

SPECIES DISTRIBUTION MODELING OF NORTHERN SEA OTTERS (*ENHYDRA LUTRIS*
KENYONI) IN A DATA-LIMITED ECOSYSTEM

By

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Abstract

Species distribution models are used to map and predict geographic distributions of animals based on environmental covariates. However, species distribution models often require high resolution habitat data and time-series data on animal locations. In data-limited regions with little animal survey data or habitat information, modeling is more challenging and often ignores important environmental attributes. For sea otters (*Enhydra lutris*), a federally protected keystone species with variable population trends across their range, predictive modeling of distributions has been successfully conducted in areas with an abundance of sea otter and habitat data. Here, we used open-access data across a single time step and leveraged a presence-only model, Maximum Entropy (MaxEnt), to investigate subtidal habitat associations (substrate and algal cover, bathymetry, and rugosity) of northern sea otters (*E. lutris kenyoni*) in a data-limited ecosystem, Kachemak Bay, Alaska. These habitat associations corroborated previous findings regarding the importance of bathymetry and understory kelp as predictors of sea otter presence. Novel associations were detected, as filamentous algae and shell litter were positively and negatively associated with sea otter presence, respectively. This study provides a quantitative framework for conducting species distribution modeling with limited temporal and spatial animal distribution and abundance data and utilized drop camera information as a novel approach to better understand habitat requirements of a stable sea otter population.

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Introduction

Quantifying habitat associations and predictive modeling of animal distributions are commonly conducted using species distribution models (SDMs). Typically, SDMs rely on known locations of species occurrences and spatially-explicit environmental information to construct mathematical relationships among these variables (i.e., model) to predict species' use of habitat across a landscape (Buckland & Elston, 1993; Drake et al., 2006; Elith et al., 2006; Guisan et al., 2002; Leathwick et al., 2006; Pearce & Boyce, 2006). There are various types of SDMs, including classical methods based on generalized linear models, generalized additive models, or Bayesian statistics, as well as more recently developed approaches based on machine learning methods, such as random forests, boosted regression trees, support vector machines, and maximum entropy. A variety of ecological questions can be addressed with SDMs, many of which have important implications for resource management. For example, SDMs can be used to guide the designation of Marine Protected Areas (MPAs), where an understanding of spatial habitat use by key species is critical for meeting MPA goals (Hameed et al., 2017). Additionally, SDMs can be used for modeling habitat suitability for invasive species (Srivastava et al., 2019), predicting species' range shifts under climate change (Zhang et al., 2020), and understanding the spatial ecology of infectious diseases (Slatculescu et al., 2020). Further, SDMs can be used to anticipate areas where wildlife might have an increased risk of human interactions due to industrial development or vessel activity (Blondin et al., 2020). Many of these models require presence/absence data. To predict potential species distributions, SDMs have been shown to perform better for modeling probability of occurrence than abundance (Lee-Yaw et al., 2022).

On land, Laser imaging, Detection, and Ranging (LiDAR) data and satellite imagery can be used for SDM habitat characterization (Koma et al., 2022). Multiple products are available on

global land cover and habitat classification (Jung et al., 2020). For marine systems, multibeam sonar data are ideal for SDMs due to their continuous spatial coverage and systematic characterization of substrate and algal cover (Monk et al., 2010). However, for many remote regions of the ocean, multibeam data are often not available due to accessibility and technical challenges. For example, Alaska's coastline makes up approximately 50% of the national coastline for the United States, but as of 2021 only 31% of Alaska's coastal waters have been mapped with single or multibeam sonar for bathymetry (Alaska Coastal Mapping Strategy Implementation Plan 2020-2030, 2022). Thus, habitat characterization of Alaska's coastal regions is particularly challenging. In the absence of sonar data, systematic drop camera surveys can serve as a replacement. Drop cameras have been widely used as non-invasive tools for measuring underwater habitat and organismal distributions when multibeam sonar data are not available (Bethoney & Stokesbury, 2018; Easton et al., 2015).

In addition to habitat data, modeling relationships between habitat and species presence across space and time (Elith & Leathwick, 2009) requires known locations for the species of interest. Often, animals are equipped with Global Positioning Systems (GPS) tags or collars to track movements to determine their locations in time and space. Advances in animal telemetry technology now allow for high resolution GPS tracking of marine and terrestrial animals (e.g., Hart et al., 2020; Kuhn et al., 2009). Sea otters (*Enhydra lutris*), the species of interest for this study, are a challenge for tracking, because GPS tags cannot be affixed to the pelage due to risk of hypothermia, if their fur is disturbed by GPS attachment (Davis et al., 2019). Very High Frequency (VHF) radio tags have been deployed in sea otters, but this method requires surgery to implant the device, does not upload data and therefore must be collected in the field, and is cost-limiting (Davis et al., 2019; Garshelis & Siniff, 1983). The current method for estimating sea

otter population abundance entails aerial surveys, where an observer marks locations and abundance of observed animals (Bodkin & Udevitz, 1999), which can be used in place of GPS locations.

Understanding habitat associations for current sea otter distributions and potential future distributions is important for a variety of reasons. First, sea otters are a keystone species, as they play a critical role in coastal ecosystem structure and function (Estes & Palmisano, 1974). For example, sea otters function as an ecosystem engineer across the North Pacific, including rocky (Estes et al., 1998), soft-sediment (Kvitek et al., 1992), and seagrass (Foster et al., 2021; Hughes et al., 2013) communities. Second, changes in the presence or absence of sea otters may impact local resource availability both for commercial and subsistence purposes (Carswell et al., 2015; Hoyt, 2015). Commercial and personal use fisheries and mariculture can be impacted by sea otter presence (Bodkin et al., 2002; Carswell et al., 2015). Lastly, federal and state permitting of anthropogenic activities, such as oil and gas development, require consideration of impacts to marine mammals, including sea otters. Thus, it is important to accurately predict how ecosystems may change under future climate scenarios, industrial development, or other anthropogenic stressors in the context of sea otter presence in an ecosystem. Predicting ecosystem change requires an understanding of habitat associations and current and future species distribution. Sea otters use nearshore waters that are associated with canopy-forming kelp, shallow depths, or preferred benthic prey (i.e., clams, crabs, etc.) (Gilkinson et al., 2011; Kenyon, 1969; Miller, 1974; Ribic, 1982; Rotterman & Simon-Jackson, 1988), but finer scale subtidal habitat use, such as subtidal algal cover, substrate composition, or bathymetric complexity, has not been fully explored for sea otter habitat associations. Finer scale habitat attributes, such as these, may increase predictability of sea otter species distribution models.

