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Predictors of Sea Otter Salt Marsh Use in Elkhorn Slough, California

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PREDICTORS OF SEA OTTER SALT MARSH USE IN ELKHORN SLOUGH, CALIFORNIA

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PREDICTORS OF SEA OTTER SALT MARSH USE IN ELKHORN SLOUGH, CALIFORNIA

Sarah M. Espinosa

Abstract

Elkhorn Slough, a small estuary located in Monterey Bay, California, has lost 50% of its salt marsh in the last 70 years (Van Dyke & Wasson 2005) and is the only estuary within the range of the threatened southern sea otter (*Enhydra lutris nereis*) that has a resident sea otter population. Recent studies suggest that estuaries provide important habitat for the recovery of southern sea otters (Hughes et al. 2013; Lindsey 2016; Eby et al. 2017; Silliman et al. 2018). Using habitat suitability modeling, this study identified important physical features of salt marsh tidal creeks for sea otter use to guide restoration projects of salt marsh habitat in Elkhorn Slough. Using ArcGIS, six tidal creek salt marsh predictor variables (channel order, width, bank slope, elevation, geometric efficiency and distance to main channel) were calculated and spatially joined to sea otter location data from abundance surveys from September 2013 through September 2017. Five generalized additive models (GAMs), a full model and four other models using subsets of data based on sea otter behavior (resting or foraging) and demographic status (female with pups vs. male and females without pups), were created with different combinations of predictor variables and evaluated against their respective null models using AIC values, in R. Results suggest that sea otter behavior influences salt marsh use more than sea otter status. Sea otters primarily use salt marsh as resting habitat and prefer resting in tidal creeks that are wider (>10 m), with elevations between 0.3 m to 2 m NAVD 88, have shallow bank slopes (10 to 20 degrees) and are close to the main channel (<300 m). The foraging models could be significantly improved in the future by including prey distributions and other habitat types, but suggest that foraging sea otters prefer feeding in flooded salt marsh or in deeper creeks (<0 m NAVD 88) close to the main channel. These methods can be used to assess salt marsh habitat suitability and identify critical habitat for sea otters in other estuaries that may soon be re-colonized.

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Introduction

Ecology is the scientific study of the interactions between organisms and their environment and forms the basis of understanding what drives the distribution and abundance of these organisms across the landscape. The physical environment relative to the species' physiological tolerances, biological interactions, and history (including the history of human interventions), can influence a species' abundance and distribution, often represented as the species' "niche". More specifically, the fundamental niche of a species can be conceptualized as its distribution within an n-dimensional hypervolume made up of all the environmental and biotic variables that have a direct influence on its physiology (Hutchinson 1957). However, a species' fundamental niche is difficult to characterize based solely on field observations because observed habitat use generally represents only a subset of the fundamental niche, often termed the "realized niche" (Holt 2009; Guisan et al. 2017).

Habitat suitability modeling is one approach used to describe the realized niche of a species throughout its distribution (Guisan & Zimmermann 2000; Franklin 2010; Guisan et al. 2017). Predicting and mapping the realized niches of species is a crucial part of wildlife management and conservation (Elith et al. 2006; Austin 2007; Morris, Proffitt & Blackburn 2015). The realized niches of marine mammals are especially challenging to measure because they can vary spatially and temporally, due to the inherent instability of the aquatic substrate, and can also be context-dependent, as marine mammals often use different portions of the marine environment for different behaviors or life history functions (Schick et al. 2011). Recent advances in technology, such as radio tracking, GPS tagging, satellite remote sensing, and geographic information systems (GIS), have facilitated the study of marine mammal habitat use, and thus supported conservation efforts but research is still logistically difficult and costly (Schick et al. 2011; Morris, Proffitt & Blackburn 2015).

Southern sea otters (*Enhydra lutris nereis*) are a threatened, keystone species that live in coastal marine habitats along the mainland coast from Half Moon Bay to Point Conception, California. Their proximity to land and the fact that they spend much of their time at the surface of the water, make them an ideal marine mammal study species. Sea otters have high energetic demands because they lack a blubber layer and rely on their dense fur for protection from the cold sea water (Kenyon 1969; Costa & Kooyman 1984). Because of their role as an apex predator in the nearshore system and their high metabolic requirements, sea otters exert a disproportionally large impact on nearshore food webs (Costa & Kooyman 1984). By limiting the abundance of sea urchins and other herbivorous invertebrate prey, sea otters indirectly provide kelp with a trophic release from grazing, resulting in more abundant kelp forests, which provide habitat for many fish, invertebrate, bird, and other marine mammals (Estes & Duggins 1995).

The behavior, ecology and habitat use of sea otters along the outer coast has been studied extensively by researchers using direct observation, radio transmitters and time-depth recorders to measure diets, movements and home-ranges (Tinker et al.

2013; Tarjan & Tinker 2016; Tinker et al. 2017). In contrast, the estuarine habitat use of sea otters is less well understood, although recent studies (Hughes et al. 2013; Hessing-Lewis et al. 2017; Silliman et al. 2018) suggest that estuaries may provide important habitats for recovering sea otter populations.

Elkhorn Slough is a small tidally influenced estuary located in the Monterey Bay, CA. Based on recent censuses, approximately 110 sea otters live in Elkhorn Slough (Tinker & Hatfield 2017), and it is the only estuary in California with a resident sea otter population. Results from a recent radio-tagging study (Lindsey 2016) suggest that sea otters use a variety of estuarine habitats in Elkhorn Slough, including salt marsh.

Salt marsh is a vegetated estuarine ecosystem that is flooded daily by the tide and is intersected by a dendritic network of tidal creeks that controls the hydrodynamics and evolution of the salt marsh (Fagherazzi 1999; 2001). Salt marsh habitats provide a number of valuable ecosystem services, including buffering adjacent areas from flooding due to storm surges, offering recreational opportunities for ecotourism, fishing and hunting, and creating important foraging and nursery habitat for fish, bird and invertebrate species (Beck 2001; Narayan 2017).

Unfortunately, many salt marsh habitats have been extensively impacted by human development: 50% of salt marsh habitats have been lost nationally, while 91% of California wetlands, including saltmarsh, have been lost to coastal development or conversion to agricultural fields (Ambrose 2000; Barbier et al. 2011). Elkhorn Slough is losing its tidal wetlands at an unprecedented rate: 50% of its original marshes have been lost in the last 70 years (Van Dyke & Wasson 2005). Increased marsh flooding and erosion due to sea level rise and increased frequency and intensity of storms is a major concern for salt marshes (Takekawa et al. 2013). In some cases where landscape barriers are not an issue, salt marsh can naturally shift inland as a response to sea level rise. Unfortunately, where natural or human constructed barriers are an issue, salt marshes may disappear completely without restoration to counteract the effects of sea level rise (Takekawa et al. 2013; Raposa et al. 2016: Thorne et al. 2016). Recognizing the importance of salt marsh habitats, the Elkhorn Slough National Estuarine Research Reserve (ESNERR) initiated a long-term Tidal Wetlands Project in 2004 to prevent marsh erosion and enhance the biodiversity and habitat functions of salt marsh in Elkhorn Slough (Wasson et al. 2015).

The potential importance of salt marsh as sea otter habitat is a relatively new finding (Lindsey 2016; Eby et al. 2017), and detailed analyses of saltmarsh habitat use by sea otters have yet to be conducted. A better understanding of how sea otters use salt marsh and tidal creeks, and which features or structures are most important, will allow ESNERR to incorporate this information into future marsh tidal creek restoration plans. ESNERR has recently completed a 20 hectare marsh restoration project and will conduct further projects in coming years; these projects could include tidal creeks optimally designed for sea otter use. Furthermore, sea otters are likely to colonize other estuaries over the coming decades, including San Francisco Bay, 150 km to the north of Elkhorn Slough, which represents the most extensive estuarine system in California. Understanding how sea otters use estuarine habitats, including salt marsh, will be useful for identifying and protecting critical habitats in these areas. Here, I examine habitat use patterns of sea otters in salt marsh, characterizing the physical features of salt marsh habitats that determine their relative degree of use by sea otters, while controlling for variation due to reproductive status and behavior.

Objectives and General Approach

To characterize sea otter salt marsh distribution and habitat use throughout Elkhorn Slough salt marsh, I used generalized additive models (GAMs) to determine key environmental variables that are predictive of sea otter use of salt marsh. First, I conducted a spatial analysis of Elkhorn Slough salt marsh tidal creeks in ArcGIS 10.5.1 (ESRI, Redlands, CA) to calculate tidal creek elevation/depth, width, bank slope, geometric efficiency, channel order, and distance to main channel. I then used GAMs to fit non-linear functions to environmental predictor variables associated with sea otter presence and randomly generated absence points. I compared the distribution of sea otters of different reproductive status (females with pups vs. males and females without pups) and behavior (foraging vs. resting and hauled out) in relation to the predictor variables to address three questions: 1) Which salt marsh tidal creek variables are most important for predicting sea otter distribution? 2) Do patterns of tidal creek use, and the relative importance of predictor variables, differ depending on sea otter behavior (foraging vs. resting)? and, 3) Do patterns of tidal creek use, and the relative importance of predictor variables, differ among males, females and females with pups?

Methods

Study Site

Elkhorn Slough is a shallow tidal estuary located approximately 150 km south of San Francisco in Moss Landing, CA on the Monterey Bay. The estuary includes an 11.5 km long main channel with salt marsh located on either side of the main channel. Sea grass beds and intertidal mudflats are also located in the main channel. Although Elkhorn Slough represents just 1% of the size of San Francisco Bay, it has 1420 hectares of marsh and tidal flats, making it the largest salt marsh in California south of the San Francisco Bay (Caffrey et al. 2002). Elkhorn Slough is also the only estuary in California with a resident population of sea otters. A male raft of about 20 sea otters first entered Elkhorn Slough in the 1980s (Kvitek et al. 1988), and the estuary was primarily used by non-territorial males until the early 2000s, when females with pups began to establish residency (Feinholz 1998). The resident Slough population grew rapidly from 2002-2013, and since then the population has fluctuated around 110 otters (USGS, unpublished data). Because most animals appear to remain exclusively within the Elkhorn Slough estuary, this population provides a unique opportunity to study how sea otters use salt marsh habitat and to identify variables that predict their distribution throughout tidal creek networks. For computational tractability we identify four main salt marsh regions for the purpose of this study: 1)

Moss Landing Wildlife Lookout, 2) Rubis, 3) Hummingbird, and 4) Yampah (Figure 1). These regions are made up of 174 hectares of salt marsh defined by permanent geographic features such as the main channel of the slough and levies that can be used as models for salt marsh restoration projects.

