CHARACTERIZING HABITAT PREFERENCE IN THREE NEARSHORE REEF-ASSOCIATED FISHES THROUGH COLLABORATIVE RESEARCH, PUBLIC DATA, AND OPEN SOURCE SOFTWARE

By

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ABSTRACT

CHARACTERIZING HABITAT PREFERENCE IN THREE NEARSHORE REEF-ASSOCIATED FISHES THROUGH COLLABORATIVE RESEARCH, PUBLIC DATA, AND OPEN SOURCE SOFTWARE

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Black rockfish (*Sebastes melanops*), canary rockfish (*S. pinniger*), and lingcod (*Ophidion elongatus*) are important species in Northern California's nearshore recreational and commercial fisheries. These species are associated with nearshore rocky reefs and are among a suite of species intended to benefit from the establishment of the marine protected area (MPA) network along the Northern California Coast in 2012.

Many aspects of the North Coast's nearshore ecosystem remain poorly studied, including the spatial distribution and habitat associations of nearshore fish species. This study used data collected from Cape Mendocino State Marine Reserve (SMR), Ten Mile SMR, and paired, nearby reference sites to investigate the habitat associations of black rockfish, canary rockfish, and lingcod on the North Coast by generating Maxent habitat suitability models for each species.

This study showed black rockfish associated with high relief, rocky habitat, less than ~30 meters in depth, lingcod associated with rocky habitat, independent of relief, deeper than 20 meters, and canary rockfish associated with high relief rocky habitat, deeper than ~35 meters. The findings of this study also investigated and supported the

findings of a previous study that found canary rockfish associated with the edge of rocky reef and sandy habitats.

Maxent modeling can increase manager's understanding of the habitat used by marine fishes and inform the establishment of MPAs, designation of Essential Fish Habitat, and regional catch limits by identifying where habitat might support more productive populations, especially for poorly studied stocks.

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INTRODUCTION

The nearshore rocky reef ecosystem of Northern California provides habitat for many commercially and recreationally important fish species. These species include Rockfishes (*Sebastes spp*.), Lingcod (*Ophidion elongatus*), Cabezon (*Scorpeanichthys marmoratus*), and Kelp Greenling (*Hexagrammos decagrammus*). The harvest of these species is regulated by a suite of management strategies, including limited access, quotas, size limits, gear restrictions, and spatial closures (Starr et al. 2016). Spatial management tools have become more common with the technological advancement of geographical information systems (GIS) which allow more precise mapping (Valavanis et al. 2008). However, these spatial management tools require an understanding of how fish populations are distributed across habitats, and of the factors that influence their distribution. Understanding the fine-scale habitat suitability of nearshore fishes could allow managers to more precisely delineate closures to allow for harvest of target species, while still minimizing the risk of bycatch of overfished species. A better understanding of the habitat used by a species, coupled with density estimates, could provide more accurate estimates of stock abundance and biomass (Starr et al. 2016). Consequently, an accurate estimation of stock size requires a model that can reliably predict habitat suitability in unsampled areas (Young et al. 2010).

Though the habitat preferences of rocky reef associated fishes have been studied elsewhere along North America’s Pacific Coast, the fish communities off the Northern California Coast (North Coast) remain poorly studied (Steinberg 2008). The North Coast is a logistically challenging study area, as there are few ports and little infrastructure to support scientific sampling (Mulligan et al. 2017). Where habitat suitability has been investigated along the California Coast, sampling has typically been conducted by SCUBA, remotely operated vehicles (ROVs), or by manned submarine (Saucedo 2017; Young et al. 2010). These methods record occurrence locations of fish by direct seafloor observation. However, direct observation methods like these are often expensive and limited in spatial extent. Sampling via hook and line may offer a complimentary approach that could cover a wider sampling area at less cost, while sacrificing some spatial precision.

This work describes a cost effective method to determine fine-scale habitat suitability for nearshore fishes, using publicly available seafloor habitat data, open-source software, and location data obtained from an existing collaborative fisheries research project.

The motivating questions of this work are:

1. Can data from our collaborative hook and line surveys, along with environmental predictors derived from California Seafloor Mapping Project bathymetry data, be used to create reasonable and useful Maxent species distribution models?
2. What environmental covariates are important for predicting habitat suitability for fish species intended to be protected by North Coast Marine Protected Areas?

Habitat Suitability Models

A habitat suitability model (HSM) attempts to describe the environmental conditions that create favorable habitat for a species. A class of HSMs known as presence/absence models compare the environmental conditions of location where the species is present, to the locations where it is not, to draw inferences about the conditions that create favorable habitat for that species (Elith et al. 2011). A significant disadvantage of presence/absence models is that accurate absence points can be challenging to collect for cryptic and/or mobile species (Elith et al. 2006).

Another class, presence/background models, compare the environmental conditions at locations where the species was observed to conditions at points distributed across the study environment to estimate habitat suitability. These background points may be distributed randomly across the study landscape, or in a manner that accounts for spatial biases in sampling (Fourcade et al. 2014).

Maxent (Phillips et al. 2006) is habitat suitability modeling software that uses presence/background data. Maxent applies maximum entropy theory to habitat modeling—the models created preserve the prior probability distribution to the extent possible, given the constraints placed on the model by the data and parameters selected (Jaynes 2003, Dudik et al. 2004). Maxent's default prior assumes an equal probability of occurrence for a species across the study landscape—background points are randomly selected from the study landscape. This prior can be adjusted by incorporating a bias layer, which accounts for spatially uneven sampling effort. Maxent's required inputs are presence locations of a species of interest, and environmental predictor data for the study landscape (Elith et al. 2011). Additionally, Maxent has been shown to perform better with small sample sizes than other presence-only methods (Wisz et al. 2008).

The output of a Maxent model is an estimation of how each predictor influences habitat suitability. The model is then used to predict habitat suitability across the study landscape, creating a raster layer of habitat suitability where the combined effects of the predictors for each pixel is used to estimate a relative habitat suitability for that location (Elith et al. 2011).

Maxent models have received criticism for overfitting data—which can be controlled by increasing the value of Maxent's beta regularization parameter. This parameter, when increased, limits the complexity of the model. Testing multiple beta parameters, and applying small sample size corrected Akaike Information Criterion (AICc) as a model selection criteria, can allow the user to maximize the generality and transferability of a Maxent model (Anderson & Gonzalez 2011, Warren & Seifert 2011, Morales et al. 2017). Overfitted models will often produce jagged response curves that appear to be modeling noise, not biological response (Figure 1).

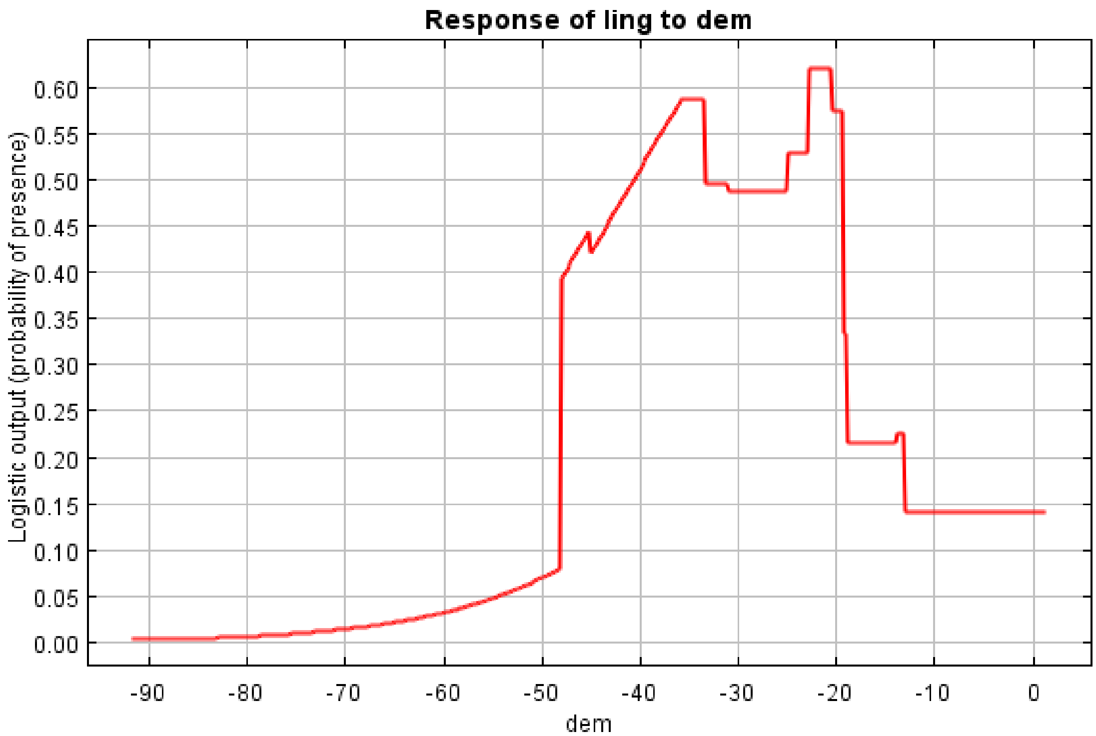

Figure 1. An example of a Maxent response curve showing evidence of overfitting from a pilot model run. Note that the curve is more erratic than would be expected if only a biological response was captured in the model.

Application of Maxent in Marine Fisheries Research

Presence/background methods are especially well suited to marine fisheries research because true absence points are difficult to collect(Jones et al. 2012). Concurrent with advances in distribution modeling, remote sensing techniques have improved, allowing the collection of more, and finer resolution, information about the marine environment. The increasing use of multi-beam sonar to map the seafloor, along with automated processing of the data collected, has allowed the investigation of seafloor habitat to extents not before possible, providing the environmental predictor variables needed to inform habitat suitability models (Valavanis et al. 2008).

In the past decade, Maxent has been applied to marine fishes around the world. These include temperate reef-associated species off of Southeastern Australia (Monk et al. 2012), commercially important demersal fishes in the North Atlantic (Jones et al. 2012), rocky-reef associated fishes in the Azores (Parra 2012), groundfish in the Gulf of Alaska (Pirtle et al. 2017), and canary rockfish off the Northern California Coast (Saucedo 2017). The Monk et al. (2012), Jones et al. (2012), and Parra (2012) studies above compared Maxent with generalized linear modeling (GLM) approaches, and found that Maxent performed as well or better than GLMs when creating habitat suitability models. These studies were able to identify habitat associations in line with what literature review and synthesis led the researchers to expect for each study species. In Pirtle et al. (2017), previously unknown habitat associations of different life stages of groundfish in the Gulf of Alaska were described. This study highlighted the utility of Maxent models to identify habitat associations with relatively few data points (when compared to GLMs) and how Maxent habitat suitability could be used in identifying Essential Fish Habitat, one of the chief charges of the National Marine Fisheries Service (Magnuson–Stevens Fishery Conservation and Management Act 1976).

