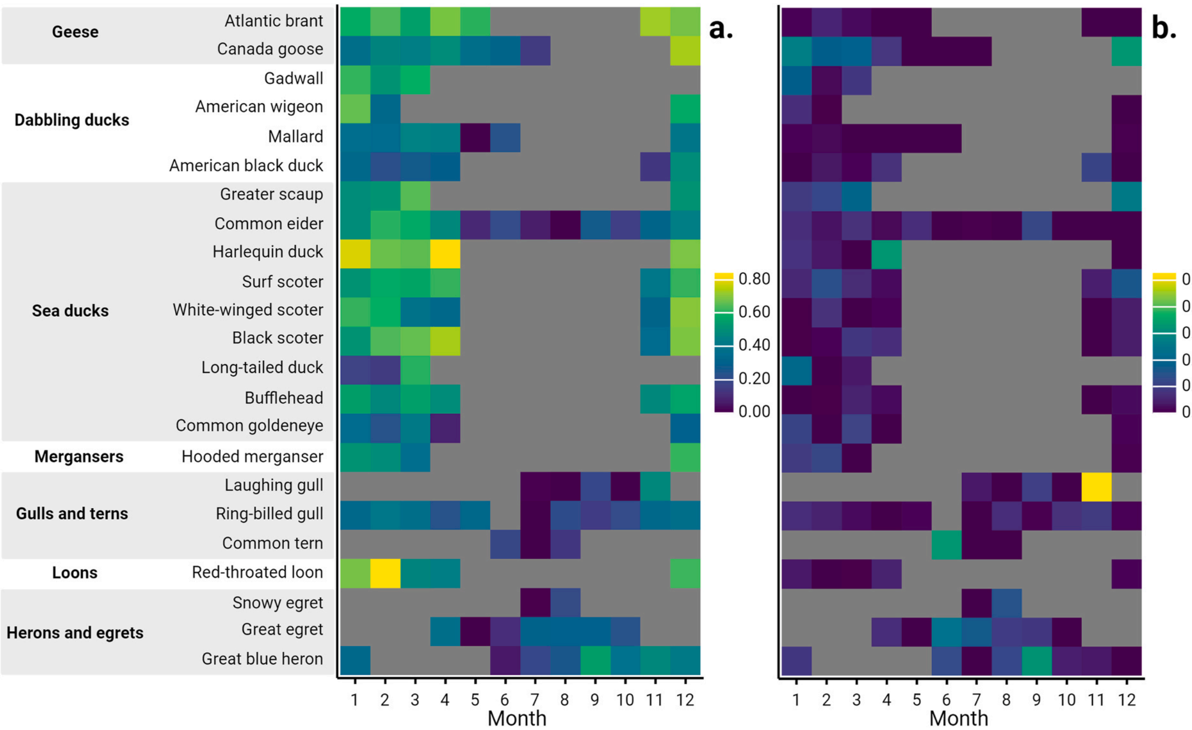

Fig. 4. Spatial variance explained by fixed effects in monthly (e.g., 1 = January 2 = February, etc.) species distribution models for waterbirds, based on data collected in Rhode Island, USA, from 2020—2023. (a) Portion of variance explained by fixed effects (distances to sand bottom, gravel bottom, shoreline, and aquaculture, along with latitude, grid cell size, and water depth) in the global model. (b) Portion of variance explained by the covariate distance to aquaculture (i.e., reduced model). Fixed effects in the global model explained an average of 44.1 % (median = 44.6 %; panel a) of the monthly variation in occurrence probabilities observed across grid cells. Distance to aquaculture explained little of this variation ($\bar{x}$ = 3.0 %, median = 1.1 %; panel b), indicating that the remaining covariates (e.g., distance to shoreline, water depth etc.) accounted for the majority of variance explained ($\bar{x}$ = 41.1 %).

the global models, we did not observe temporal trends in the variance explained by distance to aquaculture for most species. However, during different months, distance to aquaculture did account for notable levels of variation explained in some species. For example, variance explained by distance to aquaculture was 16.3 % in December, 16.3 % in April, 26.3 % in November, 16.3 % in June, and 15.9 % in September for Canada goose, harlequin duck, laughing gull, common tern, and great blue heron (*Ardea herodias*) respectively.