Sea Otter Occurrence Data and Forage Data

In 2013, the U.S. Geological Survey (USGS) and U.C. Santa Cruz, in collaboration with the ESNERR, the Monterey Bay Aquarium, and the California Department of Fish and Wildlife, initiated a four-year project to determine the population status and habitat use of sea otters in Elkhorn Slough. As part of the study, 27 wild sea otters (18 females and 9 males) were tracked using radio telemetry, after the capture and surgical implantation of VHF radio transmitters (Advanced Telemetry System Inc., Insanti, MN) and application of plastic colored Temple Tags, (Temple, TX), following standard procedures (Williams and Sinif 1983; Ames et al. 1986; Ralls, Eagle & Siniff 1996).

From September 2013 through September 2017, 79 surveys for sea otter abundance and distribution were conducted. These land-based surveys took place bi-weekly from September 2013 through September 2016 and monthly from October 2017 through September 2017. Five teams of observers, comprised of volunteers, interns and staff, made simultaneous counts of their assigned sections of the slough at a specified time to minimize double counting otters. Volunteers and interns were trained by staff from Monterey Bay Aquarium, USGS and U.C. Santa Cruz, on established survey protocols used during the annual statewide USGS sea otter survey. During Elkhorn Slough distribution surveys, the behavior, number of otters, number of pups, and habitat type were marked on a paper map following standard protocols (Tinker & Hatfield 2017). Paper maps were later digitized in ArcMap for Desktop 10.5.1. Sea otter occurrence data from these surveys was used as the response variable in the GAM models.

Using the spatial analyst toolbox in ArcMap, I created a series of kernel density maps in raster format with cell size of 400 m^2 and a kernel-smoothing window of 200 m from the survey data after grouping by behavior (foraging vs. resting) and status (females with pups vs. males and females without pups), to visually describe observed sea otter distributions throughout the salt marsh and main channel. Tidal height was grouped into three bins based on NOAA datums in NAVD 88 for Elkhorn Slough at Elkhorn (N 36º49.1’, W-121º 44.8’). For this study, low tide is below mean low water (< 0.315 m), medium tide is from 0.315 m to 1.42 m (mean tide level is 0.87 m), and high tide is above mean high water level (>1.42 m).

Over the four-year project, 16,117 successful forage dives, in which an otter was observed to capture and consume prey, were recorded out of a total of 26,429 dives. Forage data were collected opportunistically on both tagged and un-tagged sea otters. For each dive, observers recorded dive time, surface time, prey type (identified to the lowest taxonomic level possible), and prey size (measured relative to sea otter paw size). These forage data were used to determine diet composition of sea otters foraging in the salt marsh and in the main channel, using standardized analytical procedures (Tinker et al. 2012).

Spatial Analysis of Environmental Variables

To calculate environmental predictor variables, spatial analyses were conducted in ArcMap for Desktop version 10.5.1 using the ‘Spatial Analyst’, ‘3D Analysis’ and ‘Data Management’ toolboxes on a merged digital elevation model (DEM) created from two Elkhorn Slough LIDAR images at a 1 m resolution (NOAA-NGS 2004; Seafloor Mapping Lab of CSUMB 2011) and an Elkhorn Slough habitat shapefile (Van Dyke 2009).

The most recent complete topographic LIDAR image, a form of remote sensing used to create accurate DEMs of the earth’s landscape, was created for Elkhorn Slough in 2004 with 1 m resolution (NOAA – NGS). In 2011, the Seafloor Mapping Lab at California State University Monterey Bay used vessel-based LIDAR sonar to create a partial bathymetric DEM of the slough that includes the main channel, Parsons Slough, and South Marsh tributaries. The six environmental tidal creek variables calculated and used in this study are mean depth (Elevation), width, bank slope (Slope_mean), geometric efficiency (geoeff) and channel order (Chan_ord) (see detailed methods below). These six variables were selected because they need to be clearly defined during salt marsh construction and restoration projects and because they were believed to potentially influence sea otter behavior and salt marsh use.

Tidal creek stream order was assigned to a total of 846 creeks using the ‘Stream Order’ Hydrology Tool with the Strahler method, which assigns channel order based on Horton (1945). The Horton method assigns channel order from the smallest creek to the largest creeks, with the first order as the smallest creeks. However, for simplicity of interpretation and consistency with other variables, I reversed the ranking to make first order streams the largest creeks that connect directly to the main Elkhorn Slough channel and fourth order streams the smallest creeks. For example: large creeks that intersect with the main channel are first order creeks; second order creeks intersect with first order creeks and other second order creeks; and, small, dead-end channels are classified as fourth-order creeks.

Cross sections of each ordered creek were created every five meters for which the elevation, bank slope and width were calculated following protocols from Endris, Clark & O’Conner (2014). First, creek center lines were created using the ‘Polygon to Lines’ tool. Second, lines perpendicular to the creek centerlines were created every five meters to generate a total of 7607 creek cross sections and cut at creek edges to create width measurements. Buffered width lines, were used to extract the mean depth across the creek cross section and the mean slope at the creek cross section using the merged DEM layer. The Euclidean distance from each creek cross section to the main channel was calculated by spatially joining the creek cross sections to the main channel. For this study, distance to main channel was used as a proxy for distance to a primary food source.

Geometric efficiency is a measure of the morphology, branching and hydrodynamics of a salt marsh and generally indicates how well a salt marsh drains into a creek network (Marani et al. 2003). Specifically, it is a measure of the unchanneled path length, or a measure of the distance a drop of water on the marsh surface must travel before reaching a creek (Marani et al. 2003; Kearney & Fagherazzi 2016). High geometric efficiency occurs when tidal creeks are curvy and have many branches: water on the salt marsh has a short distance to travel back to a creek, as the tidal network efficiently drains the marsh, but transit through the creek network to the main channel will be tortuous and slow. Conversely, low geometric efficiency is associated with fewer branches and fewer curves in the creek network: water on the salt marsh must travel longer distances to reach a creek but then may flow quickly in and out of these creeks to the main channel. Geometric efficiency (GE) was calculated using equation (1) below, where “l_h” is the Hortonian length and “l” is the mean unchanneled path length.

$$GE = l_h / l \qquad (1)$$

$$l_h = A/L \qquad (2)$$

The Hortonian length is calculated using equation (2), where “A” is the total sub-basin area, and “L” is the sum of the channel lengths in a sub-basin.

To calculate the unchanneled path length, the ‘watershed’ hydrology tool was used to create sub-basins within each of the four areas. Channel-ordered creeks were spatially joined with a sub-basin to assign streams to a sub-basin. Using the ‘Flow

Direction' hydrology tool on the DEM, a raster layer of water flow direction was created for each watershed. A channel-ordered creek shapefile was buffered based on stream order. The buffered stream shapefile was used to clip the flow direction raster layer. Using the 'Flow Length' hydrology tool on the DEM, a raster layer of each sub-basin within each watershed was created. This final raster layer is the unchanneled path length "l". The area of each sub-basin and the sum of the channels within a sub-basin were used in equation (2), above, to calculate the geometric efficiency of tidal creeks within a sub-basin.

Joining Environmental Variables to Sea Otter Presence and Available Points

Predictive suitability habitat models have a higher success of predicting species distributions when incorporating both species presence (observed use) and species absence (un-used) locations; however, absence locations are hard to identify thus, randomly generated pseudo-absence points can be used in place of observed absence locations (Boyce et al. 2002; Brotons et al. 2004; Pearce & Boyce 2006). Distribution survey data only include sea otter presence locations so a total of 7000 pseudo-absence points, hereafter referred to as 'available points', were generated using the 'Create Random Points' Tool in ArcGIS throughout the entire salt marsh shapefile filtered to within 250 m of water. 7000 available points were generated because model results are less biased with a contamination rate of 20% or less presence points to presence and available points (Pearce & Boyce 2006; Lancaster & Imbens 1996). A total of 1703 sea otter presence points and the 7000 available points were spatially joined with the nearest tidal creek cross section to combine all environmental variables with a presence or available point. I then used boxplots of each variable to visually explore differences between sea otter presence points and available points, as a first-pass approximation of sea otter preferences for each habitat variable.

Model Analysis - Generalized Additive Models (GAMs)

Generalized Additive Models (GAMs) and Maximum Entropy (MaxEnt) models are two common types of models used in species habitat analysis because they have the best predictive performance without overfitting (Elith et al. 2006; Guisan et al. 2017). Both modeling frameworks were initially used to analyze sea otter presence and available points in relation to tidal creek salt marsh variables. However, because GAMs have higher statistical power that can be used to determine the mechanisms behind sea otter presence in tidal creeks, they are the primary focus for the remainder of the paper.

GAM models relate presence points and randomly generated pseudo-absence points to a series of environmental variables across a landscape of interest, to predict potential species' distributions by fitting non-linear functions to each environmental variable (Hastie & Tibshirani 1990; Guisan & Zimmerman 2000; Austin 2002; Elith et al. 2006). A binomial link function was used to accommodate the binary response variable, and GAM models with various combinations of predictor variables were fit to the data by randomized maximum likelihood methods, implemented using the ‘mgcv’ package (Wood 2017) in R-studio (RStudio Team 2016, version 1.1.383) using R software (R Core Team 2017, version 3.4.3). First, a full model with all six predictor variables (Elevation, Width, Slope_mean, geoeff, dist_mc and Chan_ord) was fit to the entire data set. Next, to determine how habitat use varied among sea otters of different status and as a function of behavior, GAM models were fit to four subsets of the data: 1) resting females with pups (n=470 presence points), 2) foraging females with pups (n=46 pts), 3) resting males and females without pups (n=680 pts), and 4) foraging males and females without pup (n=96 pts). Females with pups, as well as foraging and resting behaviors, were separated out because of their unique physiological constraints and their importance for indicating population health (Thometz et al. 2016). For each of these five data sets (the complete data and the four sub-sets), I evaluated GAMs having different combinations of predictor variables, comparing their performance to that of a null model (i.e. no predictor variables) by using the Akaike information criterion (AIC) to select the best-supported model (Burnham & Anderson 2002). All models, including null models, incorporated ‘region’ as a random effect, to account for disproportionate use of each salt marsh region.