North Coast MPA Baseline Study

In 2012, 19 marine protected areas were established on the Northern California coast, distributed from Point Arena in Mendocino County to the California-Oregon Border. A collaborative fisheries research project to gather baseline data on fish communities associated with nearshore rocky reefs in and near the MPAs was conducted in the summers of 2014 and 2015. The project engaged commercial passenger fishing vessels (CPFVs) and volunteers to conduct hook and line surveys in four marine protected areas and nearby reference sites: Pyramid Point State Marine Conservation Area, South Cape Mendocino State Marine Reserve (SMR), Sea Lion Gulch SMR, and Ten Mile SMR. To conduct the sampling, CPFVs and volunteers were engaged in the ports of Crescent City, Eureka, Shelter Cove, and Fort Bragg (Mulligan et al. 2017).

The data used for this study was collected as part of the collaborative fisheries project during the summer of 2015, at South Cape Mendocino SMR, Ten Mile SMR, and their associated reference sites.

Fish Species

Three fish species, black rockfish (*Sebastes melanops*), canary rockfish (*S. pinniger*), and lingcod (*Ophidion elongatus*), were selected for inclusion in this work. These species are important in the Northern California nearshore groundfish fishery, are probably attracted to different habitat features that could be elucidated by habitat suitability models, and were caught in sufficient numbers to create those models.

Black rockfish

Black rockfish are an important recreational and commercial fish in California. They are an important component of the west coast rockfish fishery but are also taken as incidental catch in other groundfish fisheries. In nearshore waters of Northern California the majority of black rockfish take occurs in the recreational fishery, north of Cape Mendocino. They have increased in importance to the recreational fishery, as salmon bag limits have declined since the 1970's. However, due to recent population declines, the recreational bag limits have been reduced (Cope et al. 2015).

The species has been observed from the Aleutian Islands to Southern California, becoming much less common south of Cape Mendocino. They are most commonly observed in association with rocky habitat less than 55 meters in depth, though they have been observed below 350 meters. Black rockfish are generally considered a midwater rockfish, and are often observed swimming in single species or mixed schools above rocky habitat (Miller & Lea 1972, Love et al. 2002).

Black rockfish show moderate site fidelity; many tagged fish are recaptured within several kilometers of their release point, even after tagging intervals exceeding

1,000 days (Starr et al. 2015, Mulligan et al. 2017). However, large displacements of several hundred kilometers are also common. Of the nine black rockfish where tag return information was available from the North Coast Baseline study, six were observed to have traveled long distances, showing northward displacements of 275 km or more (Mulligan et al. 2017). A similar tagging effort, in Central California, also documented long distance movement, with a northward displacement, in approximately half of the black rockfish which had tag information available (Starr et al. 2015).

Black rockfish were chosen for inclusion in this work because they were the most abundant species observed, are important to the fishery, and are a good example of a midwater rockfish species. Habitat suitability for black rockfish was hypothesized to be higher in shallower water, and where there is greater habitat complexity.

Canary rockfish

Canary rockfish were once an important part of the west coast groundfish fishery. They were taken in large numbers by trawlers, long liners, and recreational fishers (Love et al. 2002). Catch peaked at over 5000 metric tons (for California, Oregon, and Washington waters) in the early 1980's before declining precipitously by the early 1990's (Thorson & Wetzel 2015). In 1995, the allowable biological catch was reduced by 60% to 1,250 metric tons. Based on information from canary rockfish stock assessments in 1999, the stock was declared overfished in 2000, and regulations allowed take of canary rockfish as bycatch only. Measures taken to protect canary rockfish, and other depleted shelf rockfish species, included establishing low bycatch quotas, gear restrictions, and the creation of rockfish conservation areas. These measures decreased the productivity of the nearshore groundfish fishery as a whole. The stock was declared rebuilt in 2015, but continues to be monitored closely by management agencies (Thorson & Wetzel 2015).

Canary rockfish are medium to large bodied rockfish, with a maximum length of approximately 76cm. They live to at least 84 years of age, and most are sexually mature by age 10 (Love et al. 2002). The combination of being a long-lived, slow growing, late maturing species, which aggregate in large schools, make canary rockfish especially susceptible to overfishing. These life history traits are similar to many other rockfish species that have histories of overexploitation (Starr et al. 2016).

Canary rockfish are thought to orient themselves more strongly to the bottom than black rockfish, and observations and previous modeling suggest that they are attracted to the interface between hard and soft substrate (Saucedo 2017).

Lingcod

Lingcod are an important commercial and recreational fish species, occurring from Baja California, Mexico to Kodiak Island, Alaska. They are most commonly observed north of Point Conception and in less than 200m of water, though they are known to occur to at least 400m (Miller & Lea 1972, Haltuch et al. 2017, Bassett et al. 2018).

Lingcod are opportunistic hunters, and are among the top predators on nearshore reefs. Fisheries managers are especially interested in the health of the lingcod stock because, in addition to the value of the species to both the commercial and recreational fisheries, there is concern that a robust lingcod stock could negatively affect rockfish stocks (Beaudreau & Essington 2007). Lingcod stocks, after decades of decline, have been steadily increasing since about the late 1990's (Haltuch et al. 2017).

A survey of lingcod by remotely operated vehicle along the Central California Coast, observed adult lingcod at depths from 17 to 350m and associated with a variety of rock habitats (Bassett et al. 2018).

MATERIALS AND METHODS

Data Collection

<u>Sampling sites</u>

This study pooled species occurrence data collected in two study areas along the North Coast. The Cape Mendocino site (Figure 2, Figure 3) includes fish sampled from the South Cape Mendocino State Marine Reserve, and the nearby, unprotected, reference site designated North Cape Mendocino. The Ten Mile/Westport site (Figure 2, Figure 4) includes the Ten Mile State Marine Reserve and the Westport reference site (Mulligan et al. 2017).

At Cape Mendocino and Ten Mile/Westport, hook-and-line sampling activities were conducted in randomly selected, 500m x 500m cells that were constrained to contain at least 20% rocky reef habitat, by area, with depths between 10 and 50m.

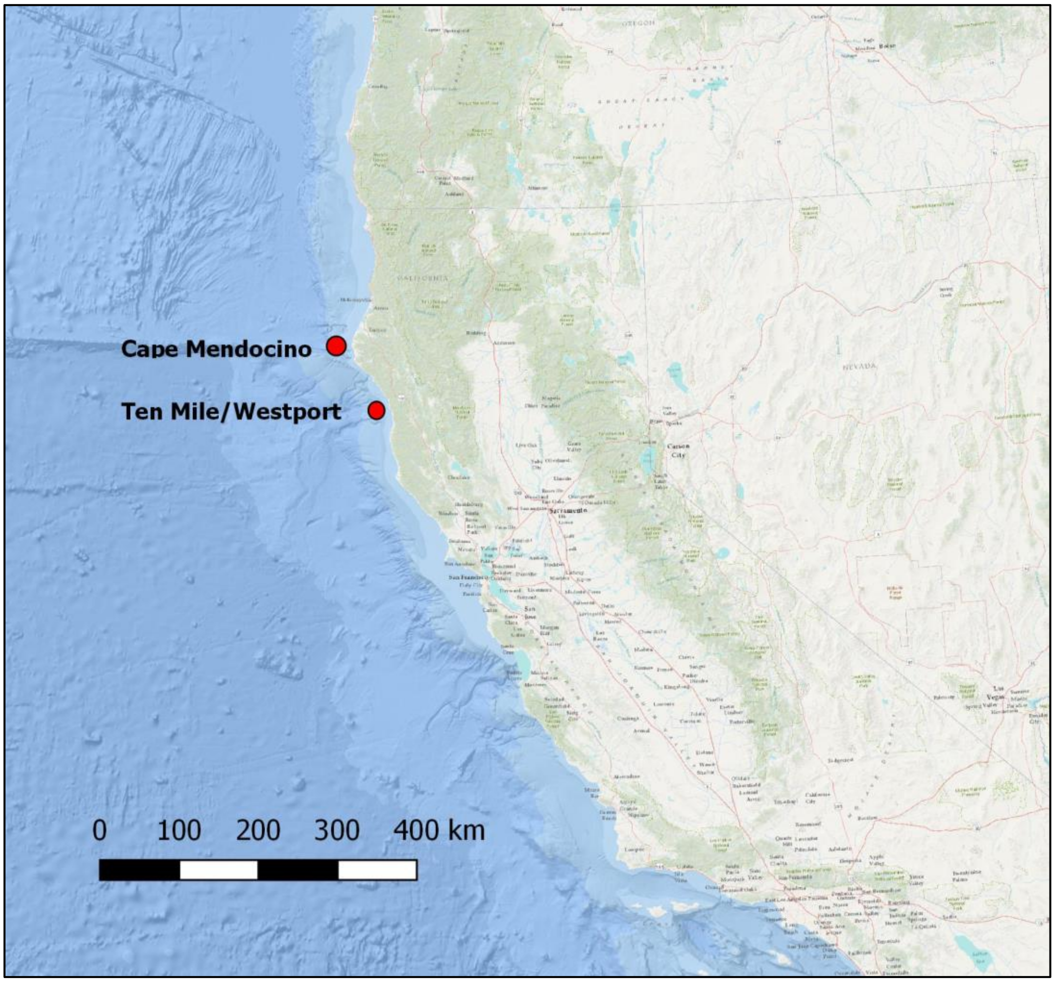

Figure 2. The location of the Cape Mendocino and Ten Mile/Westport sites (red dots), offshore of Northern California, USA.