We assessed trends in occurrence probabilities across varying distances to aquaculture during months when the variance explained metric exceeded 0 (Fig. 5). For most waterfowl species, approximately half of these relationships varied across months, while the other

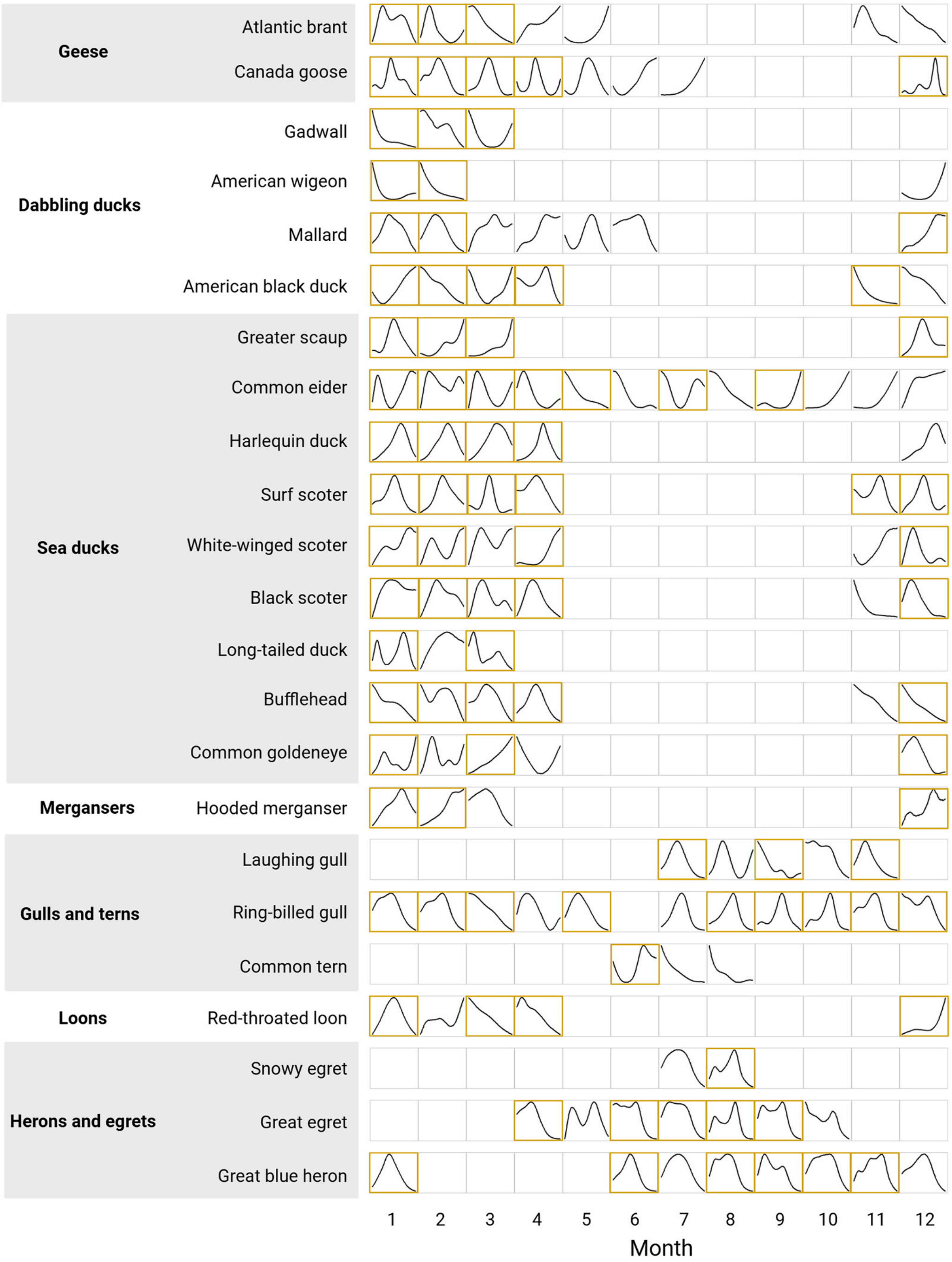

Fig. 5. Generalized additive mixed model predictions showing waterbird occurrence probabilities (y-axis) across increasing distances to shellfish aquaculture (x-axis). The x-axes are scaled to the same range of values (min = 0 km, max = 43 km), while the y-axes vary by species. Gold boxes indicate months when the distance to shellfish aquaculture explained variation in occurrence probabilities across survey grid cells.

half remained consistent. Dabbling ducks were the only waterfowl group that consistently exhibited a higher probability of occurrence near floating aquaculture, except for mallards (*Anas platyrhynchos*), which were more likely to occur slightly farther from these areas. Sea ducks and mergansers showed a preference for areas farther from floating aquaculture, often displaying bimodal peaks in occurrence probabilities at varying distances. For gulls, terns, and loons, the relationship between occurrence probabilities and distance to aquaculture varied; however, these species showed higher occurrence probabilities near floating aquaculture from January through April. Herons and egrets exhibited consistent trends in occurrence probabilities across all months they were observed, favoring shallower waters.

3.4. Aquaculture suitability model

The aquaculture suitability model displayed similar AUC values among the training and validation datasets (0.90 and 0.88 respectively), indicating the model consistently had acceptable performance. Areas most suitable for aquaculture were in shallower water depths (β = 2.30, CrI = 1.91, 2.27) and closer to shoreline (β = −0.35, CrI = −0.58, −0.11) and gravel bottom (β = −0.83, CrI = −1.02, −0.65). Distances to sand bottom and boat launches were poor predictors of aquaculture suitability (β = 0.00, CrI = −0.20, 0.19 and β = 0.01, CrI = −0.16, 0.17, respectively). The southwestern portion of our study was predicted to be the most suitable for aquaculture development (Fig. 6). This is also where most aquaculture development to date has occurred (Fig. 1).

3.5. Connecting occurrence probabilities and aquaculture suitability indices

Our ANOVAs considered 23 species with mean monthly AUC values > 0.7. Our ANOVA results suggested occurrence probabilities were significantly different (effect size > 0.5) across aquaculture suitability index values for 11 species (Fig. 7). Specifically, probability of occurrence values trended in a positive direction across aquaculture suitability bins for Canada goose, mallard, American black duck, hooded merganser (*Lophodytes cucullatus*), ring-billed gull, snowy egret (*Egretta thula*), great egret (*Ardea alba*), and great blue heron. Conversely, probability of occurrence values trended in a negative direction with increasing aquaculture suitability for white-winged scoter (*Melanitta deglandi*), black scoter, and red-throated loon (*Gavia stellata*).