Best supported GAM models for each data set (5 total) were used to predict sea otter presence by behavior and status throughout Elkhorn Slough salt marsh. Plots of the fitted smoothing functions for each continuous variable were generated to determine preferred ranges of each predictor variable. Model predictive ability was evaluated using area under the curve (AUC) values. AUC values are based on the area under the receiver operating characteristic curve (ROC) where model point predictions are plotted and connected using straight lines (Elith et al. 2006). AUC values range from 0 to 1, with an AUC of 1 indicating a model that perfectly predicts a species presence and an AUC of 0.5 indicating a model that does not predict better than random chance (Elith et al. 2006). AUC values for each GAM were derived using the 'ROCR' package (Sing et al. 2005) in R.

Results

Foraging Data

In general, most sea otter foraging occurred within 216 hectares of the main channel rather than in the surrounding 215 hectares of salt marsh (Figures 3, 5). In the main channel, foraging occurred more frequently as the tide increased while resting occurred more frequently at low tides (Figure 5). Sea otters foraged primarily on clams (55% of the diet) with intertidal crabs (*Pachygrapsus crassipes)* comprising just 12% of the diet in the main channel habitat (Figure 4). In the salt marsh, foraging occurred mostly at high tides when the pickleweed was flooded (Figure 5) and intertidal crabs made up 65% of the diet with clams making up only 6% of the diet (Figure 4).

Environmental Variable Boxplots

Visual comparison of the boxplots showing the distributions of each environmental variable for available points vs. sea otter presence points, indicate that sea otters use tidal creeks with lower channel orders (mean = 1.5, SD = 0.95) that are wider (mean=11.34, SD=4.45), with steeper bank slopes (mean=12.45, SD=3.61), lower geometric efficiencies (mean=1.80, SD= 0.47), lower elevations (mean=0.36m NAVD88, SD=0.34), and are closer to the main channel (mean=263.12, SD=72.2) (Table 1, Figure 6).

GAM Full Model

The best-supported full model (AIC=4593) included five predictor variables: elevation ($p<0.001$), bank slope ($p<0.001$), distance to main channel ($p<0.001$), geometric efficiency ($p<0.001$), channel order ($p=0.0212$) and region ($p<0.001$) as a random effect (Table 2). This model explained 47% of the deviance compared to the null model, which explained 29% of the deviance and had an AIC value of 6114 (Table 2). Plots of the GAM functions for the predictor variables indicate that sea otters prefer creeks with depths between 0 and 0.4m NAVD 88, with slopes between 12 to 20 degrees, that are somewhat close to the main channel (<265m) and with lower geometric efficiency (Figure 7). The AUC value for this model is 0.914, indicating very high predictive ability of this model. The predictive map from the best-supported full model shows high probabilities of sea otters along the main Yampah Creek, with medium probabilities throughout higher-order Yampah creeks and some main creeks in the other salt marsh regions (Figure 8).

GAM Models by Behavior and Status

The best-supported model for resting females with pups (AIC=1443) included all tidal creek predictor variables: elevation ($p<0.001$), bank slope ($p<0.001$), width (p=0.072), distance to main channel (p<0.001), geometric efficiency (p<0.001), and channel order (p=0.00303) with region as a random effect (p<0.001). This best-supported model explained 59% of the deviance, compared to the null model that explained 33% of the deviance with an AIC of 2327 (Table 2). Response curves from the model indicate that resting females with pups prefer tidal creeks that are shallower (0 to +1.5 m NAVD 88), with bank slopes of 12 to 20 degrees, lower geometric efficiency, and that are close to the main channel (<310m NAVD 88) (Figure 9). The AUC value for this model is 0.913, suggesting high predictive ability. The predictive map of resting females with pup showed high probabilities in the main creek of the Yampah Region (Figure 11).

The best-supported model for resting males and females without pups (AIC=2625) included: elevation (p<0.001), bank slope (p<0.001), width (p=0.0206), distance to main channel (p<0.001), and geometric efficiency (p=0.0276) with region as a random effect (p<0.001). This model explained 44% of the deviance compared to the null model that explained 24% of the deviance (Table 2). Response curves from the model indicate that resting males and females without pups prefer tidal creeks that are 0.3m to 1.5 m NAVD 88, with bank slopes of 12 to 20 degrees, with lower geometric efficiency, and that are close to the main channel (<330m) (Figure 9). The AUC value for this model is 0.911, suggesting high predictive ability. The predicted distribution of resting males and females without pups showed high probabilities in the main Yampah creek and medium probabilities throughout Yampah, Wildlife and Hummingbird salt marshes (Figure 11).

The best-supported model for foraging females with pups (AIC=497) included the predictor variables: elevation (p<0.001), distance to main channel (p<0.001), and channel order(p=0.0174) with region as a random effect (p<0.001) and explained 13% of the deviance compared to the null model that only explained 6% of the deviance (Table 2). Response curves of the smoothed functions indicate that sea otters can be found foraging in deep tidal creeks (<0m NAVD 88) closer to the main channel (Figure 10). The AUC value for this model is 0.882, suggesting a relatively high predictive ability. The distribution map of foraging females with pups distribution predicts medium probabilities throughout the main Yampah creek, and also in the mouths of larger creeks near the main channel in the Wildlife, Rubis and Hummingbird regions (Figure 11).

The best-supported model for foraging males and females without pups (AIC=910) included: elevation (p=0.0002), bank slope (p=0.01793) and distance to main channel (p=0.0723) with region as a random effect (p<0.001) and explained 12% of the deviance compared to the null model which explained only 6% of the deviance (Table 2). Response curves of the smoothed functions indicate foraging males and females without pups prefer foraging in deeper channels (<0 m NAVD 88). Although elevation is the only significant variable in this model, response curves indicate foraging otters can be found feeding close and far away from the main channel along wider creeks with steeper bank slopes (Figure 10). The AUC value for this model is 0.900, suggesting relatively high predictive ability. The distribution map of males and females without pups foraging predicts medium to high probability of foraging otters along the main Yampah creek and some probability of finding sea otters along large creeks throughout other regions (Figure 11).

Discussion

Sea Otter Salt Marsh Use in Elkhorn Slough

In general, sea otters in Elkhorn Slough primarily use salt marsh tidal creeks as resting habitat and the main channel as foraging habitat (Figure 5). Sea otters that rest in the salt marsh at lower tides will usually move from the marsh to the main channel at medium and high tides to forage on clams. However, during high tides some sea otters may remain in the salt marsh to forage on *Pachygrapsus crassipes* (shore crabs) that live within the submerged pickleweed in the flooded salt marsh. Elevation, in terms of both depth of tidal creeks and the height of the creek banks, and distance to main channel, a proxy used for distance to a primary food source, were included in all five of the best-supported models and appear to be the most influential environmental variables. Based on my results, sea otters appear to prefer salt marsh habitat with deeper creeks around 0.36 NAVD 88 and <300 m from the main channel (Table 2, 3).

Although observed and predicted sea otter distribution maps differed by status and behavior (Figure 11), a comparison of best-supported GAM component smooth functions suggest that creek selection is more strongly affected by sea otter behavior than by demographic status. In other words, males and females with or without pups were generally similar in terms of their tidal creek usage patterns for resting and foraging behavior, although there were some slight differences.

Sea otters in Elkhorn Slough primarily use salt marsh as resting habitat, especially at medium (0.316 to 1.42 m) and high tides (>1.42 m). Resting behavior in salt marsh includes both floating in the water of the tidal creeks and hauling out on salt marsh banks. The GAM model functions show that resting otters are found in tidal creeks with shallow sloping creek banks (13 to 20 degrees) and elevations of 0.3 m to 2 m, which corresponds closely to the height of medium and high tides and the distribution of *Salicornia virginica* (1.2 m and 2.5 m NAVD 88), the dominant vegetation of Elkhorn Slough’s salt marsh (Figures 3, 10; Van Dyke & Wasson 2005). Sea otters, while being agile swimmers, exhibit poor terrestrial locomotion (Riedman & Estes 1990) and are generally awkward at moving around on exposed salt marsh (Eby et al. 2017). Having shallow slopes to climb up may therefore facilitate movement between tidal creeks and salt marsh haul-out areas. Gradually sloped banks also coincide with slower flow rates (Allen et al. 2007), creating good resting locations and refuge spots because otters will not be swept away with an ebb tide. Sea otters also preferred resting in creeks >100 m and < 300 m from the main channel. Proximity to the main channel is likely important for allowing efficient and frequent transitions in and out of salt marsh habitats on changing tides to access food, although the humped function indicates an optimal distance of ~265 m and suggests that at least some separation from the main channel is preferred. Similarly, sea otters appear to prefer resting in wider (>10 m) creeks with low geometric efficiencies, indicating creeks with straighter and less sinuous courses (Kearney & Fagherazzi 2016). Such creeks are probably easier to navigate and have higher tidal flows facilitating transitions to the main channel.

The model-predicted resting distributions of sea otters throughout the salt marsh agree well with the observed salt marsh distributions, showing high probabilities of finding resting otters throughout Yampah salt marsh region and the main Yampah creek. One noticeable difference between demographic groups is that males and females without pups have a higher probability of resting in the first order creeks of the Wildlife, Rubis and Hummingbird salt marsh regions than females with pups, which have a higher probability of being found only in Yampah. This difference may reflect the fact that Yampah salt marsh has been off-limits to marine recreation (including kayaking, fishing, paddle boarding, and tour boats) since 2011 when signage was installed by ESNERR to close the area. Sea otters resting in salt marshes are highly vulnerable to human disturbance, due to the limited potential for escape, and females with dependent pups may be especially susceptible. Nursing mothers may thus prefer Yampah creek to other salt marsh regions because of the reduced frequency of disturbance (Eby et al. 2017).

In addition to resting, sea otters also forage in salt marsh habitats, particularly at high tides when they have swimming access to larger areas of marsh. Elkhorn Slough's salt marsh is low compared to salt marsh in other estuaries in California, and tides of >1.52 m flood the pickleweed on the marsh, enabling sea otters prime access to *Pachygrapsus* that live in the pickleweed found in lower marsh region (<1.8 m NAVD 88). Nonetheless, model results suggest that foraging sea otters are found in deeper creeks closer to the main channel (Figure 11). This likely reflects foraging in transit as sea otters return to salt marsh from feeding bouts in the main channel, when they may opportunistically feed on *Pachygrapsus* along the bank edges until they reach preferred resting spots about 300 m from the main channel. Foraging males and females without pups show a slight tendency to feed in creeks with steeper banks (12 to 20 degrees). These banks are devoid of vegetation and typically riddled with numerous crab burrows. The foraging models themselves only explain 12% to 13% of the deviance in sea otter foraging: I expect that models could be improved by adding prey distributions and abundance and including the main channel as a habitat class.