While sea otters were historically abundant across their range, their populations were severely depleted due to commercial hunting in the mid 1700's to early 1900's (Kenyon, 1969). Sea otters were protected in 1911 by the International Fur Seal Treaty, which allowed sea otter populations to begin the recovery process (Kenyon, 1969), and they have since been protected by the Endangered Species Act (Endangered Species Act, 1973) and the Marine Mammal Protection Act (The Marine Mammal Protection Act, 1972). As sea otter populations continue to change over time (through recovery, expansion into new territory, translocation, and contraction), there is a growing need to better understand the species' foraging and resting habitat requirements to manage this federally protected species and its associated ecosystems (Davis et al., 2019).

Northern sea otter (*E. lutris kenyoni*) distributions have been previously modeled in Prince William Sound, Alaska (Coletti, 2006), southeast Alaska (Eisaguirre et al., 2021; Lu et al., 2020; Tinker et al., 2019; Williams et al., 2019), Washington state (Hale et al., 2022; Laidre et al., 2002), and California (Tinker et al., 2021). These modeling efforts have employed Bayesian state-space models (Hale et al., 2022; Tinker et al., 2019) and diffusion models (Eisaguirre et al., 2021; Lu et al., 2020; Williams et al., 2019), frameworks that are possible due to the high resolution of sea otter abundance time-series data. Calculating population dynamics requires annual estimates of changes in abundance and range (Eisaguirre et al., 2021; Hale et al., 2022; Lu et al., 2020; Tinker et al., 2019, 2021; Williams et al., 2019), because sea otter populations are structured on small scales (Davis et al., 2019). Additionally, animal movement patterns, collected via telemetry, are necessary for modeling dispersal (Hale et al., 2022; Tinker et al., 2019, 2021). However, not all sea otter populations have been surveyed with such frequent temporal coverage. For example, some populations, such as Cook Inlet, Alaska, have only been surveyed once in over a decade (Garlich-Miller et al., 2018)

For minimally surveyed populations, the Maximum Entropy (MaxEnt) model (Elith et al., 2011; Phillips et al., 2006; Phillips & Dudík, 2008) may be ideal, because MaxEnt uniquely uses presence-only data compared to other common species distribution model methods (e.g., generalized additive models, Guisan et al. (2002), support vector machines, Drake et al. (2006), and random forests, Evans et al. (2011)). MaxEnt also performs better than other SDMs in its predictive ability and robustness to overfitting (Elith et al., 2006; Valavi et al., 2022), handling of small sample sizes (Kaky et al., 2020; Kaky & Gilbert, 2016; Wisz et al., 2008), and modeling complex relationships between the response and predictor variables (Elith et al., 2006). We examined the role of specific substrate and algal habitat attributes, including ones that have yet to be tested, so robustness to model complexity due to many model covariates was critical in this exploratory study. Other than MaxEnt, SDMs often assume that species occurrences across the region of interest are representative of prevalence, but this is not always the case (Elith et al., 2011). Because sea otters are highly mobile and forage underwater, it cannot be assumed that locations without sea otter observations are true absences. However, modeling presence-only in a colonized area still retains the signal of absence, because if a habitat is unsuitable for an animal, there will be no presence records (Elith et al., 2011). The MaxEnt model instead uses pseudoabsences (i.e., available space) along with occurrences to model habitat use.

To predict the potential expansion of sea otter populations, it is important to understand the species' associations with subtidal habitat types. The extent to which this can be done for a spatial and temporal data-limited ecosystem is not well resolved. Here, we evaluated whether the distribution of sea otters in Kachemak Bay, Alaska can be modeled with two years of habitat information and one year of sea otter occurrence information using MaxEnt. We also compared sea otter habitat associations in this data-limited ecosystem with other regions that are data-rich

to better understand possible generalizations between sea otters and their habitat attributes. The sea otter population of Kachemak Bay is an important model system, as this population is considered to be at carrying capacity and stable (H. Coletti pers. comm.). It is important to use a stable population for model development to understand if other uncolonized regions are suitable to support a future stable population. This study notably leverages open-access data to demonstrate how the MaxEnt framework may be applied to other ecosystems, and the ecologically relevant questions we can answer with data that are publicly available.

Methods

Study site

This research was conducted in Kachemak Bay, Alaska (Figs. 1 and 2), a highly productive, estuarine ecosystem located in southcentral Alaska that connects to Cook Inlet at the eastern coastline and supports significant macroalgal, invertebrate, fish, and marine mammal populations. Northern sea otters have inhabited Kachemak Bay since the 1970's, and the current population is thought to be stable at an estimated ~6,000 adults (Esslinger et al., 2021; Garlich-Miller et al., 2018). The distribution of sea otters has expanded from Kachemak Bay into Cook Inlet and is expanding northward further into Cook Inlet (Fig. 1) (Esslinger et al., 2021; Garlich-Miller et al., 2018).

Model components

The subtidal habitat data used in this study are publicly available through the National Oceanic and Atmospheric Administration (NOAA) (Field et al., 2020). In 2016 and 2017, NOAA collected 518 subtidal habitat videos in Kachemak Bay via a drop camera. The drop camera consisted of two cameras, one low-resolution (720 pixels) camera (Sartek Industries, Inc.) and one high-resolution (1080p) GoPro camera, and two lights for visibility at depth. Only

high-resolution camera data were characterized for this study. Instruments were mounted on a stainless-steel tripod frame. The drop camera was lowered to depths between 0-170 m with a tether and passed over the benthos for various durations of time (~2-10 minutes), while recording continuous video. Point locations of each survey were marked with a GPS device.

To obtain fine-scale habitat information for each high-resolution video, average percent cover (0-100%) of each substrate type and algal group was visually determined. Substrate utilized a modified Wentworth scale consisting of boulder, cobble, pebble, gravel, shell, sand, and mud (Wentworth, 1922). Algae consisted of understory kelp (Order: Laminariales), macroalgae (all macroalgae, not including Laminariales), filamentous/microalgae, and coralline algae. Raster surfaces for each habitat category were produced using kriging in ArcGIS (ArcGIS, 2012) to obtain continuous percent cover of each habitat attribute throughout the survey region. Raster surfaces have a cell resolution of 131 x 131 m. Bathymetry data were collected by NOAA in 2008 and 2009 (Field et al., 2020). Rugosity was derived from bathymetry using the rugosity tool in ArcGIS (ArcGIS, 2012). Multicollinearity among habitat data was assessed using a stepwise variance inflation factor method via the vif function (Naimi et al., 2014). Multicollinearity analysis was conducted using the R language environment (R Core Team, 2022).

Sea otter abundance data used in this analysis were collected by the United States Fish and Wildlife Service in 2017 (Esslinger et al., 2021; Garlich-Miller et al., 2018) via aerial abundance surveys flown using the method described by Bodkin & Udevitz (1999). Four replicate surveys consisting of a series of 400 m wide strip transects were flown during May 2017 in the north-south direction across Kachemak Bay, starting and ending at the 0 m tide line. Starting points were randomly selected and subsequent transects were flown every 4 km for each

replicate. These strip transects in Kachemak Bay cumulatively covered 40% of the total area of Kachemak Bay (Garlich-Miller et al., 2018). Observations from eastern Cook Inlet surveys that fell within NOAA's habitat study area were also included in the analysis. For the eastern Cook Inlet surveys, a series of 400 m wide strip transects were flown in the east-west direction from the 0-40 m depth contour. These surveys were flown 7 km apart and replicated three times during May 2017, resulting in a 15% coverage of the total area. Data were represented with sea otter counts at each observation point recorded as geographic coordinates (Garlich-Miller et al., 2018).