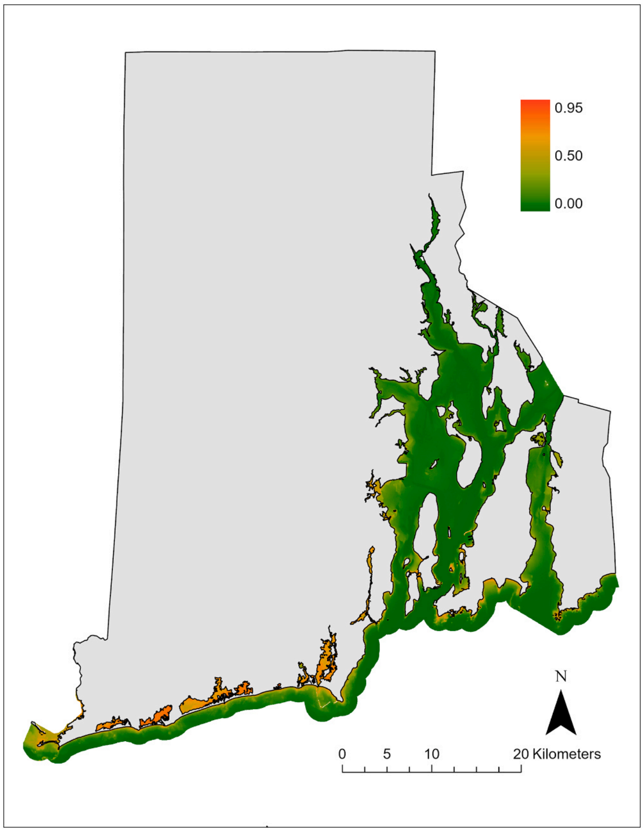

Fig. 6. Aquaculture suitability indices derived from a presence-absence model for the entire study area in Rhode Island, USA, using known aquaculture locations from 2020–2023. Higher values indicate areas more likely to be suitable for aquaculture farms.