Salt Marsh Use by Sea Otters vs. Other Animals

Although this is the first study to investigate sea otter salt marsh tidal creek use, other studies have also found salt marshes and tidal creeks to be important habitat for large animals (mammals and reptiles). Similar to sea otters in Elkhorn Slough, bottlenose dolphins in South Carolina use salt marsh tidal creeks at high tides to forage because they can access/swim though the creeks and follow their fish into creeks (Young & Phillips 2002). Nifong and Silliman (2016) created models to examine variation in tidal creek use by alligators, finding that tidal creek depth (a proxy for tide) was the most important predictor variable. They concluded that alligators preferred deep creeks because depth was maximized at high tides and the difference in tides resulted in fish becoming an easy prey source for alligators when stranded at low tides. Gradual bank slopes, creek depth, flow, channel order and distance to land were all important factors that influence fish abundance and distribution throughout salt marshes (Desmond 2000; Jin et al. 2014). Salt marshes are also used as nursery habitats for many economically important fish and invertebrate species (Beck et al. 2001; Minello et al. 2003; Jin et al. 2014). For an area to be considered nursery habitat it must have a higher contribution to juvenile age classes than predicted based on area alone (Beck et al. 2001). Based on this definition, Yampah salt marsh can be considered critical nursery habitat for sea otters because it supports higher densities of resting females with pups than any other habitat within Elkhorn Slough.

Implications for Salt Marsh Restoration

Salt marshes contribute a variety of ecological services to coastal areas. These include the mitigation of coastal flooding from storm surges; filtration of sediments and pollutants from water runoff; and feeding and breeding habitat for a variety of marine and terrestrial species (Beck 2001; Barbier et al. 2011; Narayan 2017). About 50% of the salt marsh in Elkhorn Slough has been lost in the last 70 years (Van Dyke & Wasson 2005). With rising sea levels and the increasing frequency of powerful storms, coastal ecosystems and communities are at ever-greater risk of damage by floods (Raposa et al. 2016). Enhancement and restoration of salt marsh is one strategy that has been employed to mitigate risk. Such natural or hybrid approaches to coastal protection can be cost-effective and can strengthen the ecological resilience of coasts while preventing loss of life and property (Sutton-Grier et al. 2015).

Salt marsh restoration and creation is a complex process that requires collaboration between scientific advisors from private and governmental organizations to create restoration plans that evaluate the specific needs of the communities surrounding the salt marsh and the species that depend on it (Thorne et al. 2012; Freedman et al. 2017). Recently, restoration of 20 hectares of marsh was completed at Hester Marsh located next to Yampah and more restoration is planned for the near future (ESA 2014). Results from this study can be used to guide salt marsh construction of new habitat that are optimized for sea otter use. Generally, I suggest that salt marsh restoration projects for sea otter use take into consideration the ease of access by avoiding areas where entrapment may occur, such as behind culverts or flood gates, and threats of potential disturbance by boats and cars. Specifically, using the results of the modeling, I recommend that creeks be constructed with bathymetry and elevations of at least -1 m to 2 m NAVD 88 and widths of at least 10 m with easy access to the main channel and shallow sloping banks to facilitate hauling out. Suitable resting areas (e.g. widened bends with resting pools) should be no more than 300 meters from the main channel. Also beneficial would be inclusion of areas of lower marsh that are more frequently submerged by high tides, providing foraging areas where shore crabs can be obtained while the marsh is submerged.

Use of Methods to Evaluate Value of Other Salt Marshes as Potential Sea Otter Habitat

While Elkhorn Slough is currently the only estuary with abundant sea otters using salt marshes, there are other estuaries in California where sea otters may interact with salt marshes in the future. Numerous factors affect the potential value of estuarine habitat to sea otters, including prey availability and disturbance levels, but one important factor especially for nursery habitat is salt marsh structure. Methods from this study can be used to create models that predict potential use of salt marshes by sea otters in other estuaries. I predict that marsh elevation, tidal creek depth and bank height, bank slope and accessibility to a main channel will all be important factors to consider when evaluating suitability of salt marshes in other estuaries. Salt marsh bank elevation appears to be particularly important for resting sea otters, and if banks are higher in other marshes relative to Elkhorn Slough's salt marsh, which is unusually low, this could negatively impact potential for sea otter resting.

Given the protected status of the southern sea otter, it is important to conduct a similar analysis of potential salt marsh habitat in other estuaries in California. For example, Morro Bay is an estuary located in the center of the southern sea otter range with about 150 hectares of salt marsh habitat (Thorne et al. 2016). Sea otters can be found resting and foraging in the harbor areas of Morro Bay, but now are rarely found in the salt marshes in the back bay. Morro Bay has a mean salt marsh elevation of 1.63 m NAVD 88 (Thorne et al. 2016), which is only slightly higher than Elkhorn

Slough’s mean salt marsh elevation of 1.5 m NAVD 88, suggesting that Morro Bay Estuary salt marsh could eventually support resting sea otters. However, other environmental variables and available prey sources would need to be assessed to determine suitability of Morro Bay Estuary for sea otters.

With 2493 hectares, San Francisco Bay has the largest expanse of salt marsh in California (Josselyn 1983). Pockets of salt marsh at varying elevations and with different invertebrate community composition and vegetation occur throughout the bay (Takekawa et al. 2013). The highest salt marsh is the western side of the San Pablo National Wildlife Refuge with a mean elevation of 2.0 m and a maximum of 3.49 m NAVD 88, while the lowest marsh is Colma with a mean of 1.4 m and a maximum of 2.58 m NAVD 88 (Takekawa et al. 2013). In the case of San Pablo salt marsh having high elevations, resting sea otters may only be able to haul out at high tides when the water is closer to the top of the creek banks and foraging on the marsh surface may not be possible if the salt marsh isn’t flooded. Foraging on other invertebrates found in the tidal creeks may still be possible, although this possibility needs to be investigated further. Based on elevation alone, Colma could provide ideal resting salt marsh habitat for sea otters given that the elevations are comparable to Elkhorn Slough. Because of its location, Colma marsh has high sedimentation rates and, although it is currently almost a mudflat, is projected keep pace with sea level rise and transition to low marsh by the end of the century (Takekawa et al. 2013).

Conclusions

This study is the first to examine the patterns of association behind sea otter tidal creek selection and distribution throughout salt marsh in Elkhorn Slough and in California. Sea otters prefer resting in salt marsh tidal creeks that are wide (>10 m), with elevations between 0.3 m to 2 m NAVD 88, with shallow bank slopes between 10 to 20 degrees, and with easy access out of the creeks. Foraging sea otters prefer feeding in flooded salt marsh but also feed in deeper creeks (<0 m NAVD 88) close to the main channel while swimming from their primary foraging site in the main channel to their resting site in the salt marsh. Results from this study can inform future salt marsh restoration projects in Elkhorn Slough and other estuaries, so that otter needs can be incorporated into restoration design. In addition, methods from this study can be used to create models to predict future use of salt marshes by sea otters in other estuaries throughout California.

Incorporating sea otter habitat use into future salt marsh construction and restoration plans will provide valuable habitat for sea otters as well as other species that rely on salt marsh for protection, foraging and reproduction. Salt marsh restoration and sea otter expansion into other estuaries in California with similar salt marsh may help with the recovery of the southern sea otter by providing protected nursery habitat for females to raise their pups. Salt marsh restoration will also provide people living on the coast a natural, cost-effective, buffer against flooding due to storm surges and more opportunities for recreation. In general, this study demonstrates how relatively simple wildlife surveys conducted by experienced biologists working with citizen scientists can be combined with GIS-based environmental data to conduct habitat modeling that informs conservation and habitat restoration efforts.

Tables and Figures

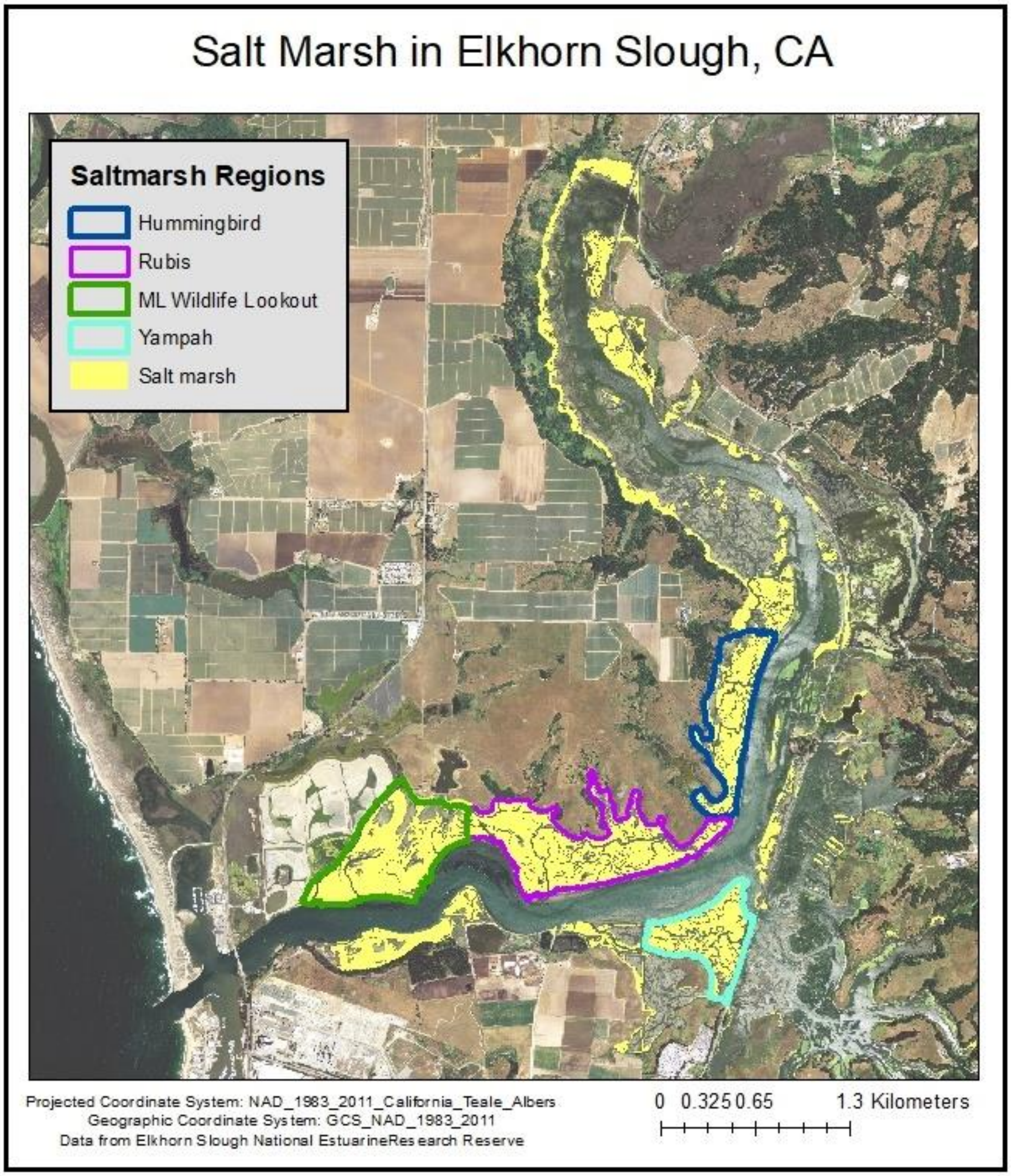


Figure 1. Elkhorn Slough salt marsh indicated in yellow with the salt marsh regions outlined as follows: 1) ML Wildlife Lookout in green, 2) Rubis in purple, 3) Hummingbird in dark blue, and 4) Yampah in light blue.