Counts were not corrected based on the intensive search unit correction factor, as described in Garlich-Miller et al. (2018), because locations alone, not counts, were used in this analysis. Replicate surveys were combined for this study to represent all observed sea otter locations in Kachemak Bay during the 2017 survey. Only on-transect sea otter observations were used for this analysis; off-transect sea otter observations were discarded, as they were opportunistic and extended beyond the 400 m transect band. Duplicate observations at any single coordinate were not included in the model, as MaxEnt will only allow one observation per grid cell to avoid pseudoreplication. Only adult sea otter locations were used, as pups are dependent on female sea otters. Polygons of sea otter survey transects were produced by creating polylines from transect start and end points (Esslinger et al., 2021). Sea otter data were constrained to the extent of habitat data.

MaxEnt model

A MaxEnt model (Elith et al., 2011; Phillips et al., 2006; Phillips & Dudík, 2008) was produced to determine subtidal habitat associations of sea otters and to provide a framework for predictive modeling of sea otter population expansion given spatial and temporal data limitations

imposed on this study. For this, we used the MaxEnt algorithm (Elith et al., 2011; Phillips et al., 2006; Phillips & Dudík, 2008) through the ENMeval package (Kass et al., 2021) in R (R Core Team, 2022). Sea otter observations collected during the 2017 USFWS sea otter aerial abundance survey (Garlich-Miller et al., 2018; Esslinger et al., 2021) were used as presence locations in the model with only one observation retained per grid cell. A total of 391 sea otter presence locations and 10,000 background points were used. Background points were randomly selected from strip transect polygons (Fig. 2), as this was considered available space of the surveyed extent. Training and testing data were separated using random k-fold partitioning with five folds or groups. Cross validation is conducted by leaving out one group at a time and calculating the out of sample predictive performance as the area under the receiver operating characteristic curve (AUC). The AUC values for training and testing are averaged over the five runs of cross validation.

Model settings were determined through model tuning in the ENMeval package, as described by Kass et al. (2021). Default MaxEnt version 3.4.3 settings were used, except for permissible types of feature classes and the regularization multiplier. Twenty models were created with varying types of feature classes (i.e., linear, hinge, and combinations of linear and quadratic, and linear, quadratic, and hinge) and regularization multipliers from 1-5. Feature class type dictates the shape of the relationship of covariates to response (Bohl et al., 2019). The regularization multiplier dictates the penalty for model complexity with a high regularization multiplier corresponding to a large penalty (Elith et al., 2011; Merow et al., 2013; Phillips & Dudík, 2008). Together, these settings influence model complexity. Model selection was conducted with two methods: a sequential method for cross-validation that favors the lowest average test omission rate and the highest average AUC (Kass et al., 2021; Radosavljevic &

Anderson, 2014), and information-theoretic methods (Akaike's Information Criterion corrected for small sample sizes, AICc; Burnham & Anderson, 2004). Sequentially selected models were compared to AICc selected models for final optimal model selection (Velasco & González-Salazar, 2019; Warren & Seifert, 2011).

Once the most parsimonious model was selected, model performance was evaluated by comparing results to a null model distribution. This allowed for testing the success of modeling species distributions for our data-limited system. Some applications of MaxEnt models report model estimates, but there is no way to evaluate performance within the algorithm. Bohl et al. (2019) developed a framework for evaluating model performance by comparing the empirical model to a null model distribution. The novelty of this approach is a null model simulation that is validated with randomly selected points, which simulate occurrences, against the same testing dataset and background points used in the empirical model. This allows for more direct comparison on model performance than in previous evaluation frameworks. As a non-parametric method, it is critical to employ an evaluation method to properly estimate effect size and model significance.

Null models were constructed over 1,000 iterations by calibrating with a random sample of points within the strip transect polygons and the same background points from the empirical model. Null models were validated with the same testing dataset as the empirical model, so that performance measures were directly comparable (Bohl et al., 2019). Model performance of the empirical and null models was evaluated with the AUC for the training (AUC_{train}) and testing (AUC_{val}) datasets, the difference between AUC_{val} and AUC_{train} (AUC_{diff}), and omission error rate (OR) with a threshold that leads to 10% omission of calibration records (Liu et al., 2005). AUC_{val} and AUC_{train} are measures of discriminatory ability and AUC_{diff} and OR are measures of

overfitting (Bohl et al., 2019). Standardized effect sizes (Ulrich & Gotelli, 2010) and p-values were calculated to test whether the empirical model performed better than the null model distribution (Bohl et al., 2019). Covariate percent contribution was gathered from the MaxEnt model output to determine the importance of habitat attributes in predicting sea otter presence. The empirical model was then applied to all grid cells in the study area (i.e., full extent of habitat raster layers) to predict the probability of sea otter occurrence based on relationships with habitat covariates and demonstrate capability for out of sample prediction. Sea otter survey results, including abundance of adult sea otters at each observed point (Garlich-Miller et al., 2018), were superimposed on the map of predicted probability of occurrence to visually assess model performance.

Results

Model components

Analysis of drop camera data revealed variation in percent cover of substrate and algal habitat attributes throughout Kachemak Bay (Fig. 3). Percent cover of larger sediment grain sizes (i.e., boulder and cobble) was higher on the south side of the bay than the north side. Percent cover of mud was higher in the inner bay, while cover of pebble, gravel, shell, and sand was lower in the outer bay. Mud was the most consistently observed habitat attribute throughout Kachemak Bay. Algal cover was found primarily in shallower waters at the edges of the bay. Understory kelp was found primarily on the south side of the bay, while macroalgae and filamentous algae were variable throughout the bay. Percent cover of coralline algae was higher in the outer bay than the inner bay.

Sea otter aerial abundance survey results are summarized in Garlich-Miller et al. (2018). Briefly, there are an estimated 6,000 adult sea otters inhabiting Kachemak Bay with an estimated

population density of 6.37 sea otters/km², not including the section of the eastern Cook Inlet survey that overlapped with the NOAA habitat study area. Sea otter abundance observations of adults and pups were variable throughout Kachemak Bay (Garlich-Miller et al., 2018).

Model performance

The evaluation of model settings with the sequential method resulted in selection of features set to linear and the regularization multiplier set to one as optimal settings (Fig. 4). The sequentially selected model resulted in an omission rate of 0.0996 and an AUC_{val} of 0.681. The AICc model selection method suggested features set to linear and quadratic and a regularization multiplier set to one, resulting in a more complex model than the sequentially selected model due to additional feature types. Comparatively, the omission rate of the AICc selected model was 0.110 and the AUC_{val} was 0.676, demonstrating a model that is more overfit than the sequentially selected model with a slightly lower discriminatory ability. The sequentially selected model with features set to linear and the regularization multiplier set to one was deemed to be optimal and is the empirical model referred to hereafter.