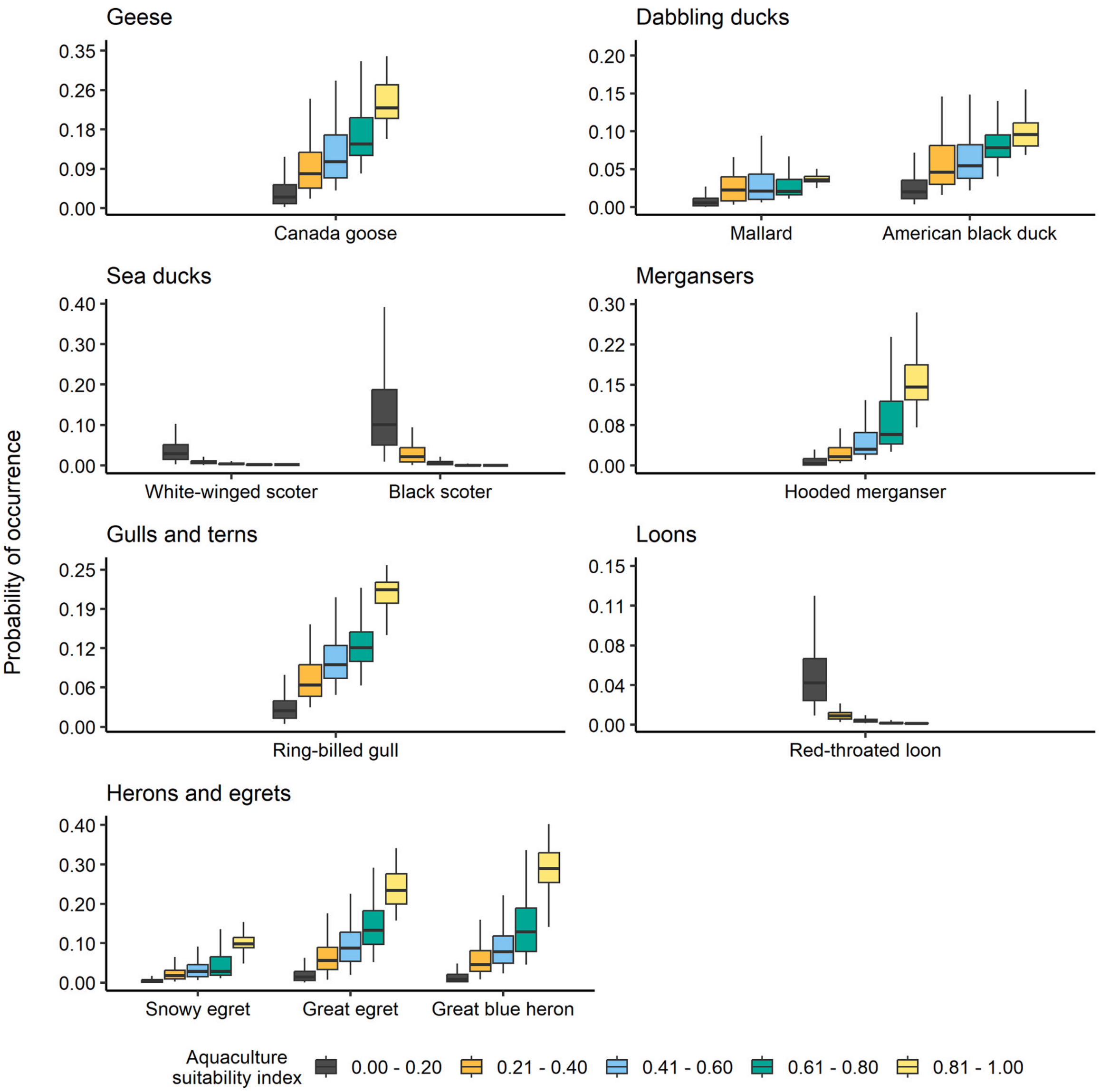

Fig. 7. Probability of occurrence values across different bins, each representing a specific range of aquaculture suitability indices. The probability of occurrence values for species represented in each plot showed significant differences in aquaculture suitability bins according to ANOVA tests with moderate to large effect sizes (i.e., > 0.5).

4. Discussion

Our results suggest that the monthly distribution patterns of most waterbird species in Rhode Island were predicted by key resources layers. However, distance to shellfish aquaculture contributed little to explaining variation in waterbird distribution patterns observed across grid cells throughout the annual cycle (Fig. 4b), indicating that other abiotic and biotic parameters (e.g., water depth, distance to shoreline, etc.) were more influential. Our results concur with previous studies that found little evidence for spatial associations between aquaculture and different waterbird species (Cheng et al., 2022, Mezebish Quinn et al., 2024). The absence of strong associations with aquaculture in our study may be partly due to the sizeable populations of common waterbird species in our study as anthropogenic disturbances typically have a more pronounced negative impact on smaller, more vulnerable populations (e.g., threatened species; Wang et al., 2018, 2022). Unlike many regions where waterbird-aquaculture research has been conducted (Zou et al., 2016; Cheng et al., 2022; Wang et al., 2022), the density of shellfish aquaculture farms across our study area is not consistently high. Additionally, our study area was dominated by caged shellfish aquaculture, potentially offering limited waterbird foraging options compared to more diverse operations in regions like China, where the cultivation of shellfish, crustaceans, and finfish likely supports a richer and more diverse food supply (Zou et al., 2016; Cheng et al., 2022). While certain locations have substantial aquaculture development, much of Narragansett Bay and the coastal lagoons in Rhode Island remain relatively undeveloped (Fig. 1), making it difficult to assess the overall impact of shellfish aquaculture on waterbird distributions.