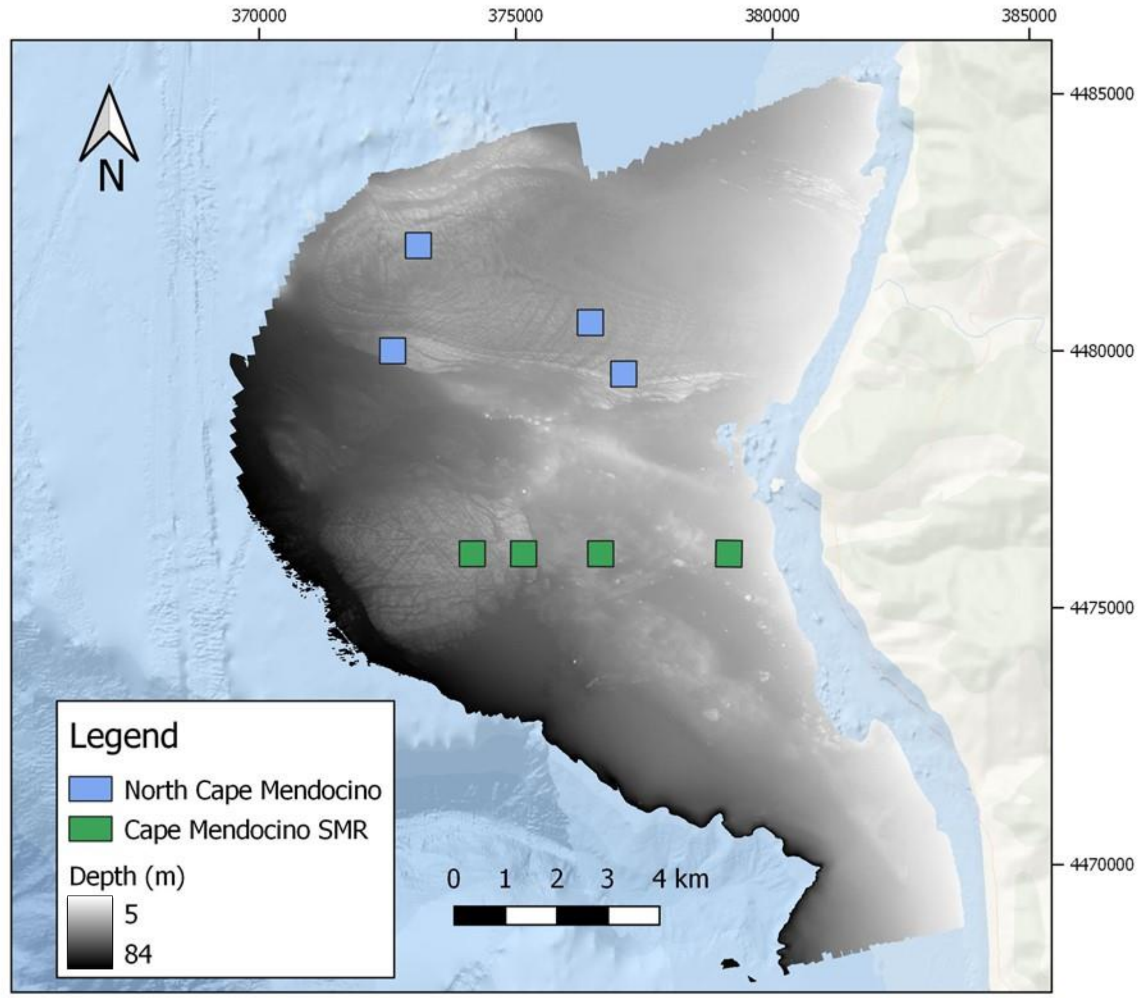

Figure 3. The location of the eight, 500 meter x 500 meter sampling stations where presence locations were gathered for this study, within the South Cape Mendocino State Marine Reserve (SMR) and North Cape Mendocino Reference Area. The locations are overlaid on a digital bathymetry model, showing the depth of the seafloor.

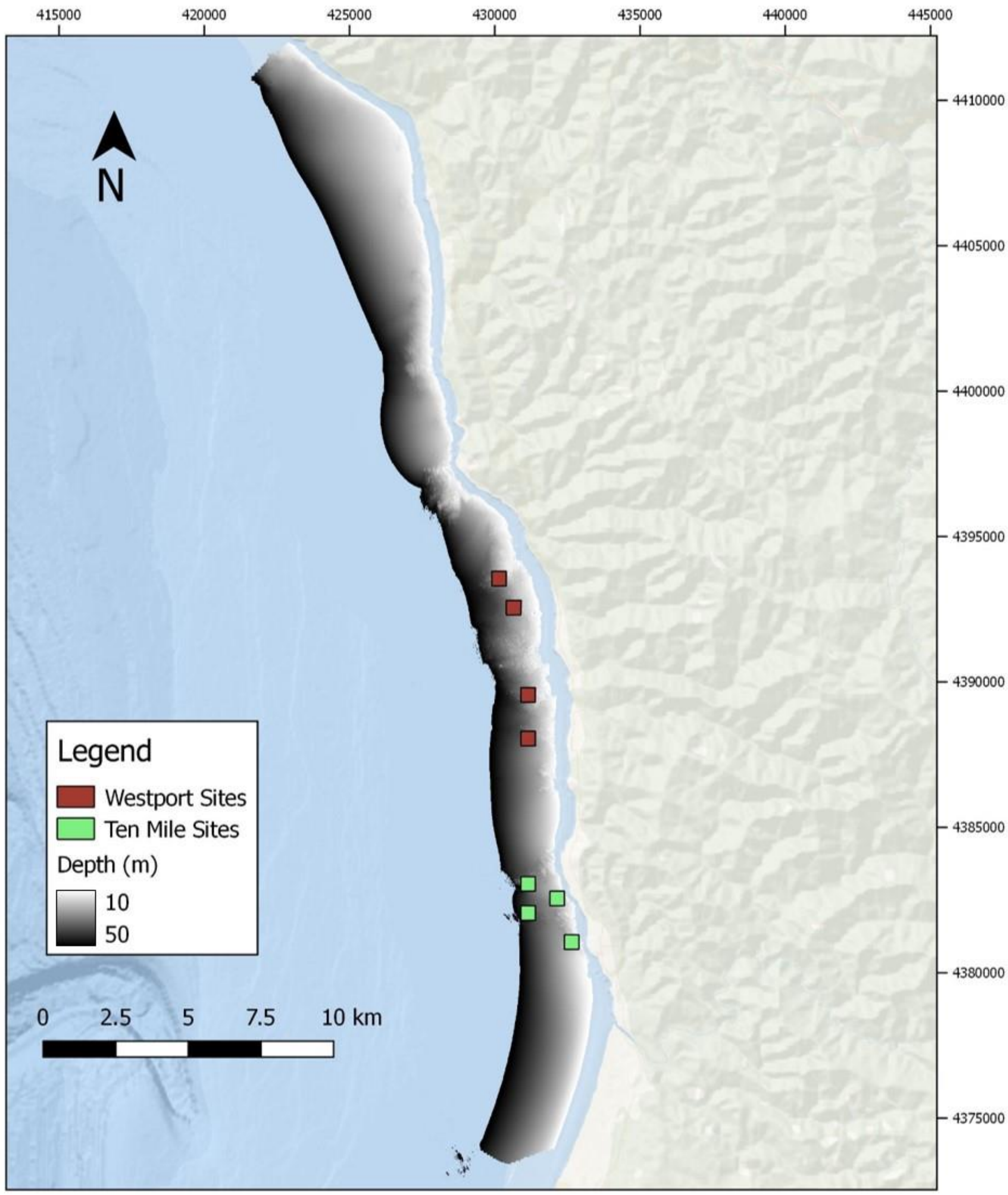

Figure 4. The location of the eight, 500 meter x 500 meter sampling stations where presence locations were gathered for this study, within the Ten Mile State Marine Reserve (SMR) and Westport reference area. The locations are overlaid on a digital bathymetry model, showing the depth of the seafloor.

Hook and line sampling

The data for this effort was collected in summer during the second year of the North Coast Baseline Marine Protected Area Monitoring Project. Each site was visited two times during the summer months (Mulligan et al. 2017; IACUC # 13/14.F.01-A).

Hook and line sampling trips were conducted from chartered commercial passenger fishing vessels from the port of Eureka, CA for Cape Mendocino and Fort Bragg, CA for Ten Mile/Westport. Each sampling trip had a scientific crew of six: four anglers and two science team members that identified, measured, tagged fish, and recorded data. Anglers were either volunteers from a pool of local fishers, undergraduate research technicians, or deckhands. Volunteer anglers were recruited from local fishing clubs, online fishing websites, previous collaborative fisheries projects, Humboldt State University marine science programs (e.g. Fisheries Biology, Oceanography, Marine Biology), as well as from public outreach events conducted as part of the project. Efforts were made to include as many different volunteer anglers from the community as possible over the entire course of the project.

Fishes were collected using hook-and-line gear designed to mimic methods used by local recreational fishers. Each of the four cells in a site was sampled by four anglers, each using a different category of standardized hook-and-line fishing gear. Each cell was actively fished for a total of 45 minutes during each sampling event. The four categories of standardized sampling gear used were: 1) two red or white size 4/0 shrimp-flies baited with a 3-6 cm strip of squid, 2) two un-baited red or white size 4/0 shrimp-flies, 3) a diamond or bar style metal jig paired with a single un-baited red or white size 4/0 shrimp-fly tied 60-120 cm above the jig, 4) a lead jig-head fitted with a scampi or swimbait style soft plastic jig paired with a single size 4/0 red or white un-baited shrimp-fly tied 60-120 cm above the jig (Figure 5). Upon capture, fish were identified to species, measured to the nearest millimeter in total length, and most fish that were in good condition and greater than 240mm in total length were tagged with an external T-bar anchor tag. Fish in good condition were released at the surface; those showing signs of barotrauma, protected species, and species observed to be especially susceptible to barotrauma were released at depth using a descending device.

Figure 5. Photos of fishing gear used during hook-and-line sampling. Left: red and white size 4/0 shrimp-flies; Top right: Bar style metal jig; Bottom right: swimbait style soft plastic jig.

<u>Location data</u>

The small scientific crew, necessitated by the use of vessels limited to six passengers, made it impractical to record coordinates, or take global positioning system (GPS) waypoints, for each individual fish, especially during periods of high catch rates. To obtain these coordinates, while minimizing extra crew workload, a GoPro camera was mounted in a location that provided a clear view of the work area on the deck of the vessel. At the beginning of each sampling period, the camera was activated, and a Garmin GPSmap 76csx handheld GPS unit with the time displayed was held up to the camera. The same GPS unit was programmed to log vessel position every 30 seconds.

After sampling, video footage from the GoPro camera was downloaded to obtain the time of capture for each fish, which was defined as the time when the fish was brought over the rail of the boat. The time of capture was compared to the vessel position log to obtain the location of capture for each fish.

Environmental Predictors

Environmental predictor values were obtained or derived from the California Seafloor Mapping Program's (CSMP) 2009 Northern California Survey. Predictors for Cape Mendocino were obtained from the Block H11975 / Vicinity of Cape Mendocino data package from the California Seafloor Mapping Program; predictors for Ten Mile/Westport were obtained from the Block H11969 / De Haven to Laguna Point and Block H11970 / Big White Rock to Abalone Point data packages. The two data packages used for Ten Mile/Westport were merged for use in the in the Maxent models.

To characterize the habitat available to the species of interest, background points were randomly selected from an area including the 500m x 500m sampling stations that were used or were available for random selection, as well as from areas within 100m of a station. The 100m buffer around each station was included because examination of the occurrence locations revealed significant sampling effort had occurred outside the established sampling stations.