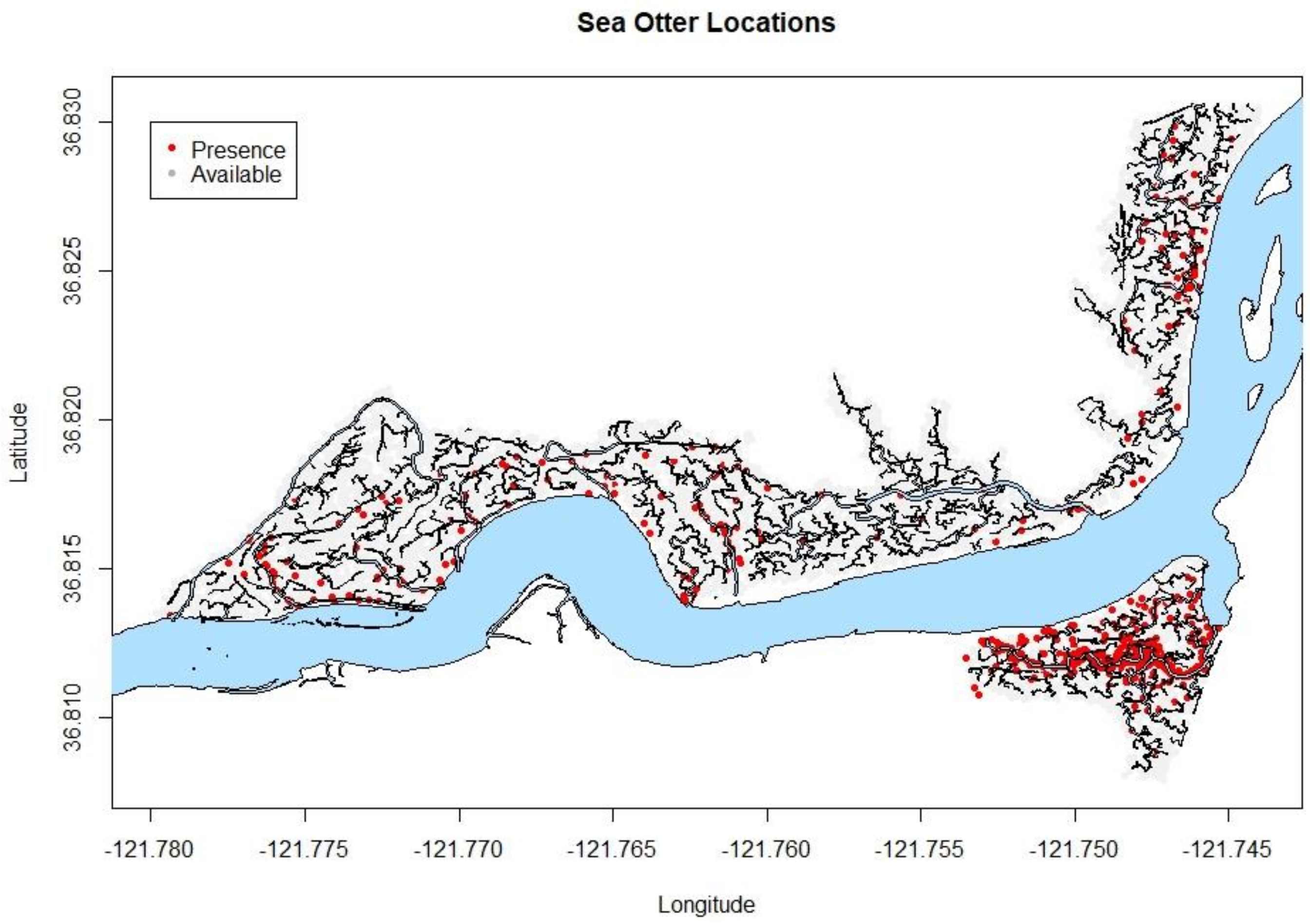


Figure 2. Map of sea otter presence and available points. Map of Elkhorn Slough main channel and salt marsh tidal creeks showing the presence (red) and available (grey) points used in GAM models.

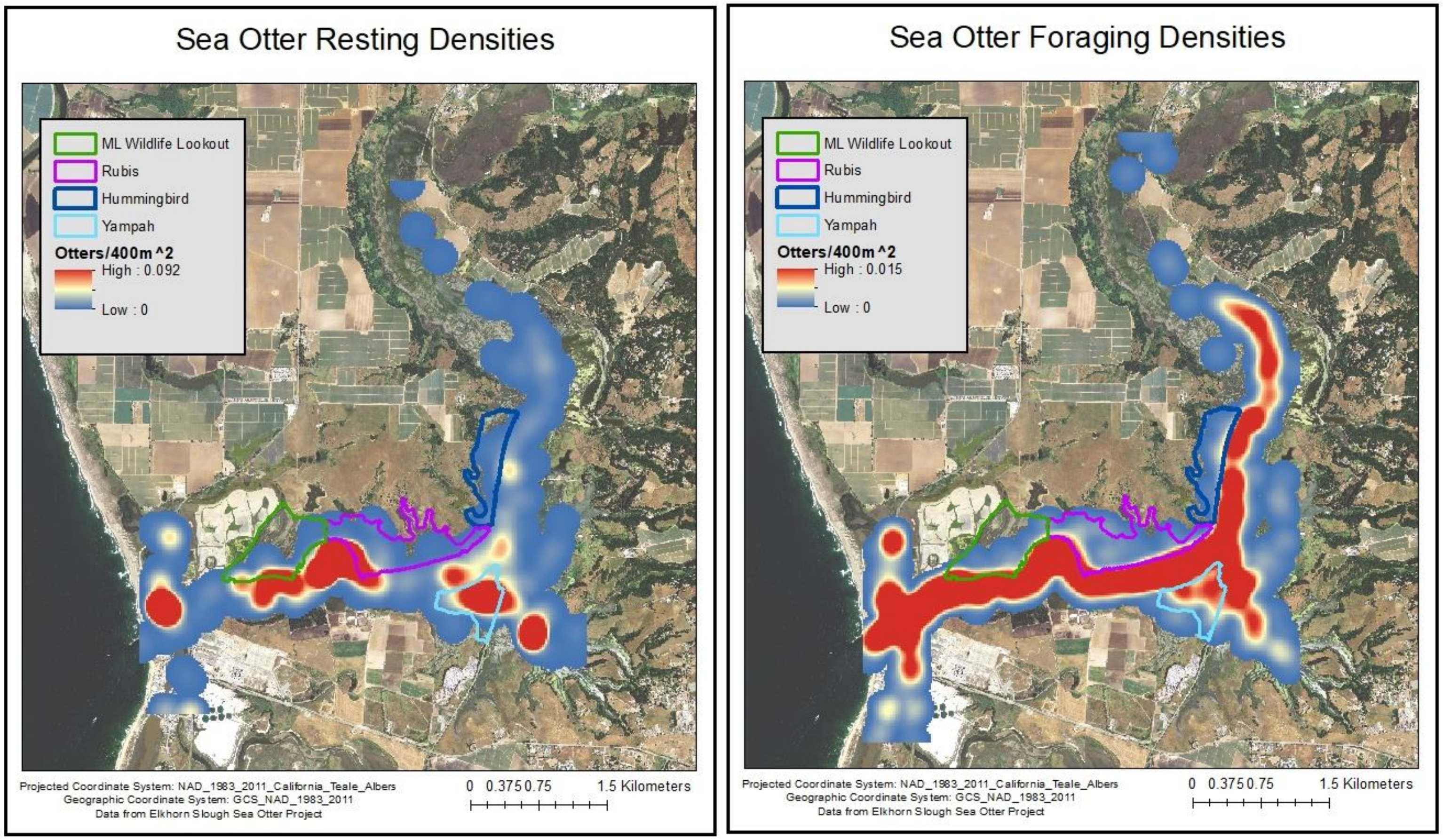


Figure 3. Kernel density maps showing the observed densities of otters over the four year study from 2013-2017. Densities of otters resting (left) and foraging (right) with salt marsh regions outlined as follows: 1) ML Wildlife Lookout in green, 2) Rubis in purple, 3) Hummingbird in dark blue, and 4) Yampah in light blue.