Waterfowl are resource specialists, with different species fulfilling distinct niche roles (Pöysä, 1983, 1984; Guillemain et al., 2002). Anthropogenic disturbances can shift waterfowl distributions, resulting in changes in access to preferred resources (Loesch et al., 2013; Singer et al., 2020). Our variance-explained-analysis indicated shellfish aquaculture likely had a negligible effect on most waterfowl distributions in our study area. However, we found evidence that some dabbling ducks were more likely to occur near shellfish aquaculture (Fig. 5), likely due to their preference for foraging in shallow water bodies, which are also favorable for aquaculture development. Interestingly, the variance-explained values were high for Canada geese and harlequin ducks (Fig. 4b). For these species, the higher variance-explained was likely due to the consistent trends in their occurrence probabilities across varying distance to shellfish aquaculture values.

Distribution models performed worse for gulls and terns compared to waterfowl species. However, models for migratory species like laughing gull (Burger, 2020) and ring-billed gull (Pollet et al., 2020) had better performance, while models for resident species such as herring gull (Weseloh et al., 2024) and great black-backed gull (Good, 2020) performed poorly. Gull and tern species are resource generalists, allowing them to be more widely distributed throughout their annual cycle (Burger and Gochfeld, 2019). Because generalists are typically widely distributed and more adaptable to anthropogenic landscapes due to their use of diverse resources (Gaston et al., 2000), it is not surprising that our distribution models performed poorly for these species (Fig. 3); an outcome similar to other studies that have attempted to predict distribution patterns for generalists (Connor et al., 2018). Interestingly, we found that distance to shellfish aquaculture explained more variation in the occurrence probabilities of gulls and terns compared to waterfowl groups although this varied across months. We frequently observed large congregations of gull and tern species at floating shellfish aquaculture farms during the post-breeding season (i.e., July — August), as they use floating gear as roost sites (Caron et al., 2023). Thus, it is counterintuitive to find that these species were not more likely to occur closer to shellfish aquaculture during these months. However, distribution models provide no information on abundance, highlighting the need for future studies to focus on the local abundance of these species to gain more informative insights.