The environmental predictors used in this modeling effort were:

- Depth: The depth, in meters, of the seafloor.
- Slope: The slope, in degrees, of the seafloor.
- Distance to rough/smooth interface (Edge): the distance, in meters to an interface of rough and smooth substrate, as delineated by the California Seafloor mapping program.
- Aspect: The direction of a slope face, in degrees.
- Vector Ruggedness (VRM): A measure of the complexity of the seafloor, independent of slope. The VRM layer was processed and provided by the CSMP, using a three by three neighborhood to calculate the values of each pixel.
- Curvature: The rate of change of the slope.
- Bathymetric position index (BPI): A categorical classification of seafloor, relative to its surroundings. 1- Valley/Crevice, 2- Lower Slope, 3- Flat, 4- Middle Slope, 5- Upper Slope, 6- Peak/Ridge (Young et al. 2010). This study used BPI at two scale factors: Fine-scale BPI had a scale factor of 20m, broad-scale BPI had a

scale factor of 250 meters. The scale factor is the radius of the area the BPI algorithm considers when determining the relative position of the pixel on the landscape (Weiss 2001).

Except for the distance to the rough/smooth interface variable, these predictors represent common characteristics used in habitat modeling of reef-associated fishes (Anderson & Yoklavich 2007, Monk et al. 2010, Simon J. Pittman & Brown 2011, Jones et al. 2012, Parra 2012, Pirtle et al. 2017, Saucedo 2017). The distance to rough/smooth interface variable was included because results from Saucedo (2017) suggest that transitions between hard and soft substrate are important for canary rockfish. The interface between rough and smooth habitat, as defined by the CSMP, serves as a proxy for that transition here. The environmental predictor rasters were resampled from two meter resolution to 10 meter resolution to more realistically reflect the spatial precision of the occurrence data.

Model Construction and Selection

Data manipulation and analysis was conducted in R (R Core Team 2017). Maxent models were run using the "Maxent Variable Selection" package (Jueterbock et al. 2016). The package attempts to identify the most important, range-limiting environmental predictor variables by eliminating correlated variables, examining the effects of different settings of Maxent's beta regularization parameter, and applying either area under the receiver operating curve (AUC; Fielding & Bell 1997) or small sample size corrected Akaike Information Criterion (AICc; Akaike 1974) as a model selection parameter.

The user must specify several parameters in the “VariableSelection” function that executes the model selection algorithm:

- The **contribution threshold**, which instructs the algorithm to eliminate variables based on relative contribution to the predictive power of the model, regularized to a scale of 0-100%. Variables that fall below the specified contribution threshold are not included in subsequent model runs.
- The **correlation threshold**. The algorithm applies a Pearson’s correlation test to the predictor variables used in each model. If the Pearson’s correlation coefficient for any set of two predictor variables is above the correlation threshold, the variable that contributed less to the model is discarded for the next model run.
- A set of **Beta Parameter Values** for the algorithm to test.

For each beta parameter, an initial Maxent model is run with all variables included. Variables are then excluded in subsequent models based on the parameters described above. For each iteration, the algorithm calculates an average AUC from ten individual Maxent models, where a random selection of 50 percent of the presence points are withheld from the model for testing. AICc for the model is then calculated using a single Maxent model generated using all of the presence points. When no further variables can be eliminated according to the parameters specified, the algorithm terminates (Jueterbock et al. 2016).

For this study, the contribution threshold was set to 5%, and the correlation threshold was set to 0.9. These are the suggested defaults for the package (Jueterbock et al. 2016). The beta parameter values tested were 1,2,3,4,5. The primary metric used to evaluate model performance was AICc. AICc has been shown to be more informative than AUC when the goal of the modeler is to understand the environmental drivers of habitat suitability (Anderson & Gonzalez 2011, Warren & Seifert 2011, Morales et al. 2017) Further, AUC favors models that correctly predict presence/absence in the given data, so using AUC for model selection with Maxent, which uses background or pseudoabsence points instead of true absence points, may lead to over fitted models in some cases (Warren & Seifert 2011, Jiménez-Valverde 2012).

RESULTS

Black Rockfish

The model set for black rockfish was constructed using 64 presence points and 10,000 background points. Two models had drastically lower AICc scores than the rest of the model set; these models estimated more parameters than the presence points used to fit the models. Burnham and Anderson (2002) state that over-parameterized models are often not the models that best approximate real world relationships. Visual inspection of the response curves showed the models to be over-fitted; consequently, they were rejected from consideration on that basis. The best supported model for black rockfish had a beta parameter of four and contained three predictors: aspect, depth, and edge (Table 1). Depth contributed to 52% of the model's predictive power, followed by edge (39%) and aspect (10%) (Table 2).

The marginal response curves showed that the model predicted higher relative habitat suitability at depths between 10 and 30 meters, and nearer to the interface of smooth and rough substrate. Rote interpretation of the model suggests a slight preference for northeastern facing slopes, though aspect accounted for a small percentage of the gain of the model, and examination of the response curve reveals a significant difference in predicted relative suitability between 359 and 0 degrees, indicating the model may not be describing a realistic relationship between aspect and habitat suitability (Figure 6).

Figure 7 and Figure 8 show the model predicted across the seafloor in proximity to the two study areas at Cape Mendocino and Ten Mile/Westport. The figures highlight the relatively shallow and rugose habitat that is predicted to be highly suitable by the model.

Table 1. Maxent habitat suitability models for black rockfish (*Sebastes melanops*) offshore of Northern California. Variables: The environmental predictor variables included in the model. Beta: The beta regularization parameter of the model. Params: The number of parameters in the model. AICc: Small sample size corrected Akaike Information Criterion. dAICc: The difference between the AICc of the model and the lowest AICc score in the model set. AUC.Test: Area under the receiver operating curve (AUC) for data held for testing a trained model. AUC.Train: AUC for data used to train the model. AUC.Diff: Difference between testing and training AUCs. The best supported model is denoted with and asterisk(*).

Variables	Beta	Params	AICc	dAICc	AUC.Test	AUC.Train	AUC.Diff
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	1	84	-1661.656	0.000	0.865	0.917	0.051
aspect, depth, edge, vrm	1	94	676.872	2338.529	0.864	0.911	0.047
*aspect, depth, edge	4	9	1875.292	3536.949	0.822	0.832	0.011
aspect, depth, edge	5	11	1888.998	3550.654	0.810	0.833	0.024
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	5	23	1899.068	3560.724	0.822	0.842	0.020
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	4	32	1923.464	3585.120	0.833	0.856	0.024
aspect, depth, edge, vrm	2	40	1955.547	3617.204	0.867	0.896	0.029
aspect, depth, edge, vrm	3	42	1983.723	3645.380	0.850	0.874	0.023
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	2	49	2040.385	3702.041	0.862	0.903	0.041
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	3	48	2042.459	3704.116	0.862	0.884	0.022

Table 2. Relative contribution of environmental predictor variables to model predictive power for the best supported Maxent habitat suitability models for black rockfish (*Sebastes melanops*) offshore of Northern California.

Variable	Contribution (%)
depth	51.8
edge	38.5
aspect	9.7

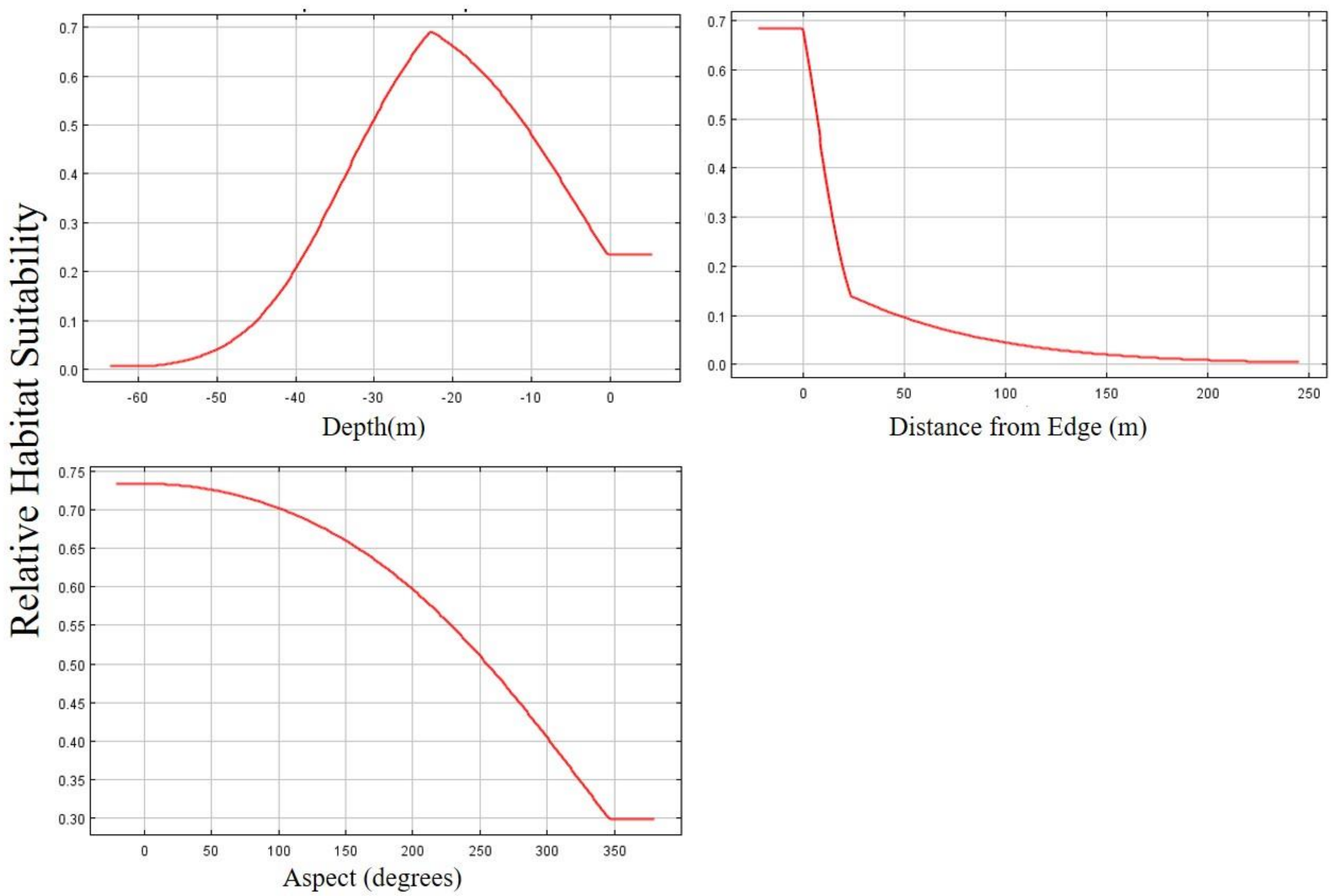

Figure 6. Marginal response curves for the best supported Maxent habitat suitability models for black rockfish (*Sebastes melanops*) offshore of Cape Mendocino, Northern California. Response variable axis is the Maxent logistic output, independent variable axis is top left: Depth (meters). Top right: Distance from rough/smooth interface (meters). Bottom: Aspect (degrees).