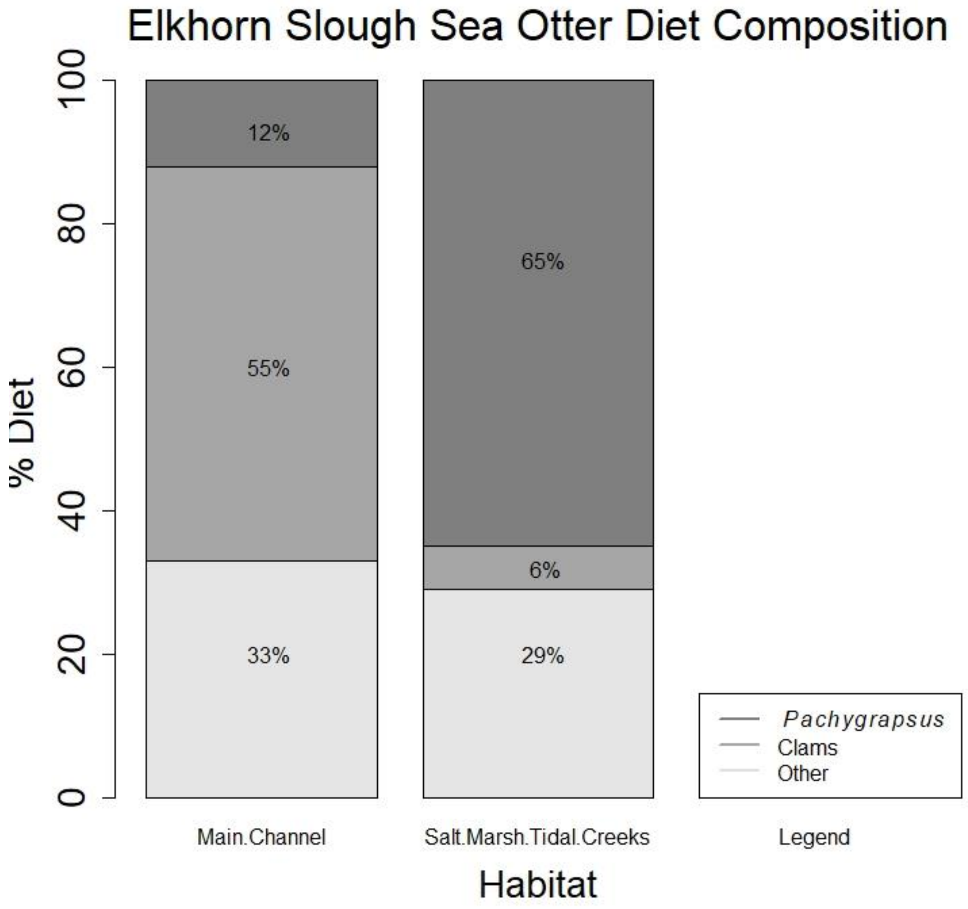


Figure 4. Diet composition of sea otters in Elkhorn Slough in the Main Channel and in the salt marsh by major prey groupings: 1) *Pachygrapsus*, 2) Clams (*Tresus nuttallii* and *Saxidomus),* 3) Other (unidentified clams, other crabs, and fat innkeeper worms, *Urechis unicinctus*).

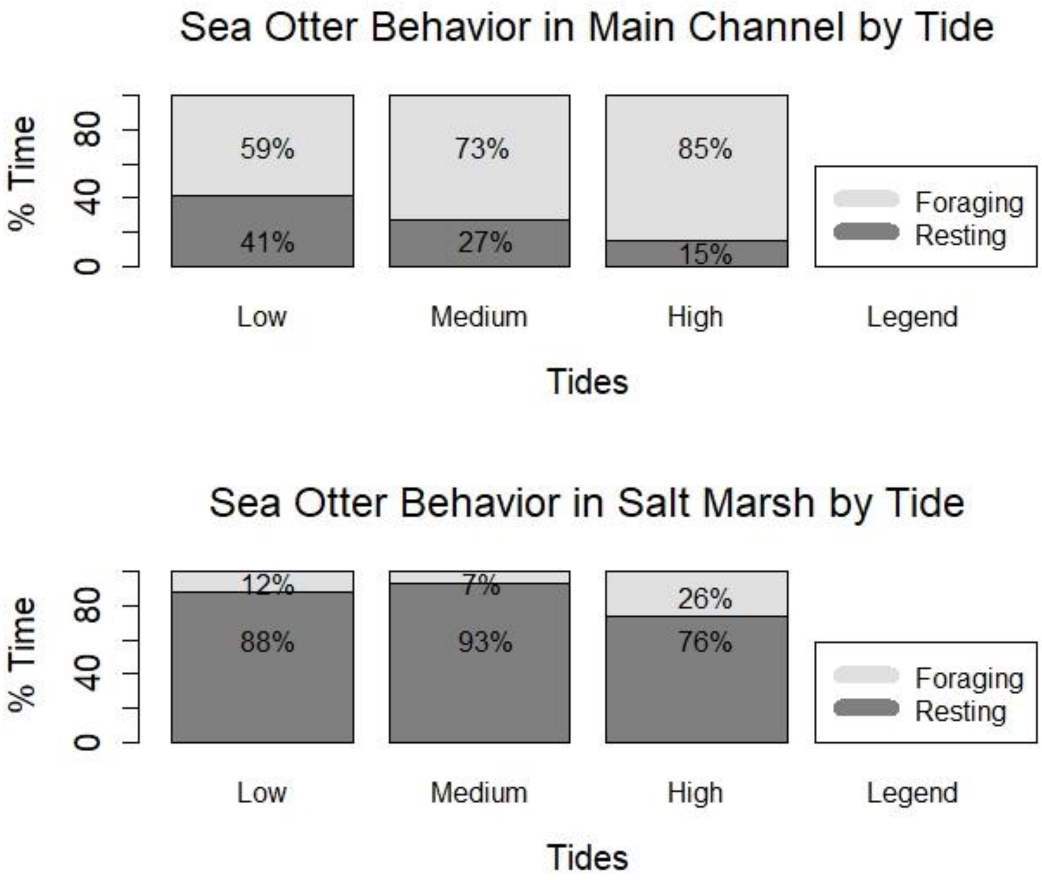


Figure 5. Variation in sea otter behavior foraging (light gray) and resting (dark gray) as a function of tidal height in the Main Channel (top) and in salt marsh (bottom).

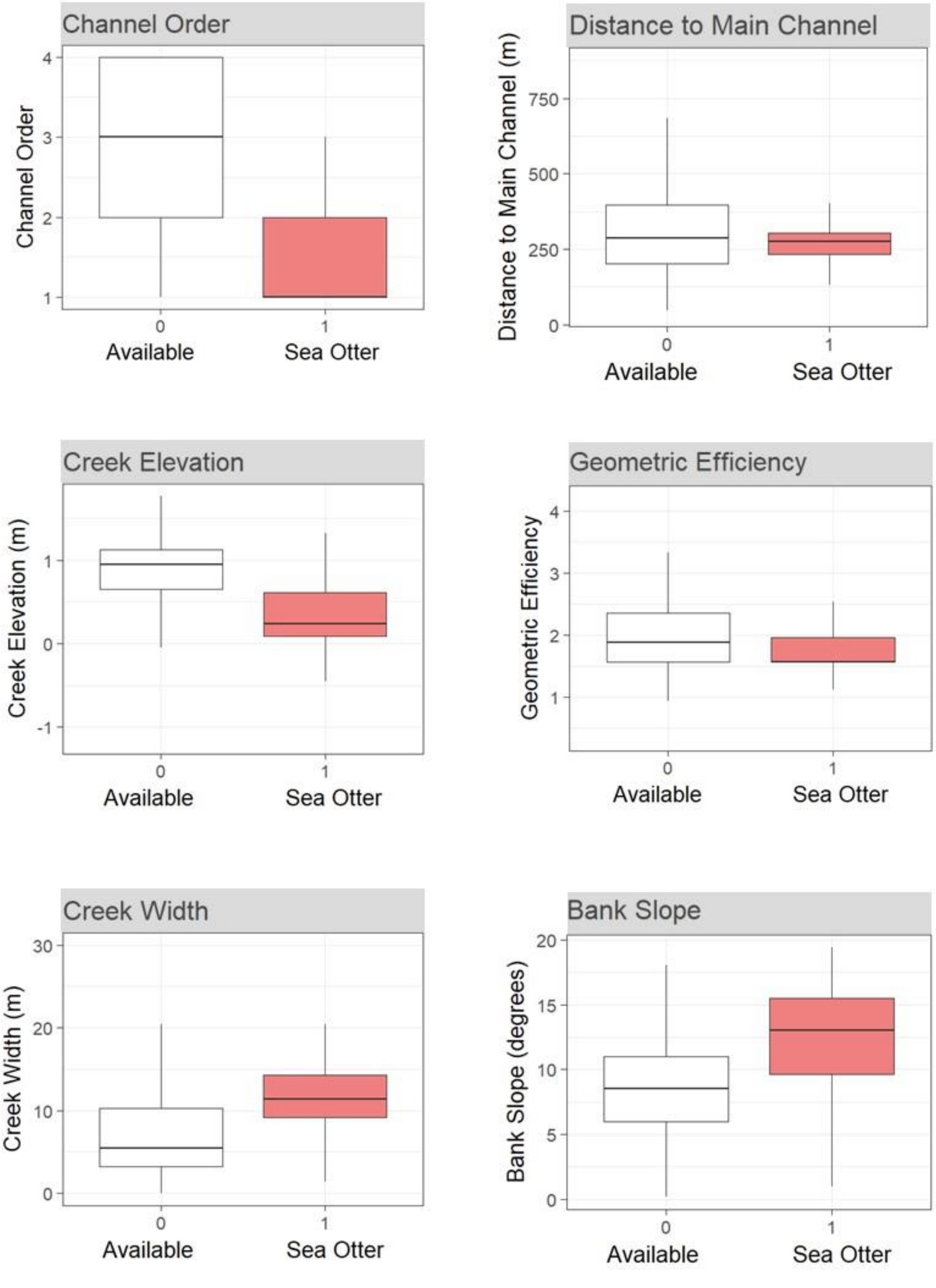


Figure 6. Boxplot comparison of sea otter use verses availability of each environmental variable. The boxes represent the middle 50% of the values for each. Horizontal lines within the boxes represent the median value. Lines extending above and below the boxes represent maximum and minimum values, respectively.

Table 1. Mean and standard deviation for each environmental variable by availability, sea otter presence points and GAM model output from component smooth functions.

Variables	**Available (mean; sd)**	**Presence (mean; sd)**	**Full GAM Model Results**
Elevation (m)	0.86; 0.34	0.36; 0.34	0.20 (range 0 to 0.4)
Width (m)	7.54; 5.81	11.34; 4.45	wider
Slope_mean (degrees)	8.40; 3.57	12.45; 3.61	12 to 20
Distance to Main Channel (m)	310.21; 141.96	263.12; 72.2	265
Geometric Efficiency	2.03; 0.57	1.80; 0.47	lower
Creek Channel Order	2.68; 1.1	1.52; 0.95	lower
Main Channel Area (ha)	216.65	na	na
Salt Marsh Area (ha)	215.31	na	174.22

Table 2. Model Results: AIC, AUC, and p-values for each variable included in the best fit GAMs are listed for 5 models and their respective null model, which includes ‘Region’ as a random variable. AUC values were calculated to determine ability to predict sea otter presence.