Of the remaining groups, the most notable trends in variance explained across grid cells come from herons and egrets (Fig. 4b). The variance explained by distance to shellfish aquaculture was minimal for these species during most months they were present in our study area. However, the distribution of occurrence probabilities for these species was skewed towards shorter distances to shellfish aquaculture. This pattern suggests a potential beneficial relationship between these species and aquaculture, as it may provide a prey resource for piscivores (Barrett et al., 2019). Numerous studies have documented higher fish abundance near aquaculture cages, which likely supports these species (Goodbrand et al., 2013; Barrett et al., 2019). Alternatively, this finding could be related to the water depth preferences of these species, as they were most frequently observed in the shallow coastal lagoons where shellfish aquaculture is most common in Rhode Island.

Our aquaculture suitability model indicated areas most suitable for shellfish farming are typically located at shallow water depths and closer to shoreline and gravel bottoms (Fig. 6). Apart from gravel substrates, these characteristics align closely with the preferred resources of Canada goose, mallard, American black duck, hooded merganser (Baldassarre, 2014), snowy egret, great egret (Trocki and Paton, 2006), and great blue heron (Vennesland and Butler, 2020). We found all these species were more likely to occur in areas better suited for shellfish aquaculture development. Both white-winged scoter and black scoter were more likely to occur in areas poorly suited for aquaculture, likely due to their preference for resources that are located at greater distances from shorelines in deeper waters (Baldassarre, 2014). Our assessment of waterbird occurrence probabilities in relation to aquaculture suitability provides an effective method that can be used to assess the effects of future aquaculture development on species of conservation interest.

Our research provides valuable insights into how proximity to existing and proposed shellfish aquaculture influences waterbird distributions. Our findings suggest that although current aquaculture operations are not having substantial impacts on species distribution patterns, future development will likely conflict with the many bird species that favor shallow waters, as these areas are also most suitable for aquaculture expansion. It will be important for managers to consider these findings when evaluating additional proposed aquaculture farms to help conserve waterbird habitat. Furthermore, our research can also be used by aquaculture farmers to understand which areas should be avoided to reduce human-waterbird conflict (Caron et al., 2023). An important next step would be to assess abundance patterns of waterbirds in relation to aquaculture in part because overabundant waterbirds can pose potential threats to bird populations and human health (i.e., *Campylobacter jejuni* infected oysters consumed by humans; Caron et al., 2023). Our study identified few instances where variation in species distribution patterns was explained by their distance to aquaculture farms and even fewer indicate significant spatial overlap between birds and aquaculture (Fig. 5). However, several waterbird species were more likely to occur in areas highly suited for aquaculture. Future research that offers in-depth assessments of the positive and negative associations between birds and aquaculture at the species level would provide crucial insights into the specific mechanisms driving these patterns. Such research is vital for developing targeted management strategies that mitigate conflicts, ensuring the sustainability of both aquaculture and bird populations.

Ethics

Not applicable: This manuscript does not include human or animal research.

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CRediT authorship contribution statement

Dylan L. Bakner: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Tori Mezebish Quinn:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Martina S. Müller:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Peter W. Paton:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation. **Jennifer E. Kilburn:** Writing – original draft, Supervision, Resources, Funding acquisition, Conceptualization, Funding acquisition, Conceptualization. **Scott R. McWilliams:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare no competing interests.