The null model distribution was used to evaluate multiple model metrics against the empirical model. Discriminatory metrics, AUC_{train} and AUC_{val} for the empirical model were 0.686 and 0.681, respectively, and 0.545 and 0.524 for the null model distribution, respectively. The p-values from a one-sided test evaluating whether the AUC_{train} and AUC_{val} were larger for the empirical model than the null model distribution were $p < 0.001$ and $p < 0.001$, respectively (Table 1). Empirical AUC_{train} and AUC_{val} fall outside of the 99th quantile of the null model distribution, showing significantly better ($\alpha = 0.05$) model performance than models with randomly generated presence locations in the survey area (Fig. 5). Metrics of overfitting, AUC_{diff} and omission rate, for the empirical model were 0.0226 and 0.0996, respectively, and 0.0599 and

0.137 for the null model distribution, respectively. The p-values from a one-sided test evaluating whether the AUC_{diff} and omission rate were smaller for the empirical model than the null model distribution, $p < 0.01$ and $p < 0.05$, respectively (Table 1). Empirical AUC_{diff} and omission rate demonstrated significantly different degrees of overfitting ($\alpha = 0.05$) from null models with randomly generated presence locations in the survey area (Fig. 5, Table 1). The out of sample prediction for Kachemak Bay had 68.1% (AUC_{val}) predictive accuracy with a standard deviation of 2.61% (Table 1).

Habitat associations

The optimal model resulted in bathymetry, shell, and filamentous algae as the three most influential habitat attributes predicting current probability of sea otter occurrence in Kachemak Bay, Alaska, with 43.0%, 18.2%, and 18.0% contribution, respectively (Table 2). Shallower depths and increasing percent cover of filamentous algae had positive relationships with probability of sea otter occurrence. Increasing percent cover of shell had a negative relationship with probability of sea otter occurrence (Table 2). Understory kelp was the next most important habitat attribute at 6.20% contribution and had a positive relationship with probability of sea otter occurrence, though there was a substantial decrease in percent contribution between filamentous algae and understory kelp (Table 2). Rugosity, boulder, and sand had no predictive value for sea otter occurrence. Gravel, pebble, coralline algae, cobble, and macroalgae (in order of importance) had low ($< 6\%$) contributions for predicting sea otter occurrence (Table 2). Permutational importance over 120 iterations also followed these trends, except for pebble, macroalgae, and sand, which had zero permutational importance (Table 2). Mud was excluded from the analysis, as it was highly correlated with other environmental covariates. The empirical model was used to predict probability of sea otter occurrence throughout Kachemak Bay based

on substrate, algae, and bathymetry (Fig. 6A). These results reveal hotspots (i.e., high use areas) with high probability of sea otter occurrence in Kachemak Bay. Based on subtidal habitat associations, sea otters are likely to occur in the northwest, northeast, south-southwest, and southwest areas of Kachemak Bay; however, there are variable hotspots throughout the bay (Fig. 6A). These hotspots visually follow patterns of sea otter observations (Fig. 6B) (Garlich-Miller et al., 2018; Esslinger et al., 2021).

Discussion

Model performance

This study importantly leveraged open access data and demonstrated that sea otter species distribution modeling is feasible with temporally and spatially limited data. The MaxEnt model was quantitatively evaluated to perform better than random using the methods described by Bohl et al. (2019). Further, the ecological relevance of the detected habitat associations was qualitatively assessed by comparing our results with other sea otter modeling studies, as well as comparing the MaxEnt-predicted occurrence probabilities to known sea otter abundance observations. Results reported here confirm previously known sea otter habitat associations, such as an association with shallow depth (Bodkin et al., 2004; Coletti, 2006; Eisaguirre et al., 2021; Gilkinson et al., 2011; Williams et al., 2019; Yeates et al., 2007), and a positive association with understory kelp (Estes & Duggins, 1995; Foster & Schiel, 1988). We also found novel associations, such as a positive association with filamentous algae and a negative association with shell cover. Notably, areas within the study region that were predicted to have a higher probability of sea otter occurrence based on habitat associations also visually corresponded to areas with observations of greater sea otter abundance (Garlich-Miller et al., 2018). This result would not be expected, if the modeled habitat associations were not relevant to true sea otter

distributions. Sea otter species distribution modeling, including variables, such as depth, rocky substrate, canopy kelp, and other environmental variables, has been conducted for California southern sea otters (*Enhydra lutris nereis*) using a model that required continuous habitat data and multiple years of sea otter abundance survey data (Tinker et al., 2021). Such extensive spatial and temporal data are rarely available for modeling. Hence, our approach serves as a way forward for systems with more limited data.

In this exercise, model performance was evaluated to ensure that the model settings were the most appropriate. The optimal empirical model was selected from a suite of candidate models by testing various evaluation metrics using two evaluation methods: sequential selection and AICc selection (Burnham & Anderson, 2004; Kass et al., 2021; Radosavljevic & Anderson, 2014). The final MaxEnt model that was selected had linear features and a regularization multiplier of one. A lower regularization multiplier corresponds to a weaker penalty on the model for complexity, resulting in a more complex framework (Merow et al., 2013). When comparing the AUC scores for both final candidate MaxEnt models, they both performed similarly in predictive accuracy with $AUC_{val}=0.681$ for the sequentially selected model and $AUC_{val}=0.676$ for the AICc selected model. However, the omission rate of 0.0996 for the sequentially selected model and 0.110 for the AICc selected model indicates a difference in overfitting. An omission rate higher than the given threshold (10%) indicates overfitting (Radosavljevic & Anderson, 2014). The sequentially selected model does not indicate overfitting, while the AICc selected model does. This comparison demonstrates the improved ability of the sequential method in limiting overfit models over the commonly used AICc method, which corroborates previous findings (Bohl et al., 2019; Kass et al., 2021; Radosavljevic & Anderson, 2014). The sequentially selected model is the model referred to hereafter. The

model AUC_{val} score of 0.681 indicates prediction that deviates from random (AUC = 0.5) but is between “poor” and “fair” performance (Swets, 1988).

The results of the empirical to null model distribution comparison demonstrate that the discriminatory ability and the degree of overfitting of the empirical model are significantly better than the null model distribution at $\alpha=0.05$. This result conveys that the model can predict the probability of sea otter occurrence based on the observed locations better than a model based on randomly selected data and is less overfit than a model based on randomly selected data.