Models	Variables							Deviance Explained	AIC	AUC
	Elevation	Bank Slope	Width	Dist_mc	GeoEff	Chan_Ord	‘Region’ as Random Var.			
Full Null Model							<0.001	29%	6113	
Full Model	<0.001	<0.001		<0.001	<0.001	0.0212	<0.001	47%	4593	0.914
Resting Females with Pups Null Model							<0.001	34%	2327	
Resting Females with Pups	<0.001	<0.001	0.072	<0.001	<0.001	0.0030	<0.001	60%	1444	0.913
Resting Males & Females no pups Null Model							<0.001	24%	3500	
Resting Males & Females no pups	<0.001	<0.001	0.0206	<0.001	0.0276		<0.001	44%	2625	0.911
Foraging Females with Pups Null Model							<0.001	6%	531	
Foraging Females with Pups	<0.001			<0.001		0.0174	<0.001	13%	497	0.882
Foraging Males & Females no pups Null Model							<0.001	6%	968	
Foraging Males & Females no pups	0.00602	0.01793		0.0723			<0.001	12%	910	0.900

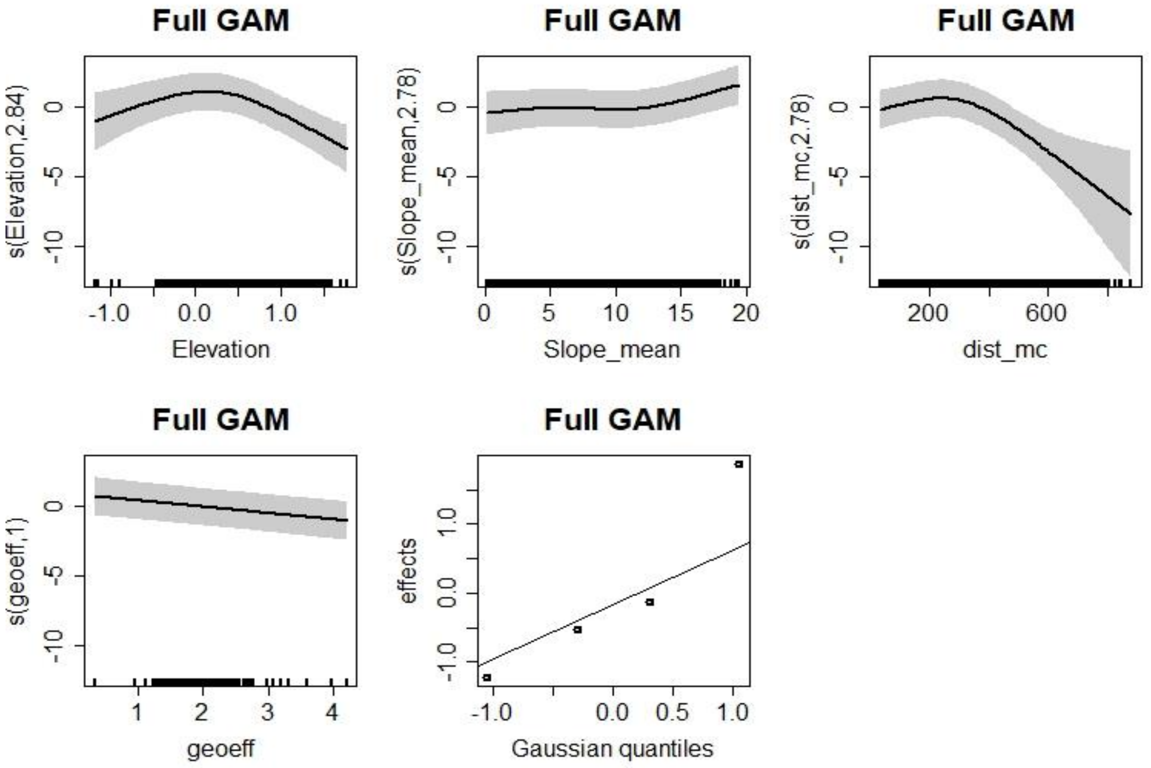


Figure 7. Component smooth functions for covariates from the full GAM. Shaded confidence intervals indicate the uncertainty around the overall mean. Y-axis is expressed in a logit scale. Rug plots along the x-axis show the specific values for the covariate.

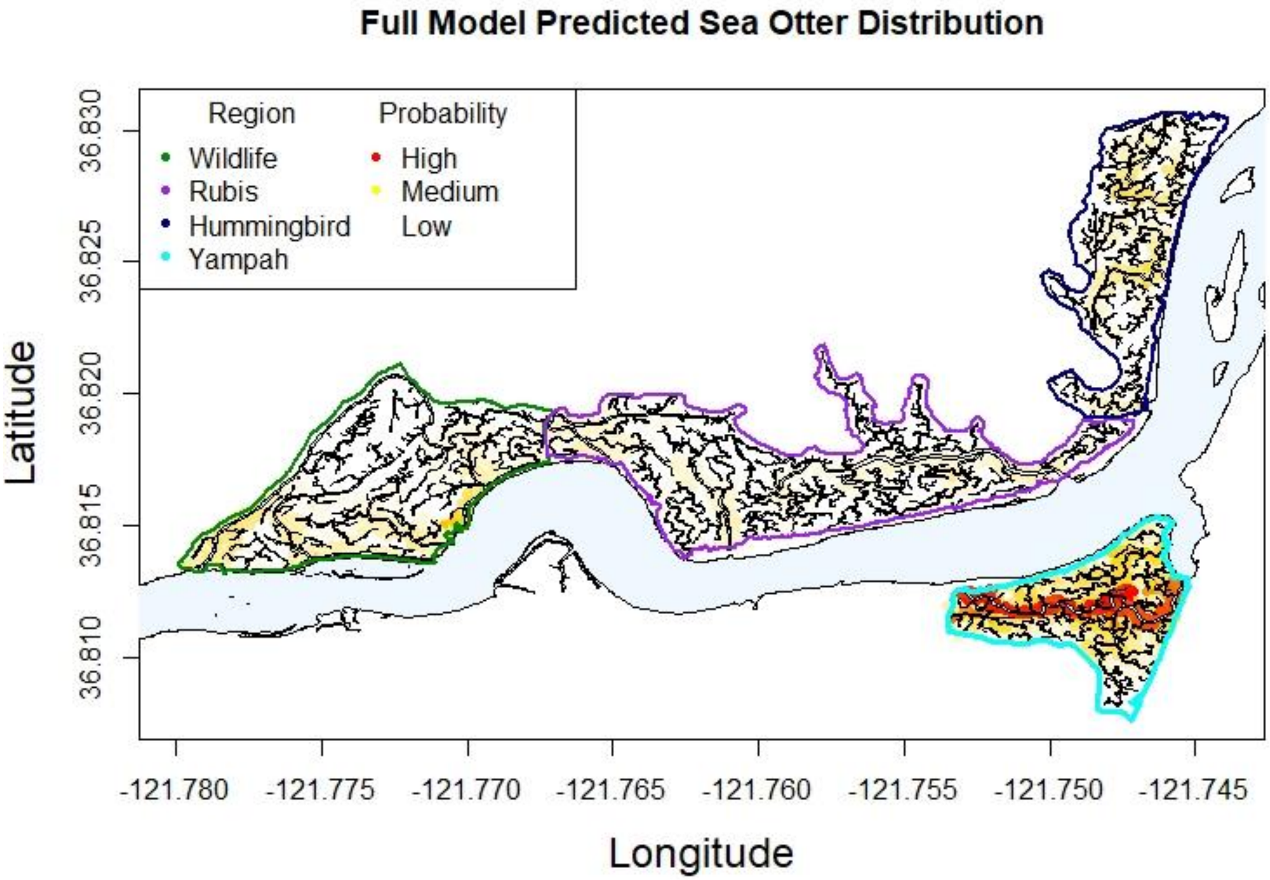
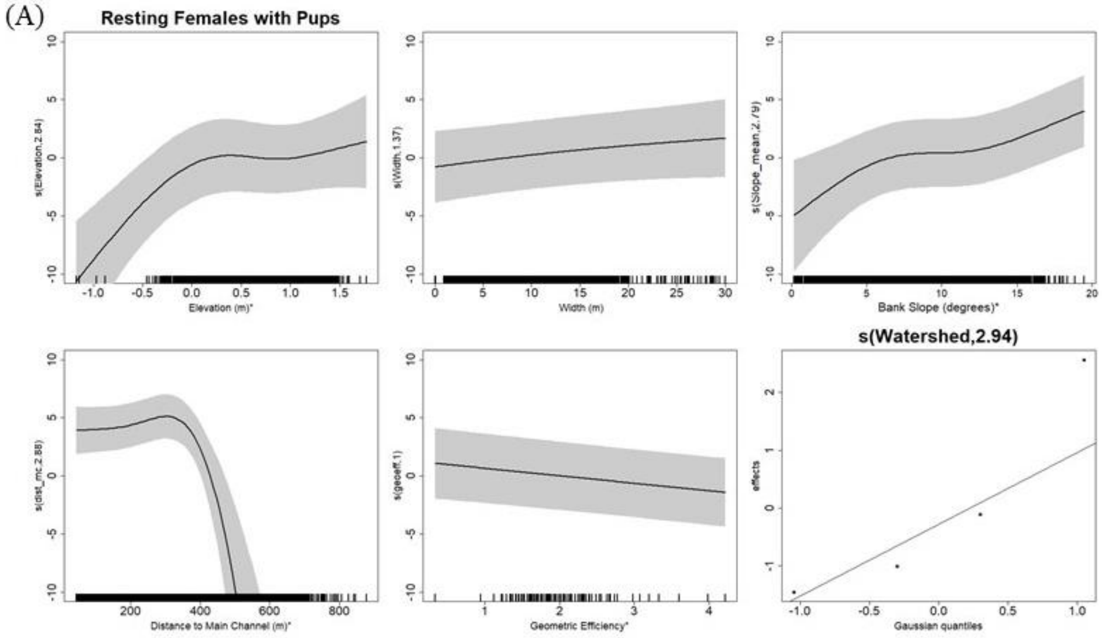


Figure 8. Habitat suitability map for sea otters in Elkhorn Slough salt marsh predicted by the GAM Full model. Red indicates high probability of occurrence, yellow medium probability of occurrence.