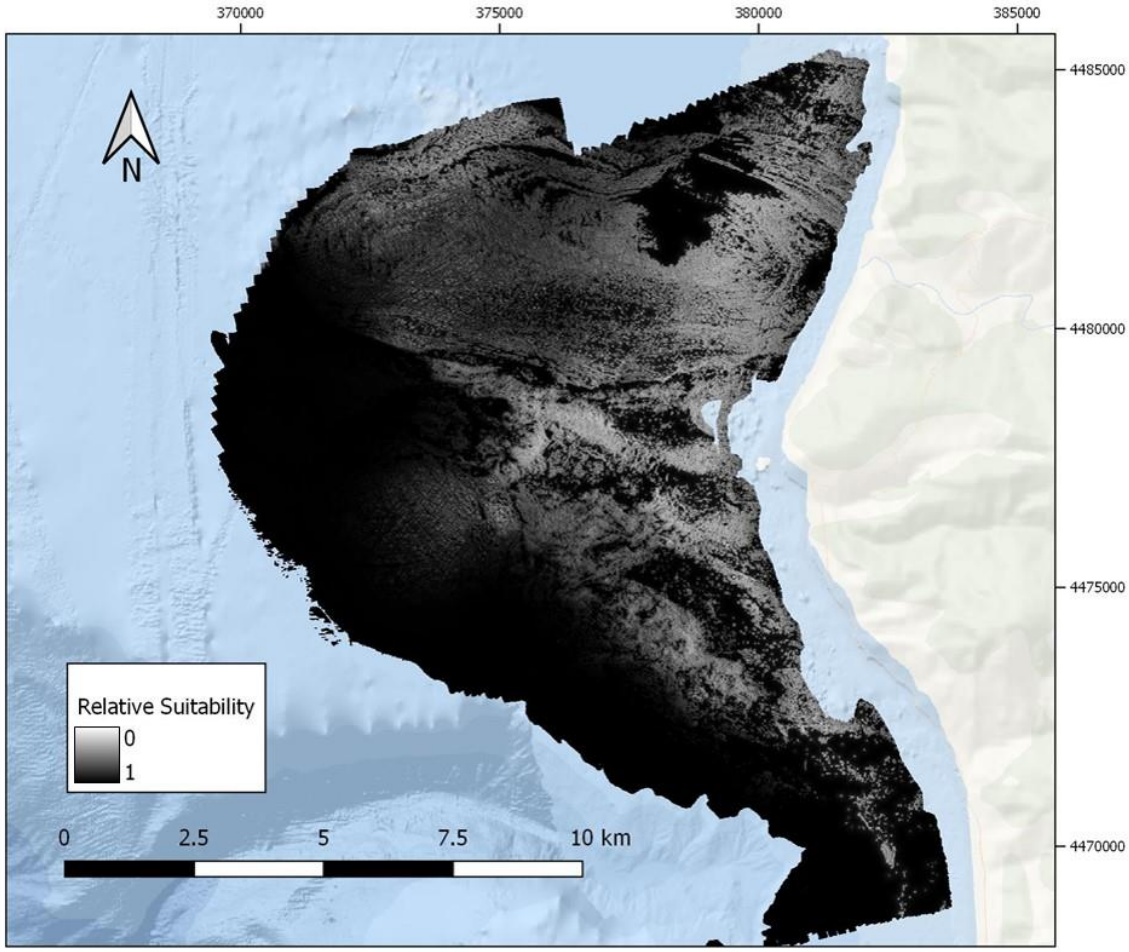

Figure 7. Predicted relative habitat suitability from the best supported Maxent habitat suitability models for black rockfish (*Sebastes melanops*) offshore of Cape Mendocino, Northern California. Lighter-colored habitat is more suitable.

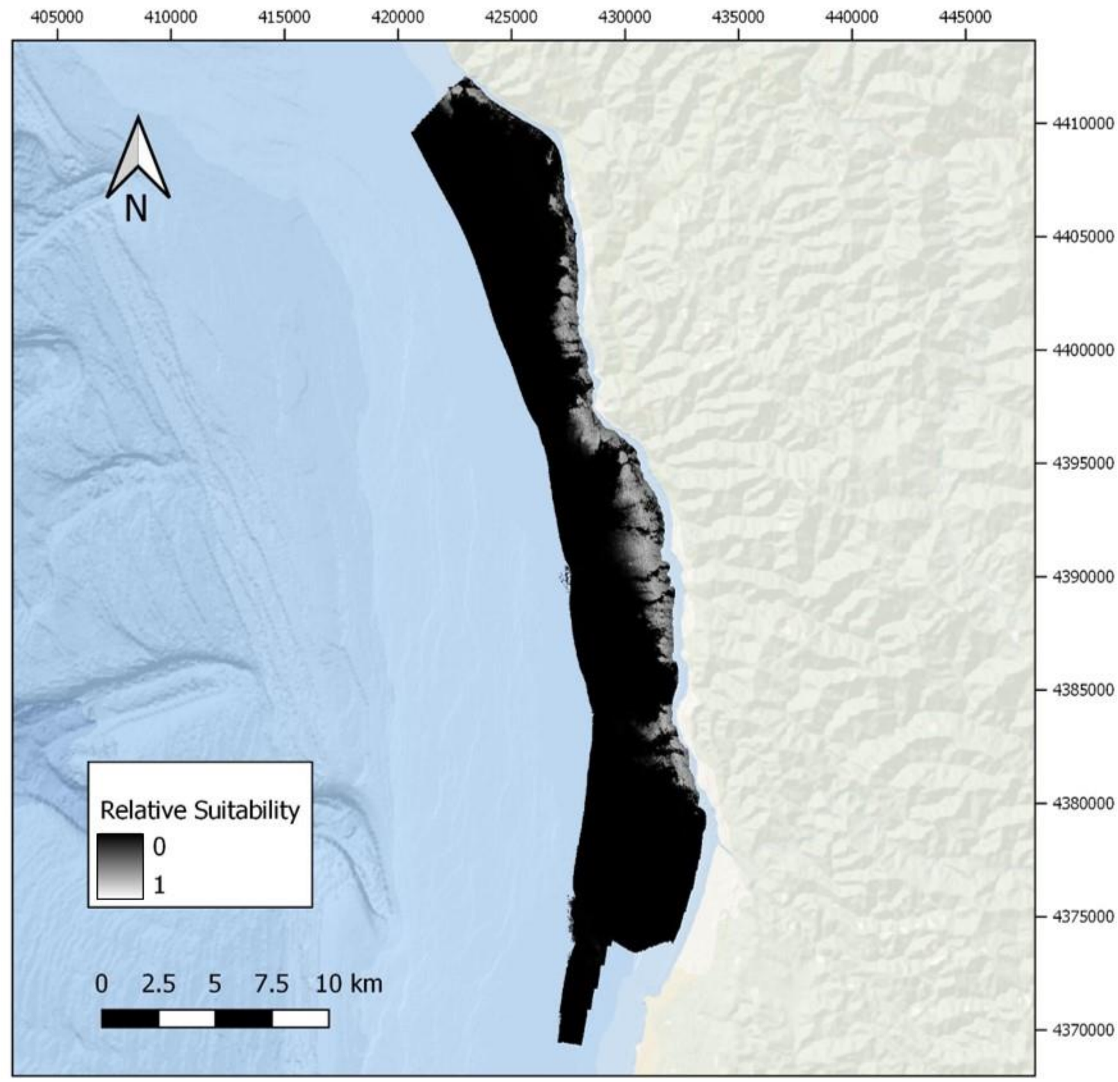

Figure 8. Predicted relative habitat suitability from the best supported Maxent habitat suitability models for black rockfish (*Sebastes melanops*) at the Ten Mile/Westport study area, Northern California. Lighter-colored habitat is more suitable.

Canary Rockfish

The model set for canary rockfish was created using 67 presence points and 10,000 background points. As with black rockfish, the model with the lowest AICc score appeared over-parameterized and was rejected. The best supported model had a beta parameter of three and contained three environmental predictors: depth, which contributed 76% of the model's predictive power, distance to rough/smooth interface (14%), and vector ruggedness (10%) (Table 3, Table 4).

The marginal response curves show the model predicts habitat suitability to increase with depth from 20 meters to 40 meters, after which it declines towards the deeper end of the range. Predicted suitability dropped off suddenly with increasing distance from the interface of rough and smooth substrate, and also had a negative relationship to vector rugosity (Figure 9).

Figure 10 and Figure 11 show the model predicted across seafloor in proximity to the two study areas at Cape Mendocino and Ten Mile/Westport. Compared with black rockfish, the most suitable habitat for canary rockfish is predicted to lie further offshore.

Table 3. Maxent habitat suitability models for canary rockfish (*Sebastes pinniger*) offshore of Northern California. Variables: The environmental predictor variables included in the model. Beta: The beta regularization parameter of the model. Params: The number of parameters in the model. AICc: Small sample size corrected Akaike Information Criterion. dAICc: The difference between the AICc of the model and the lowest AICc score in the model set. AUC.Test: Area under the receiver operating curve (AUC) for data held for testing a trained model. AUC.Train: AUC for data used to train the model. AUC.Diff: Difference between testing and training AUCs. The best supported model is denoted with and asterisk(*).

Variables	Beta	Params	AICc	dAICc	AUC.Test	AUC.Train	AUC.Diff
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	1	72	-3481.768	0.000	0.748	0.873	0.125
*depth, edge, vrm	3	7	1692.177	5173.945	0.752	0.780	0.028
depth, edge, vrm	4	6	1694.648	5176.416	0.730	0.762	0.032
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	3	12	1700.565	5182.333	0.759	0.808	0.049
bpibroad, depth, edge, vrm	4	9	1701.488	5183.256	0.743	0.801	0.058
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	4	10	1703.234	5185.002	0.700	0.780	0.080
depth, edge, vrm	5	7	1703.675	5185.443	0.7108	0.7394	0.0286
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	5	10	1710.757	5192.525	0.700	0.737	0.037
depth, edge, vrm	2	17	1716.152	5197.920	0.768	0.810	0.043
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	2	20	1716.369	5198.137	0.763	0.841	0.078
aspect, depth, edge, vrm	1	55	2161.208	5642.976	0.782	0.852	0.070

Table 4. Relative contribution of environmental predictor variables to model predictive power for the best supported Maxent habitat suitability models for canary rockfish (*Sebastes pinniger*) offshore of Northern California.