Additional explanatory covariates, such as prey availability (Davis et al., 2019), distance from shore (Coletti, 2006), presence of canopy kelp (Tinker et al., 2021), and demography (Laidre et al., 2009; Tinker et al., 2008) may also increase the predictive power of the model, which would be demonstrated by an increase in AUC score above the 0.70 threshold of “fair” into the “good” range (Swets, 1988) and may further decrease the degree of overfitting by reducing complex relationships with less important covariates. However, this study demonstrates that the MaxEnt model produced here is quantitatively effective for species distribution modeling based on two years of open-access environmental data and one year of species observation data and identified the importance of subtidal substrate and algal composition for predicting the probability of sea otter occurrence.

Habitat associations

Similar to other studies (Bodkin et al., 2004; Coletti, 2006; Eisaguirre et al., 2021; Gilkinson et al., 2011; Williams et al., 2019; Yeates et al., 2007), bathymetry was found to be the most influential habitat attribute for predicting the probability of sea otter occurrence.

Bathymetry had a positive relationship with probability of sea otter occurrence, such that sea otters are most likely to be present in shallower waters. Sea otters use shallower water depths (0-

40 m) potentially due to a higher abundance of available prey compared to deeper waters (Bodkin et al., 2004; Gilkinson et al., 2011) and lower energetic costs of shallower dives (Yeates et al., 2007). Other studies have assumed that abundance and carrying capacity estimates can be applied to areas with similar habitat; however, similar habitat has previously been defined predominantly with depth alone (0-40 m; Laidre et al., 2002; Burn et al., 2003; Garlich-Miller et al., 2018). Depth may represent access to prey with minimal physiological diving stress and thermoregulatory cost (Yeates et al., 2007), but infaunal and epifaunal prey are variable in distribution and density across similar habitats (Barber et al., 2012; Cates, 2022; Eggleston et al., 1992; Seitz et al., 2001; Sponaugle & Lawton, 1990; Turner et al., 1997). Hence, this may result in over- or under-estimation of equilibrium density and abundance, if habitat is more or less suitable in modeled areas based on variables other than depth.

Although sea otters forage on clams and deposit empty shells on the benthos, shell litter has not been mentioned in other habitat association studies. Here, shell litter was the second most important attribute in predicting probability of sea otter occurrence. Shell had a negative relationship with probability of sea otter occurrence, such that an increase in percent cover of shell litter corresponded to a decrease in probability of sea otter occurrence. This relationship may indicate that areas with high shell cover no longer have an abundance of available bivalve prey. Areas with high shell cover may have limited remaining large live clams, thus causing sea otters to prey switch or forage in new locations, as has been observed when preferred prey stocks are depleted (Ostfeld, 1982).

Filamentous algae have not been considered in other sea otter habitat studies but were detected as the third most important attribute in predicting probability of sea otter presence in this study. Filamentous algae had a positive relationship with probability of sea otter occurrence,

such that an increase in percent cover of filamentous algae corresponded to an increase in probability of sea otter occurrence. This association may be due to a positive feedback loop, where sea otters modify substrate and increase settlement of algal spores (Fletcher & Callow, 1992). Sea otters often feed in consolidated substrate habitat, where filamentous algae may recruit well and have low competition with larger/perennial algae (Stewart & Konar, 2012). Another hypothesis is that filamentous algae may be serving as a proxy for another factor that may be affecting sea otters more directly, such as prey abundance. Sea otters prey on herbivorous invertebrates (e.g., sea urchins) that may be feeding on filamentous algae (Dethier & Duggins, 1988; Vadas, 1977). In addition, filamentous algae may increase the amount of particulate organic carbon in the water column for filter-feeding prey items (e.g., bivalves) to take up (Page, 1997; Riera & Richard, 1996). Additional covariates, such as invertebrate abundance and particulate organic carbon, would help distinguish the driving factor of the observed filamentous algal relationship but were not collected in this study.

Some, but not all, of the remaining covariates in the model only contributed minimally when predicting the probability of sea otter occurrence. Understory kelp was the fourth most influential attribute predicting sea otter occurrence, but only at 6.20% contribution, which supports findings from other studies of sea otters associating with understory kelp (Estes & Duggins, 1995; Foster & Schiel, 1988). Previous modeling studies have found canopy forming kelp associations with sea otters (Estes et al., 2010; Tinker et al., 2021), however, the current study only used non-canopy forming algae, so results are not directly comparable. Of the remaining habitat attributes, gravel, pebble, and cobble only have minimal and negative relationships with probability of sea otter occurrence at 5.30%, 3.40% and 2.30% contribution, respectively, and coralline algae has a minimal positive relationship with probability of sea otter

presence at 2.90% contribution. Although percent contribution was $< 6\%$ for these habitat attributes, this result demonstrates the prominence of habitat complexity in ecological relationships. Macroalgae, boulder, rugosity, and sand did not contribute to predicting probability of sea otter presence indicating that Kachemak Bay, Alaska, does not appear to function as a rocky ecosystem based on substrate composition (Stewart et al., 2014).

Additional studies using habitat data have included substrate and distance to other known important features (e.g., distance to shore and distance to closest protected shoreline) as covariates in estimating density and distribution (Coletti, 2006; DeMaster et al., 1996; Eisaguirre et al., 2021; Laidre et al., 2002; Lu et al., 2020; Tinker et al., 2021; Williams et al., 2019). Specifically, distance to shore and distance to the closest protected shoreline have inverse relationships with sea otter density (Coletti, 2006). In addition, rocky, sandy, and mixed substrate types have been associated with varying degrees of sea otter carrying capacity (DeMaster et al., 1996; Laidre et al., 2001), though substrate, other than shell litter, was not a strong driving factor for predicting probability of sea otter occurrence in this study. Other sea otter distribution modeling studies have relied on population growth dynamics, which requires many consecutive years of sea otter surveys (Eisaguirre et al., 2021; Hale et al., 2022; Lu et al., 2020; Tinker et al., 2019; Williams et al., 2019).

Variation in results between this study and others may be due to survey method and data types. The use of drop cameras instead of multibeam sonar might lead to a discrepancy in scale. Drop camera data allow for a fine-scale characterization of habitat and may provide benefits for studies emphasizing environmental complexity. In addition, leveraging technology, such as drop cameras, allows for increased survey extent without an increase in field effort, such as *in situ* survey methods, i.e., SCUBA diving, due to ease of use. Increasing the spatial extent of habitat

data would broaden our range for predictions of animal distributions. The habitat associations in this study are based on a single summer season during one year of sea otter aerial abundance surveys, which is a snapshot in time for habitat use and does not capture seasonal or inter-annual habitat use. Because the MaxEnt algorithm uses available space as background points for comparison, the resulting associations are still robust estimates of preferential habitat use. However, these associations are being drawn from data on both resting and foraging animals; these two behaviors might result in variable use of habitat types (Finerty et al., 2009). Tracking information would provide more detailed estimates of sea otter habitat use to correlate known behaviors and movement across space and time, though these data are challenging to collect for sea otters, especially in remote locations (Davis et al., 2019).