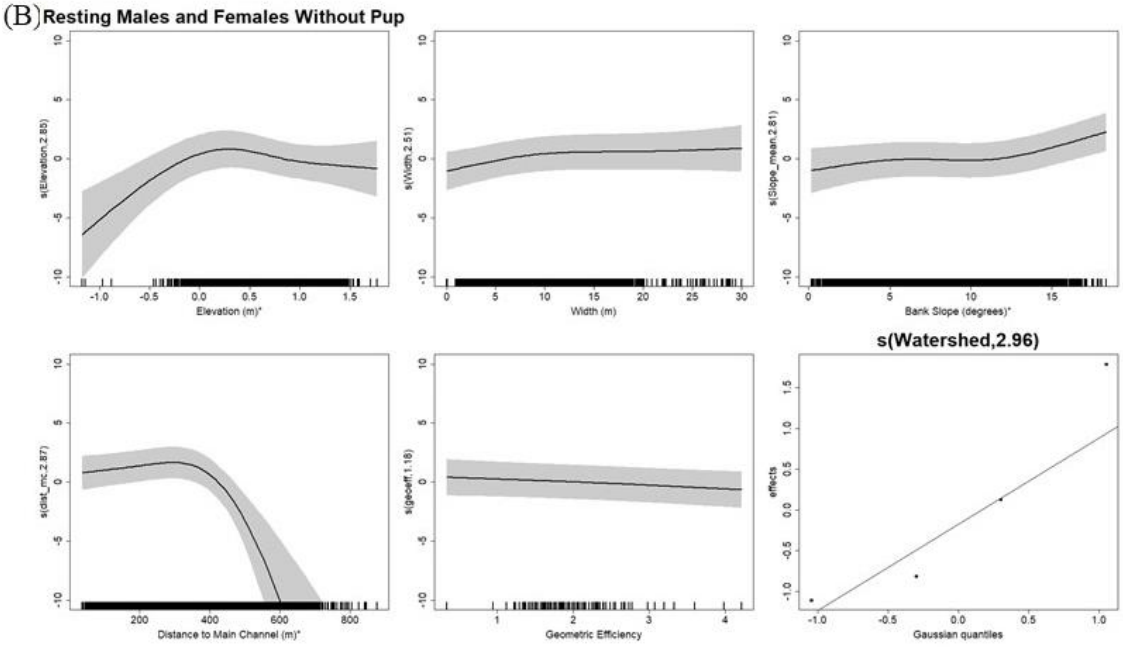


Figure 9. GAM Component Smooth Functions: Resting – Component smooth functions for covariates from the resting females with pups (A) and resting males and females without pups (B) GAMs including shaded confidence intervals around the uncertainty of the overall mean and rug plots along the x-axis show the specific values for the covariate. Y-axis is expressed in a logit scale.

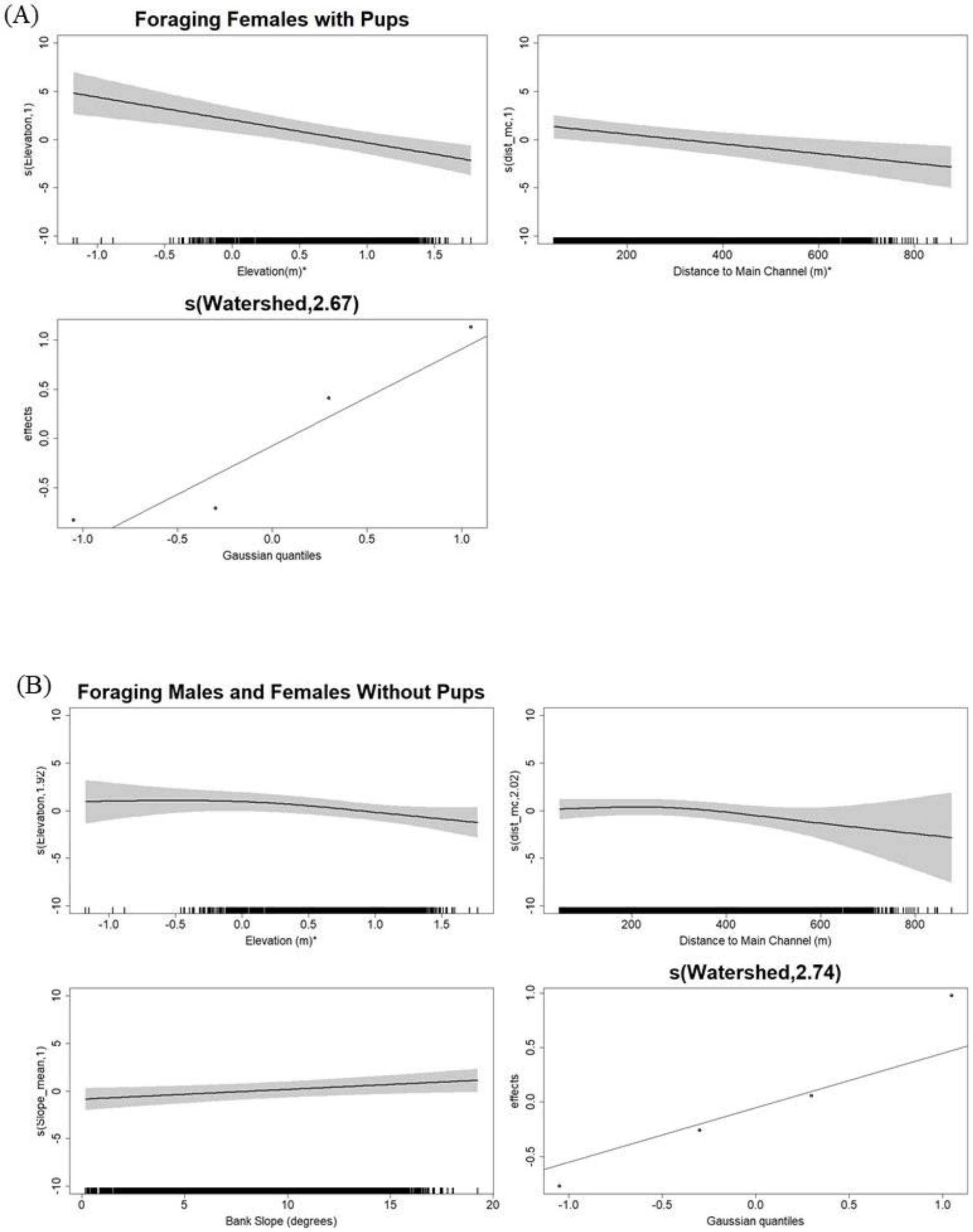


Figure 10. GAM Component Smooth Functions: Foraging – Component smooth functions for the covariates in the foraging females with pups (A) and foraging males and females without pups (B). GAMs including shaded confidence intervals around the uncertainty of the overall mean and rug plots along the x-axis show the specific values for the covariate. Y-axis is expressed in a logit scale.

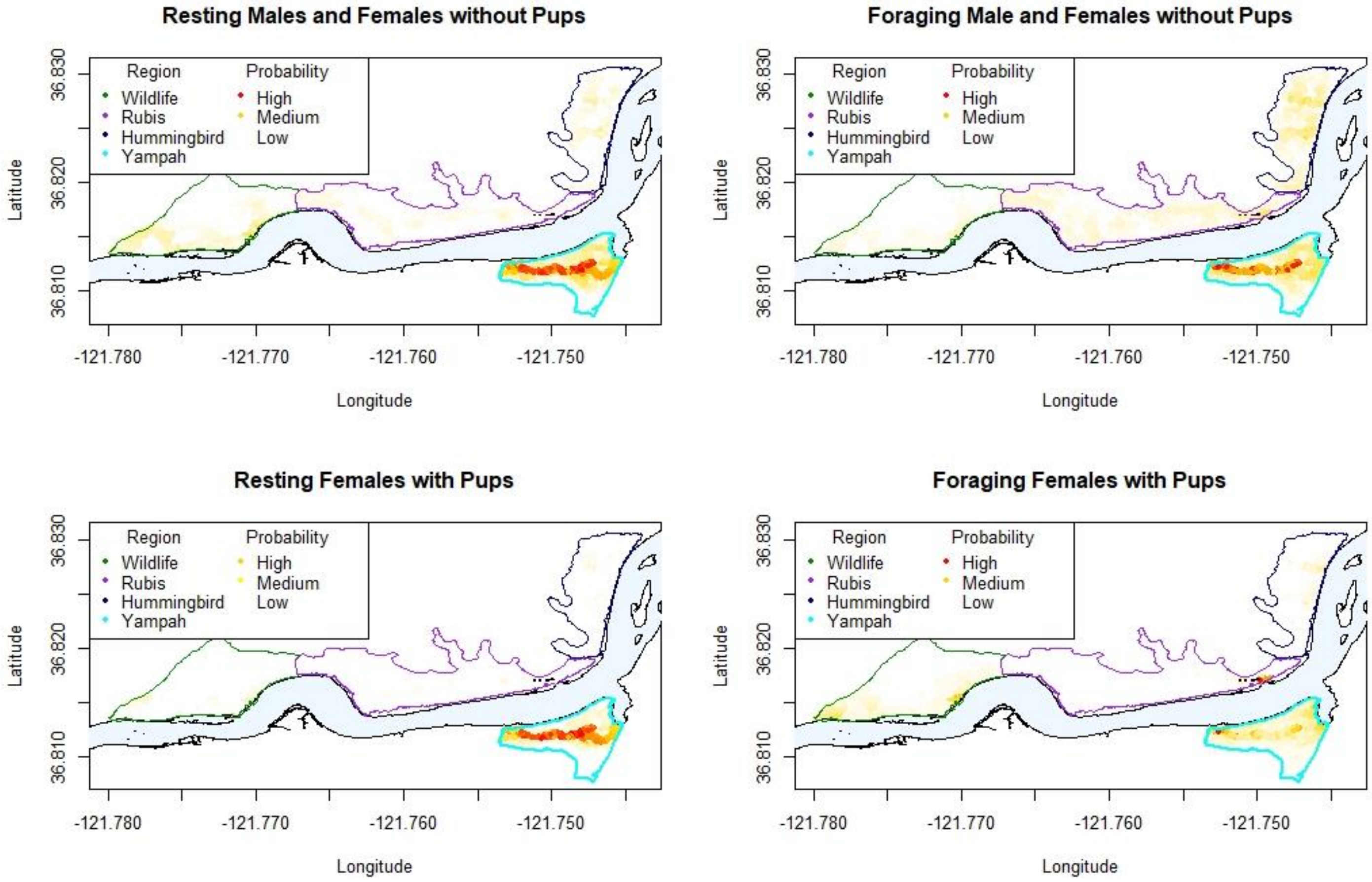


Figure 11. Habitat suitability maps based on sea otter status and behavior in Elkhorn Slough salt marsh predicted by GAMs. Red indicates high probability of occurrence, yellow indicates medium probability of occurrence. Salt marsh regions outlined in respective color: Wildlife is green, Rubis is purple, Hummingbird is dark blue and Yampah is bright blue.

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