Variable	Contribution (%)
depth	76.0
edge	13.8
vrm	10.2

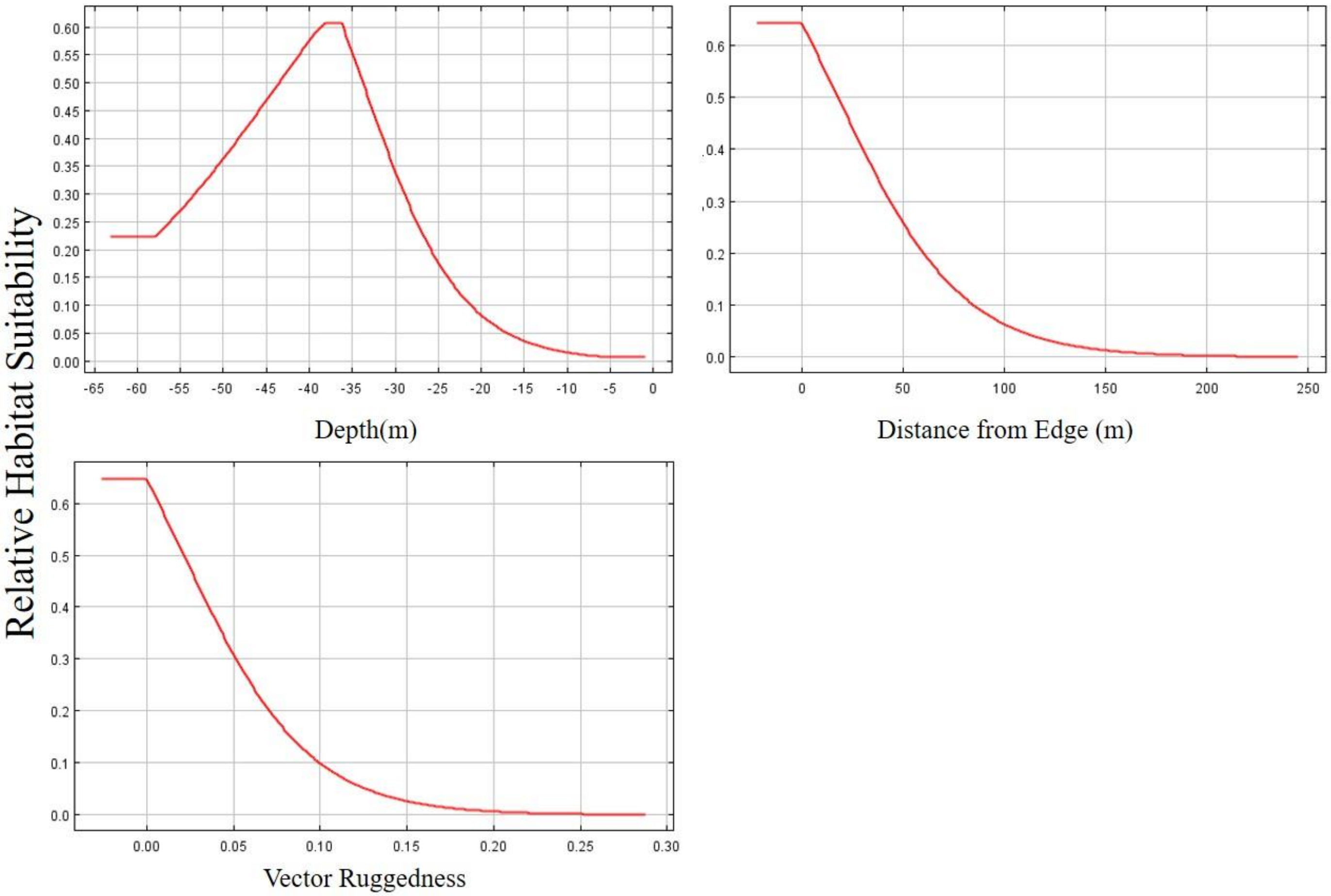

Figure 9. Marginal response curves for the best supported Maxent habitat suitability models for canary rockfish (*Sebastes pinniger*) offshore of Northern California. Response variable axis is the Maxent logistic output, independent variable axis is top left: Depth (meters). Top right: Distance from an intersection of rough and smooth substrate (meters). Bottom: Vector Ruggedness (unitless).

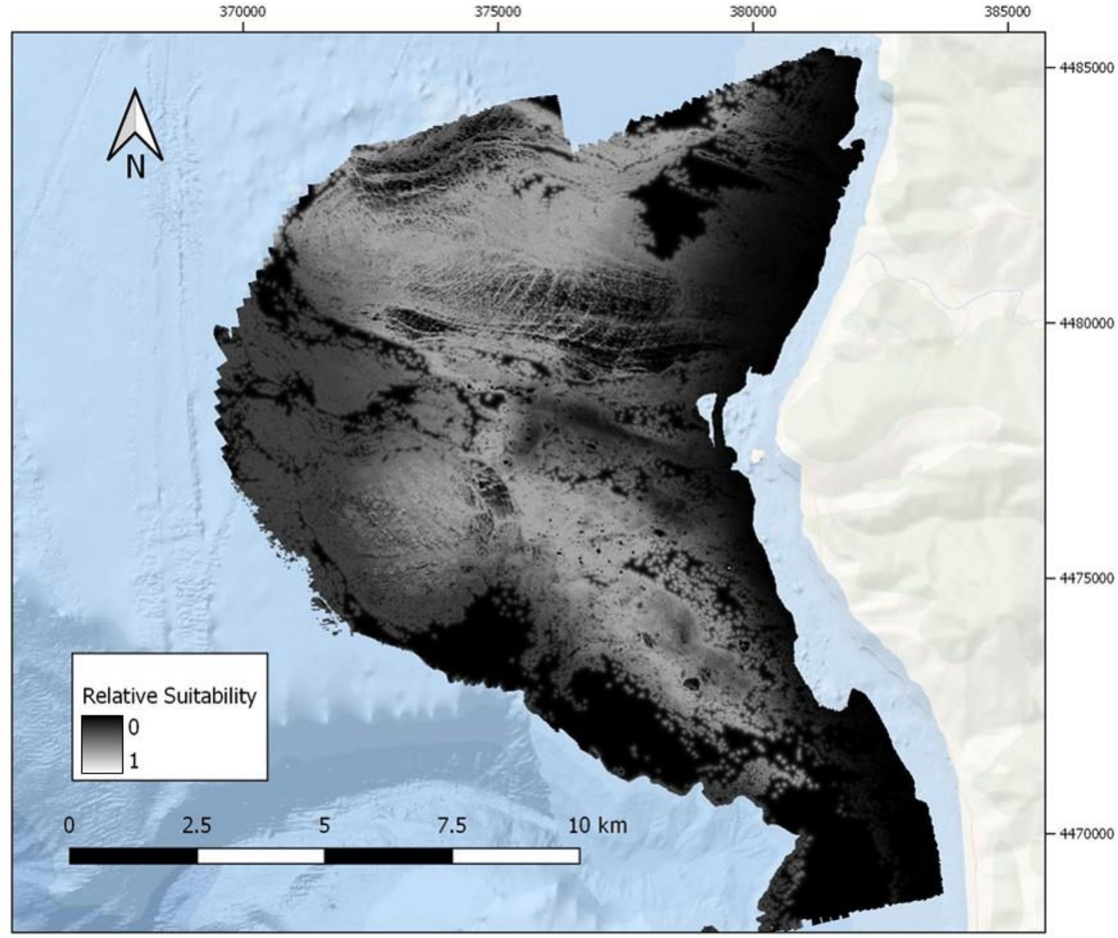

Figure 10. Predicted relative habitat suitability from the best supported Maxent habitat suitability models for canary rockfish (*Sebastes pinniger*) offshore of Cape Mendocino, Northern California. Lighter shaded habitat is more suitable.

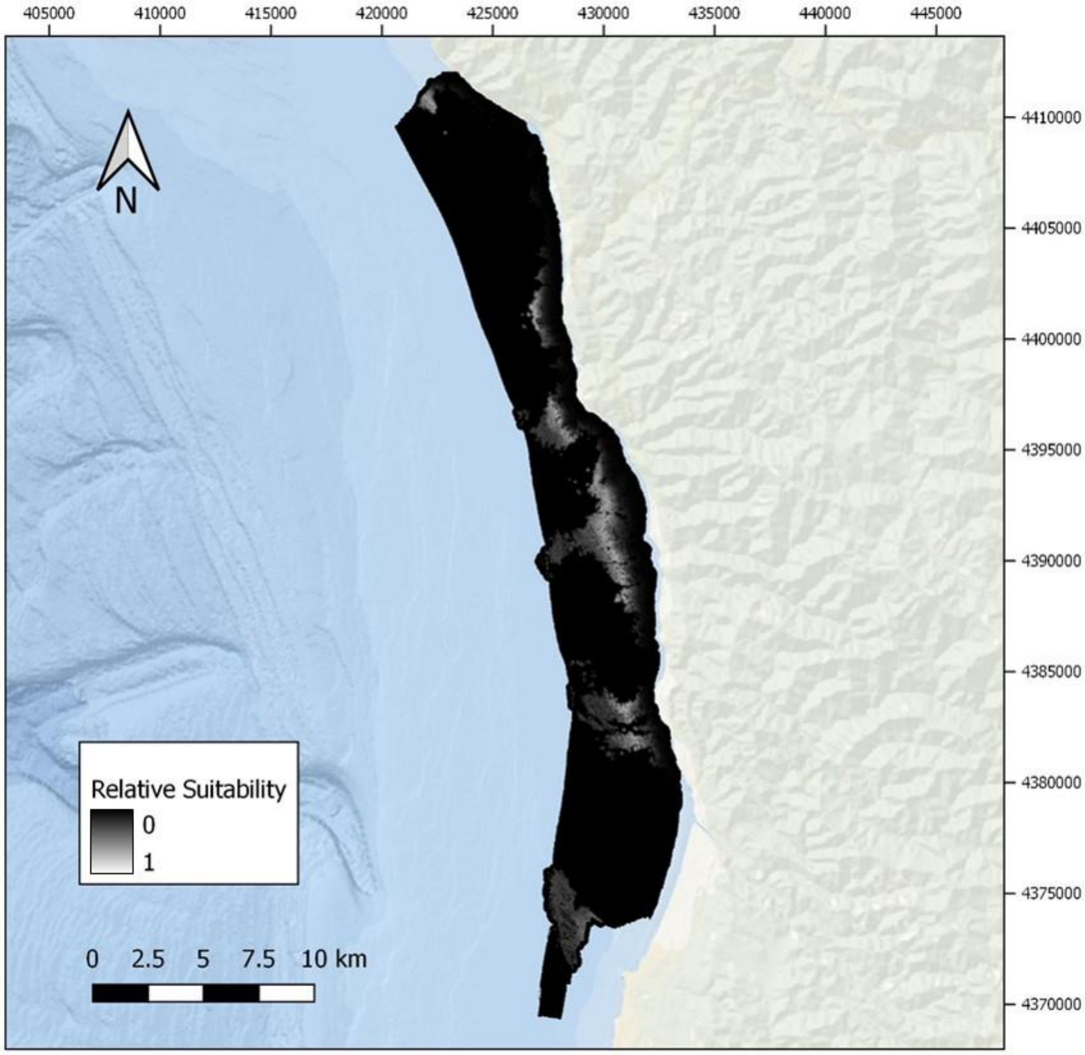

Figure 11. Predicted relative habitat suitability from the best supported Maxent habitat suitability models for canary rockfish (*Sebastes pinniger*) at the Ten Mile/Westport study area, Northern California. Lighter shaded habitat is more suitable.