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Appendix

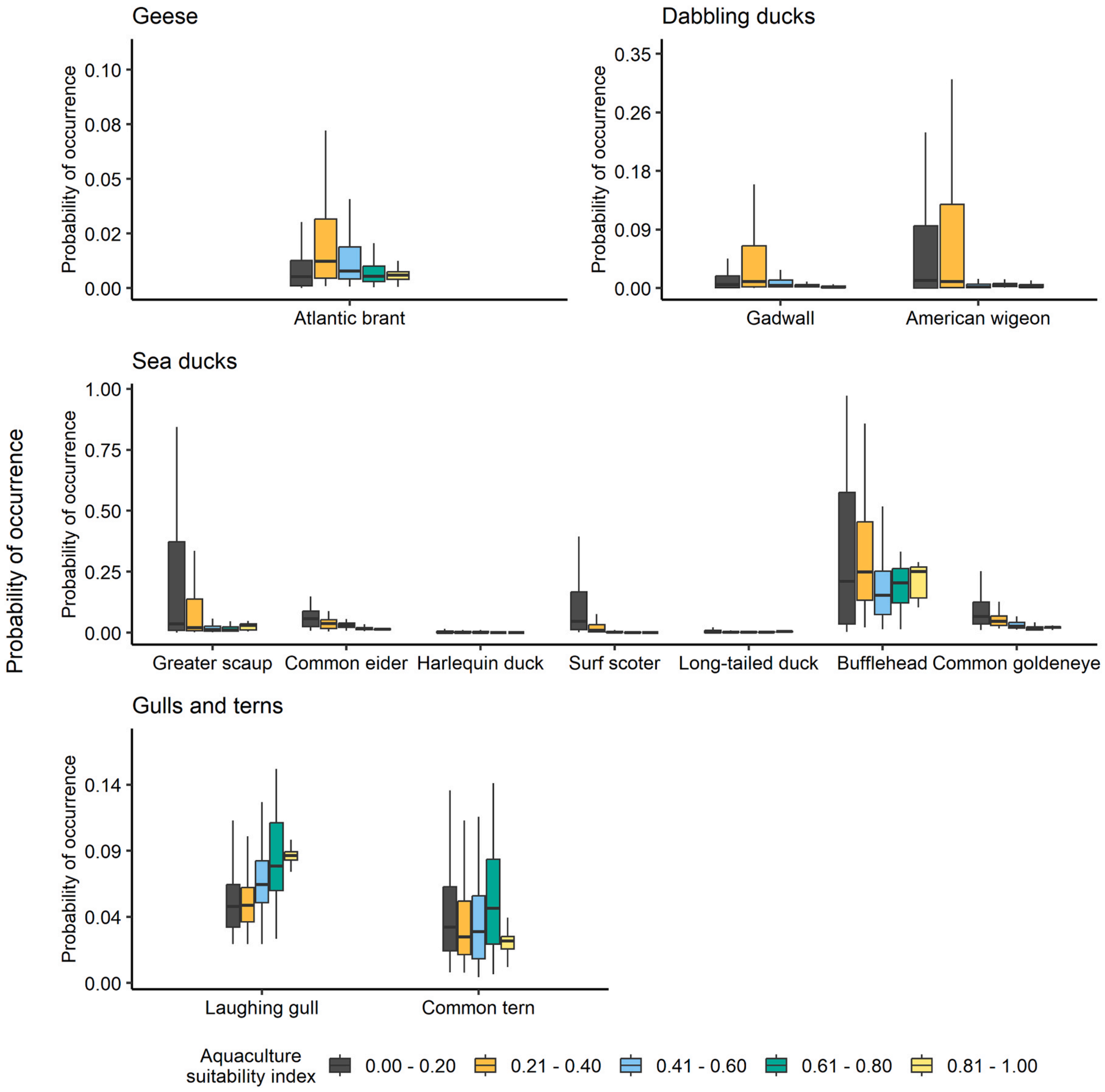

Figure A.1. Probability of occurrence values across different bins, each representing a specific range of aquaculture suitability indices. The probability of occurrence values for species represented in each plot showed significant differences in aquaculture suitability bins according to ANOVA tests with less than moderate (i.e., ≤ 0.5)

Data availability

Data will be made available on request.

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