This study is a step forward in exploring additional habitat features that may be important for estimating northern sea otter carrying capacity in southcentral Alaska, as has been done in California with southern sea otters (Tinker et al., 2021). However, a component necessary for carrying capacity estimates is prey availability data, which influences equilibrium densities of sea otters (Davis et al., 2021; Dean et al., 2002). Despite large efforts to model carrying capacity in other regions, many studies (Eisaguirre et al., 2021; Hale et al., 2022; Lu et al., 2020; Tinker et al., 2019, 2021; Williams et al., 2019), including the one presented here, have not incorporated sea otter prey information directly, which is recommended for future modeling efforts (Davis et al., 2019). An important linkage is the association of subtidal habitat, specifically substrate and algal cover, with sea otter prey. Including estimates of available prey energy are also critical for accurately estimating equilibrium density of sea otters. Regions with stable sea otter populations have been found to increase in abundance after being considered standards for equilibrium densities, pointing to prey availability as a more reliable metric (Davis et al., 2021; Hale et al.,

2019, 2022). We recommend combining a suite of known sea otter-associated metrics in future studies. Additional advancements in survey technology, including remote and autonomous survey platforms, may improve access to information in data-limited systems. Much can be learned about the function of ecosystems by including physical habitat variables (Pittman, 2017).

Identifying habitat requirements is important for species management and conservation. As this study has shown, it is promising that modeling species distributions and habitat associations is possible in data-limited ecosystems. Much is still unknown about our oceans, and the ability to answer questions with open access data can help fill key information gaps. Beyond sea otters, this framework can be beneficial for species distribution modeling of other mobile marine megafauna. Specifically, understanding the habitat requirements of protected species and predicting distributions can mitigate future conflicts of resource competition or disturbance. The minimal data requirements of animal presence and dispersed habitat data over an area of interest can lead to significant gains in knowledge for management and conservation by using MaxEnt for species distribution modeling in data-limited ecosystems.

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Tables

Table 1: MaxEnt model evaluation metrics for the empirical model and null model distribution for sea otter habitat suitability in Kachemak Bay, Alaska, using data from 2016 and 2017. Z scores and p-values compare the empirical model to the null model distribution with a one-sided test. NA stands for not applicable, AUC stands for the area under the receiver operator curve and is evaluated for training data, testing data, and the difference between training and testing, and OR stands for the omission rate.

Statistic	AUC_{train}	AUC_{val}	AUC_{diff}	OR
Empirical mean	0.686	0.681	0.0226	0.0996
Empirical standard deviation	NA	0.0226	0.0195	0.0548
Null mean	0.545	0.524	0.0599	0.137
Null standard deviation	0.0107	0.0151	0.0130	0.0168
Z score	13.2	10.5	-2.86	-2.23
p-value	5.14×10^{-40}	5.13×10^{-26}	0.00211	0.0129

Table 2: Percent contribution, permutational importance, and relationship direction of habitat attributes in predicting sea otter presence. NA stands for not applicable.

Variable	Percent contribution	Permutation importance	Relationship direction
Bathymetry	43.0	25.2	Positive
Shell	18.2	23.4	Negative
Filamentous algae	18.0	11.9	Positive
Understory kelp	6.20	8.40	Positive
Gravel	5.30	5.80	Negative
Pebble	3.40	0	Negative
Coralline algae	2.90	13.1	Positive
Cobble	2.30	11.9	Negative
Macroalgae	0.600	0	Positive
Boulder	0	0.200	NA
Rugosity	0	0.200	NA
Sand	0	0	NA

Figures



Figure 1: Map of Cook Inlet, located in southcentral, Alaska. Kachemak Bay is located on the eastern side of Cook Inlet.

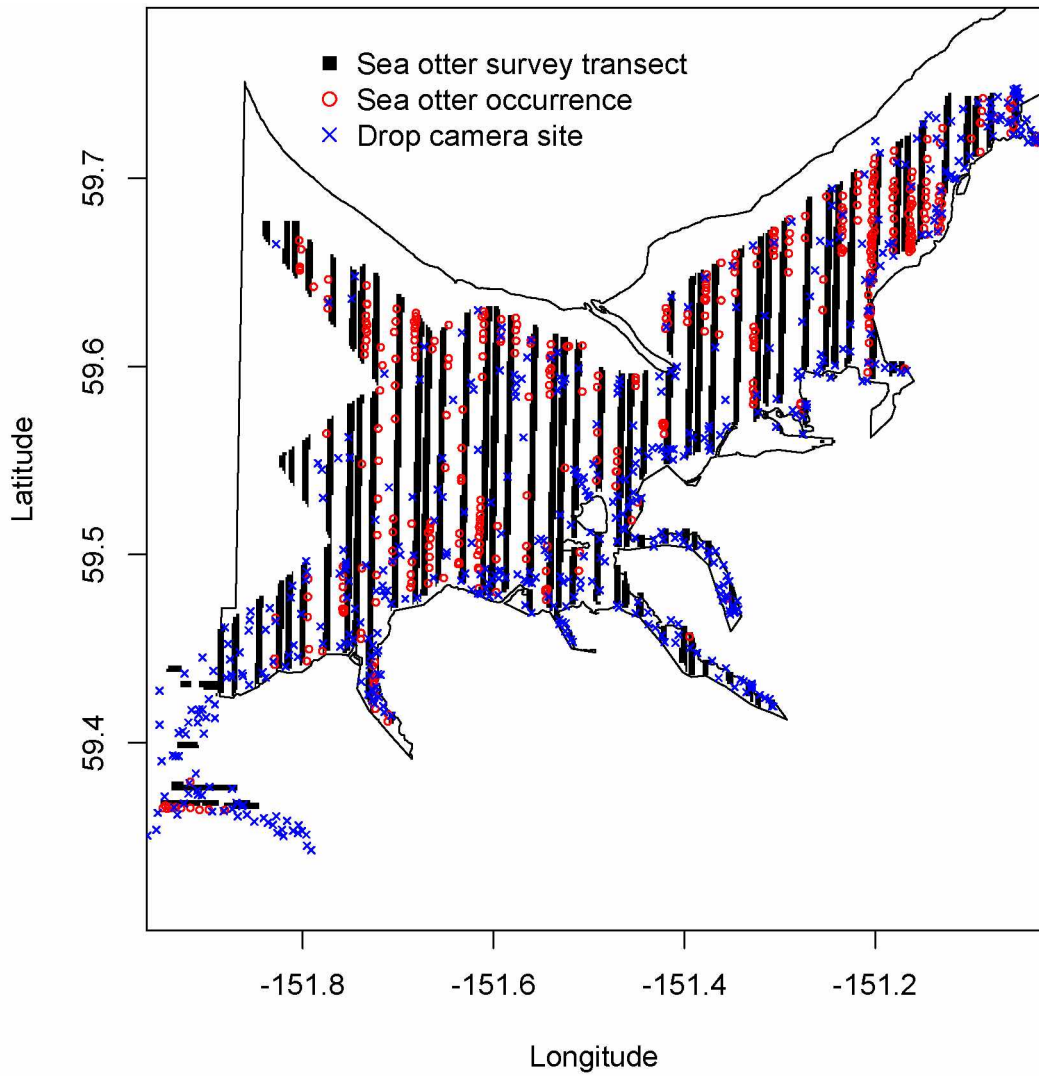


Figure 2: Map of the Kachemak Bay, Alaska, study site. The thin black line represents the outline of Kachemak Bay. The thick black lines indicate surveyed areas for sea otter abundance in 2017. Red circles (o) indicate northern sea otter sightings and blue crosses (x) indicate drop camera sites.