Lingcod

The model set for lingcod was constructed using 99 presence points and 10,000 background points. The best supported model had a beta parameter of two and contained three variables: distance from rough/smooth interface, which accounted for 69% of the model's predictive power, broad-scale BPI (20%) and depth (11%); (Table 5, Table 6).

The marginal response curves for the model showed high predicted relative habitat suitability near a rough/smooth interface, with a rapid decrease with increasing distance from an interface. Suitability was predicted to be higher at the broad-scale BPI values that represent valleys/crevice, upper slope, and peaks/ridges than on flat areas and middle slopes. Lower slope areas were predicted to have the lowest relative habitat suitability. The marginal response curve for depth predicts relatively high suitability between 20 and 40 meters, with a steep drop off in shallower waters and a more gradual decrease towards the deeper end of the sampled range (Figure 12).

Figure 13 and Figure 14 show the model predicted across the seafloor in proximity to the two study areas at Cape Mendocino and Ten Mile/Westport. Compared with the two rockfish species, lingcod are predicted to occur more evenly across depths in the study area.

Table 5. Maxent habitat suitability models for lingcod (*Ophidion elongatus*) offshore of Northern California. Variables: The environmental predictor variables included in the model. Beta: The beta regularization parameter of the model. Params: The number of parameters in the model. AICc: Small sample size corrected Akaike Information Criterion. dAICc: The difference between the AICc of the model and the lowest AICc score in the model set. AUC.Test: Area under the receiver operating curve (AUC) for data held for testing a trained model. AUC.Train: AUC for data used to train the model. AUC.Diff: Difference between testing and training AUCs.

Variables	Beta	Params	AICc	dAICc	AUC.Test	AUC.Train	AUC.Diff
*****bpibroad, depth, edge	2	19	2389.830	0.000	0.747	0.776	0.029
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	3	30	2416.409	26.578	0.723	0.759	0.035
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	4	30	2432.218	42.388	0.722	0.736	0.014
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	2	38	2437.325	47.495	0.743	0.783	0.040
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	5	29	2443.139	53.309	0.710	0.741	0.031
aspect, depth, edge, vrm	1	53	2545.404	155.573	0.750	0.791	0.041
aspect, bpibroad, bpifine, curvature, depth, edge, slope, vrm	1	67	2704.57195	314.742	0.7636	0.8182	0.0546

Table 6. Relative contribution of environmental predictor variables to model predictive power for Maxent habitat suitability models for lingcod (*Ophidion elongatus*) offshore of Northern California.

Variable	Contribution (%)
edge	68.7
bpibroad	20.1
depth	11.2

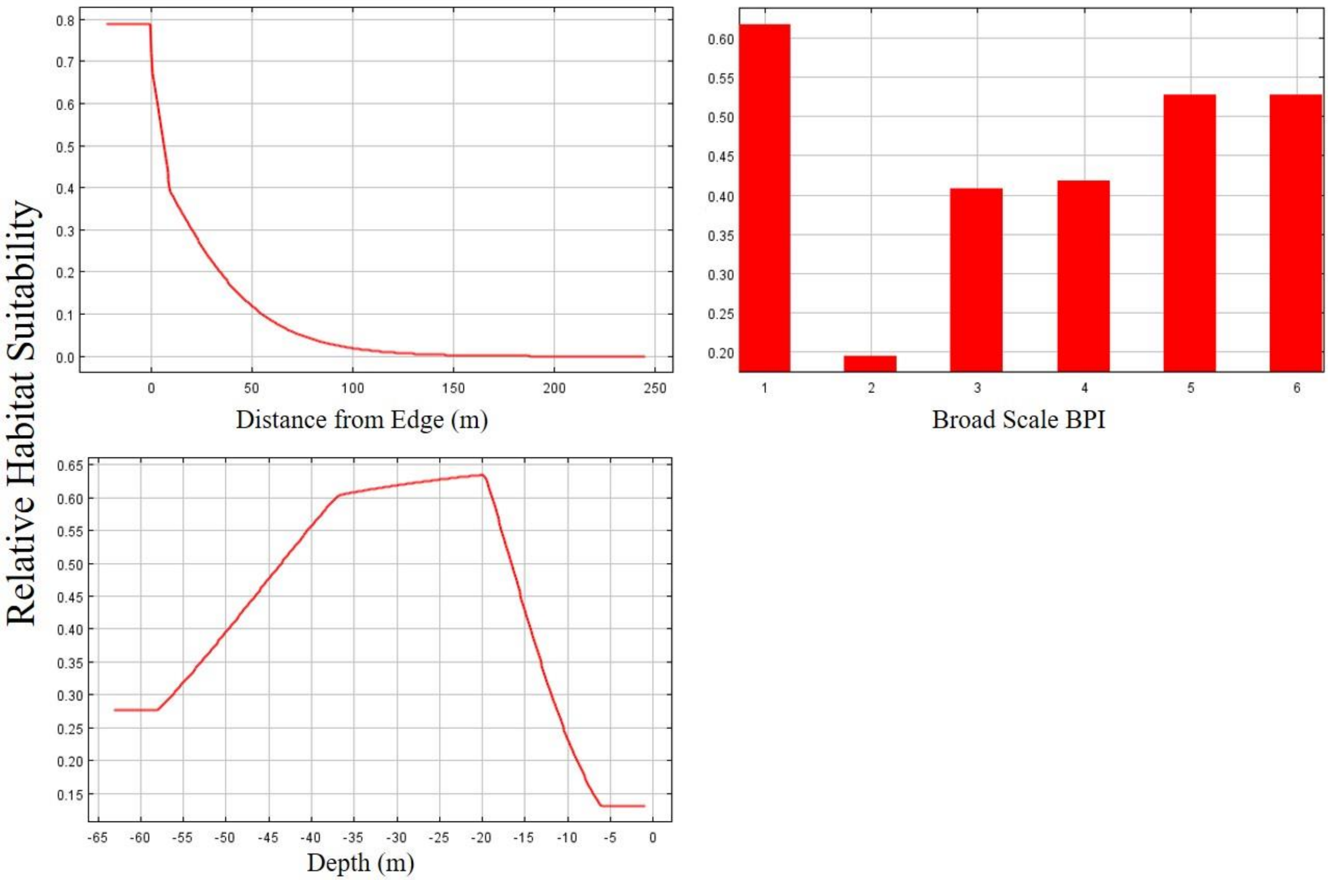

Figure 12. Marginal response curves for the best supported Maxent habitat suitability models for lingcod (*Ophidion elongatus*) offshore of Northern California. Response variable axis is the Maxent logistic output, independent variable axis is: Top left: Distance from rough/smooth intereface (meteres). Top right: Broad-scale bathymetric position index (1- Valley/Crevice, 2- Lower Slope, 3- Flat, 4- Middle Slope, 5- Upper Slope, 6- Peak/Ridge). Bottom: Depth (meters).

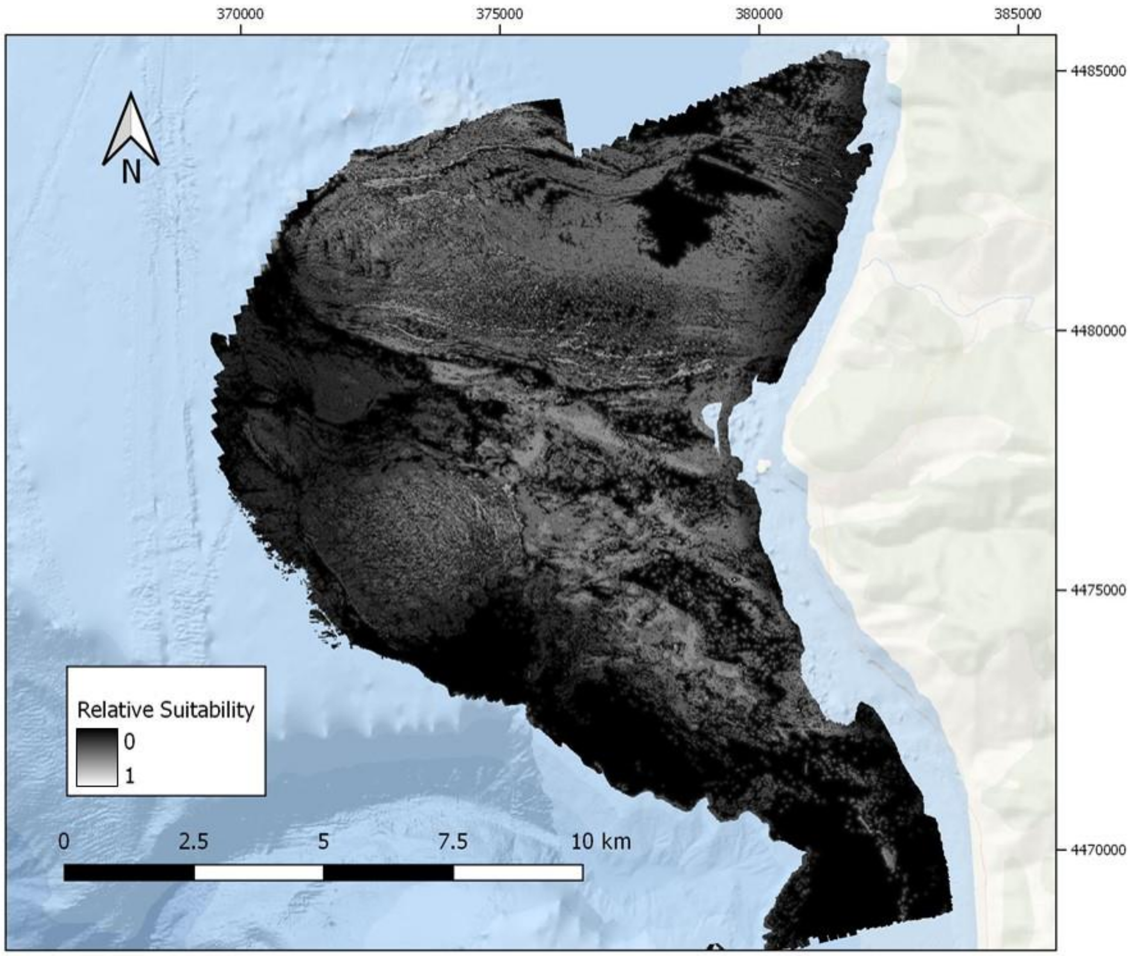

Figure 13. Predicted relative habitat suitability from the best supported Maxent habitat suitability models for lingcod (*Ophidion elongatus*) offshore of Cape Mendocino, Northern California. Lighter shaded habitat is more suitable.