Figure 3: Raster surfaces for each substrate (boulder, cobble, pebble, gravel, shell, sand, and mud) and algal (understory kelp, macroalgae, filamentous algae, and coralline algae) attribute throughout the survey region in Kachemak Bay, Alaska. Darker colors represent higher percent cover and lighter colors represent lower percent cover.

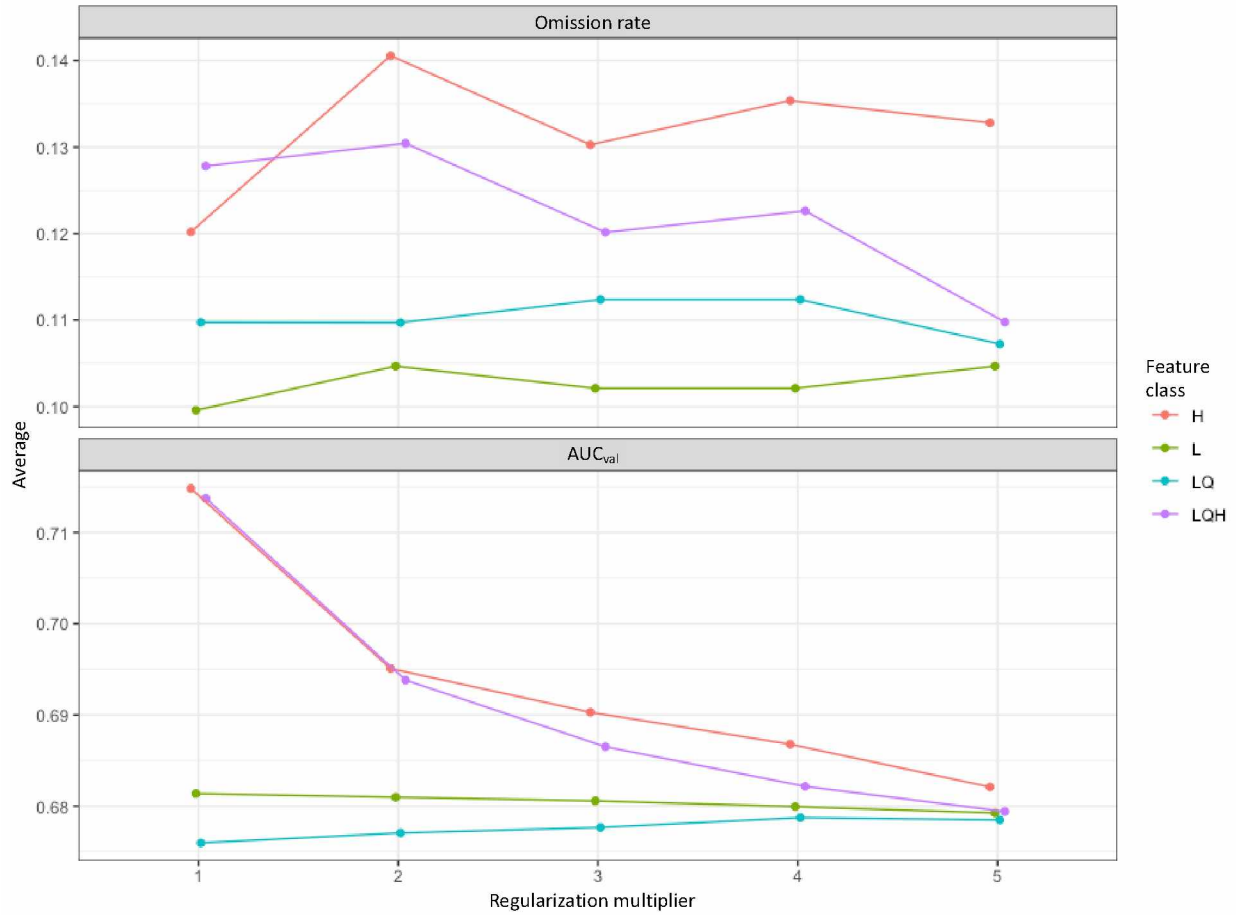


Figure 4: Line graphs of candidate model settings for model tuning. Lines are colored by feature settings (H: hinge, L: linear, LQ: linear and quadratic, LQH: linear, quadratic, and hinge). The x-axis indicates the regularization multiplier (1-5), and the y-axis indicates the evaluation metric value with omission rate on the top panel and AUC_{val} (area under the receiver operator curve for the test dataset) on the bottom panel.

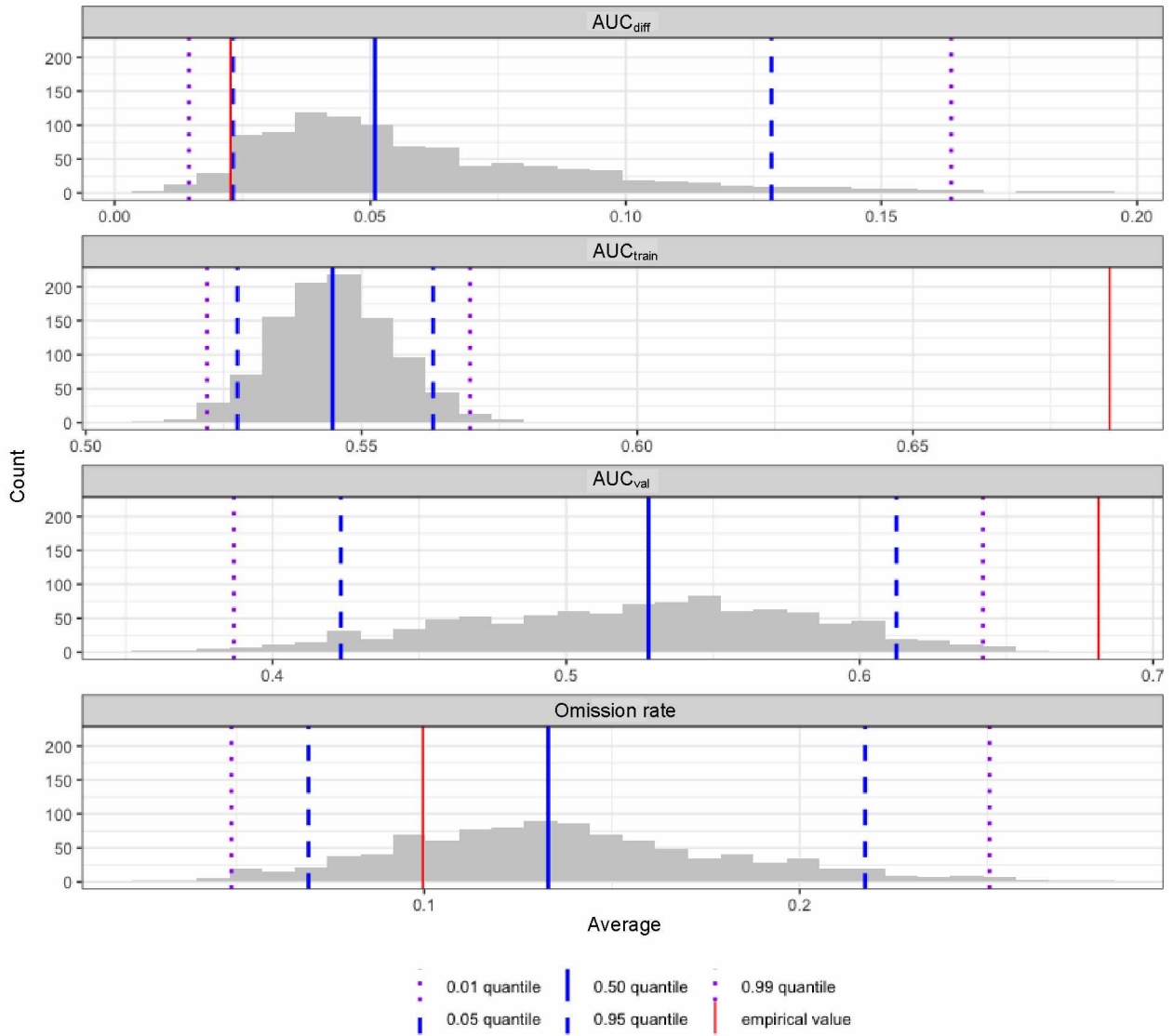


Figure 5: Null model distribution histograms for evaluation of MaxEnt model performance. The red line indicates evaluation metric values for the empirical model. Dashed blue lines indicate the 0.05 and 0.95 quantiles, purple indicates the 0.01 and 0.99 quantiles, and the solid blue line indicates the median of the null model distribution. The x-axis of each panel corresponds to the AUC_{diff} , AUC_{train} , AUC_{val} (i.e., the area under the receiver operator curve for the training data, testing data, and the difference between training and testing), and omission rate value from top to bottom, respectively. The y-axis indicates frequency.

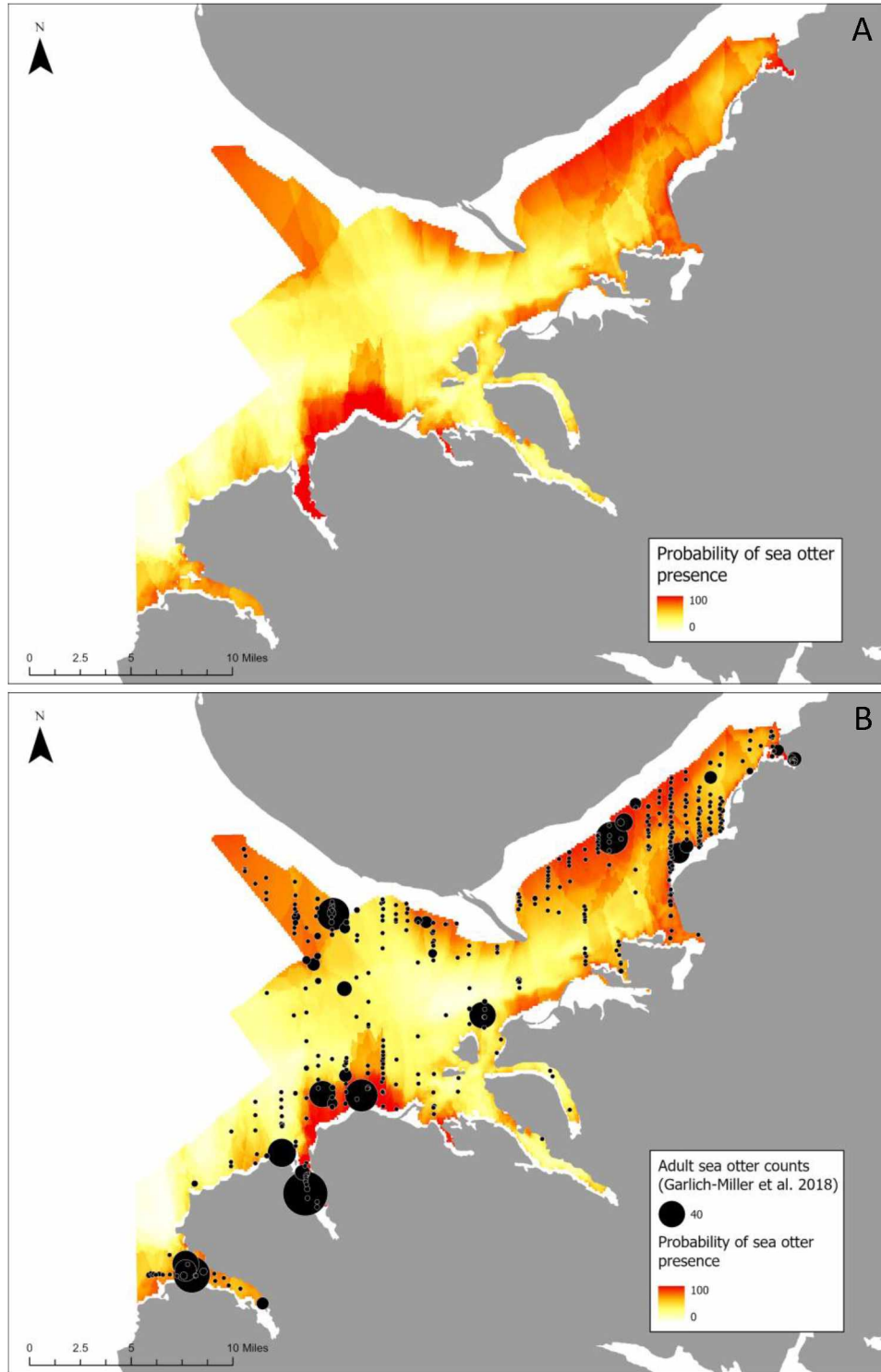


Figure 6: (A) Map of the probability of sea otter presence in Kachemak Bay based on MaxEnt model predictions. Probability ranges 0-100% from white to red. (B) Map of probability of sea otter presence in Kachemak Bay based on model predictions with sea otter survey results superimposed. Points represent adult sea otter observations and point size represents relative abundance with the point in the bottom legend representing 40 sea otters (Garlich-Miller et al., 2018).