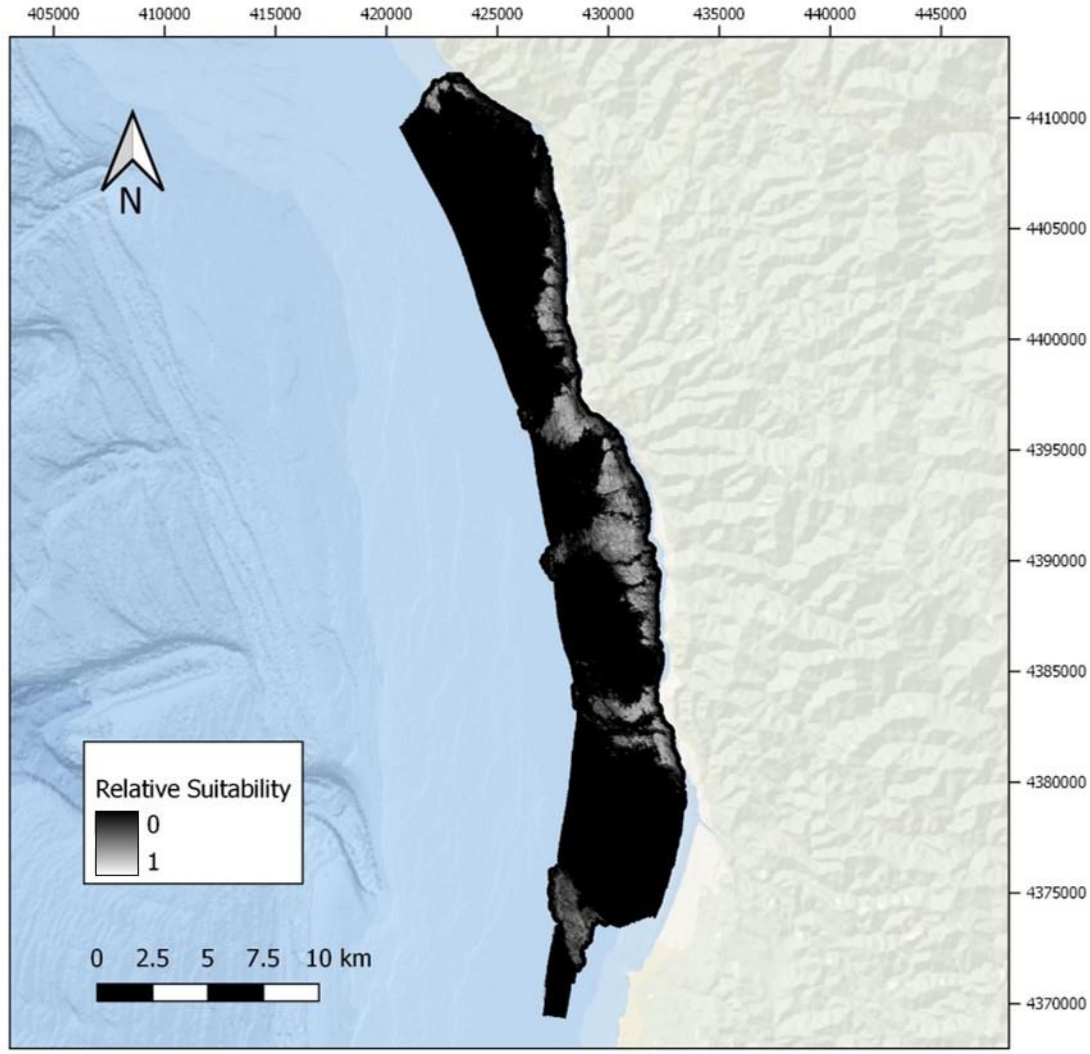

Figure 14. Predicted relative habitat suitability from the best supported Maxent habitat suitability models for lingcod (*Ophidion elongatus*) at the Ten Mile/Westport study area, Northern California. Lighter shaded habitat is more suitable.

DISCUSSION

Black Rockfish

The best supported model for black rockfish predicted higher relative habitat suitability for the species at depths shallower than about 30 meters, and near the interface between rough and smooth habitat. This is consistent with previous studies that show preference for relatively shallow, complex, rocky habitat (Miller & Lea 1972, Love et al. 2002, Green & Starr 2011). The biological significance of the relationship of black rockfish to the reef edge is unclear. The edge predictor may be more effective in this case at serving as a proxy for habitat complexity than VRM, possibly driven by the patchiness of the reefs, especially at the Ten Mile/Westport site.

Aspect accounted for about 10% of the predictive power of the model, but aspect itself is probably not a driver of habitat suitability. The aspect signal may be a result of fish selectively seeking, or seeking refuge from, a prevailing current. It may also be a result of fish seeking different light conditions to hunt prey, or hide from predators. The shape of the response curve for aspect does not lend itself to easy interpretation of what aspect, if any, the species is seeking. Relative suitability is predicted to be highest at 0 degrees, and lowest at 359 degrees. If the fish were seeking a north-facing slope, increased relative suitability would be expected on northwest facing slopes. The response curve for aspect was a similar shape in the second-best supported model, which contained the same environmental predictors (aspect, depth, edge) with a beta parameter of five, as well as in the model with all predictors, and a beta of one. Specific northness and eastness terms could be used to further investigate the importance of slope aspect in predicting relative habitat suitability.

Canary Rockfish

The most substantial difference in the characteristics of habitat with a high predicted relative suitability for canary rockfish, compared to black rockfish, is in depth. Higher suitability habitat for canary rockfish is predicted to occur in waters deeper than 30 meters. In addition to depth, the algorithm identified the distance from the interface of rough and smooth substrates and vector ruggedness as important predictors. The inclusion of the "edge" variable was done to test the conclusions of a study of canary rockfish habitat suitability on the North Coast, which found the species to be drawn to the edge of rocky reefs, possibly to take advantage of favorable currents or cover (Saucedo 2017). Edge accounts for 14% of the predictive power of the model, and the model better predicts the occurrence of canary rockfish with edge included, than if it is excluded.

An unexpected feature of the response curve for depth (Figure 9, top left), is that predicted habitat suitability declines after peaking at about 40 meters. Canary rockfish are known to occur much deeper than the 50-meter maximum depth of the survey (Love et al. 2002, Saucedo 2017). There are a few possible explanations:

1) The deeper areas of the study area (40-50m) were not sampled as comprehensively, and fish that occur there were not detected. Spatial bias in sampling is a common problem in species distribution modeling (Fourcade et

al. 2014), and perhaps it was not adequately controlled. Deeper sites are more difficult to sample by hook and line because they are typically further offshore and more subject to wind and current, which in turn make it more difficult to keep a fishing lure close to the bottom during sampling.

2) Many of the canary rockfish captured were juveniles or sub-adults. These life stages are known to occur in shallower water (Love et al. 2002). The model may reflect the habitat preferences of these stages, rather than adults.
3) The is little suitable habitat between 40-50 meters and the fish do not occur there.

Saucedo (2017) found habitat suitability, for canary rockfish, to be highest at about 60 meters' depth at Cape Mendocino, so it is likely that spatial bias in the hook and line survey is to blame for the discrepancy. Also of note is that predicted suitability in that study declined on the deep side of the survey range, and is near zero at 80 meters. Though relative suitability may start to decrease at that depth, the species is thought to be common to 100 meters, and occasionally observed as deep as 300 meters (Miller & Lea 1972, Love et al. 2002). Staton et al. (2017) used generalized additive models to test the effects of depth on catch per unit effort (CPUE) of canary rockfish captured during the North Coast MPA baseline study, and did not observe the same sort of steep drop-off below 40m. Though CPUE and relative habitat suitability are not directly comparable, this may also be an indicator of sensitivity to a spatial sampling bias in depth in this work and Saucedo (2017).

Lingcod

The drivers of higher suitability habitat for lingcod are different than the two rockfish species. Depth accounted for only 11% of the predictive power of the model, while distance to rough/smooth interface accounted for 69%, with the remaining 20% explained by broad-scale BPI. The literature suggests depth should not be a strong driver of habitat suitability at the 10-50 meter depth range surveyed, as lingcod are thought to be common at those depths (Miller & Lea 1972, Bassett et al. 2018). The response curve for depth showed a decrease in predicted relative habitat suitability below about 45 meters. Staton et al. (2017) observed increasing CPUE with depth to 50m. Like in the canary rockfish model, this may also be indicative of spatial sampling bias.

(Bassett et al. 2018) observed lingcod associated with both high- and mid-relief habitat, and hard and mixed hard/soft substrates. The distance to rough/smooth interface may be capturing the association of lingcod with rocky structure of any type.

The model predicted at least moderate levels of relative habitat suitability at all categories of broad scale BPI except lower slope. It is possible that the other categories provide better opportunities for camouflage and ambush. At the scale the variable is calculated, the “flat” category could include boulder fields and other smaller features that provide cover. There may be an advantage to lingcod either being well hidden in a crevice/valley, where potential prey could be taking refuge, or further upslope where access to midwater species, common prey, is more available (Beaudreau & Essington 2007).

Using Best Practices for Model Fitting and Selection

The gross over-parameterization of several of the models for black and canary rockfish demonstrate the importance of not relying on any single metric of model performance to select a model most reflective of real-world relationships between species and their habitat. Testing a suite of beta parameters, and visually inspecting the response curves, allows the investigator a more robust understanding of the relationships between the predictors, model settings, and habitat suitability.

Spatial Bias and Error

An unresolved question of this work is the amount of spatial error in the occurrence locations. The occurrence locations contain both systematic (line scope, vessel drift) and random error inherent in GPS locations.

To attempt to account for some of the systematic error, I calculated AICc scores for a suite of models for each of the three species where the occurrence locations were assigned to the location of the vessel at the time of landing (“no delay” models), 30 seconds prior to landing, and 60 seconds prior to landing. For black and canary rockfish, AICc scores were consistently lower for the no delay models with the same predictors and beta parameters compared to the 30 and 60 second models. While there was not a consistent pattern in lingcod between the no delay and 30 second models, though both sets had lower AICc scores than the 60 second models. Based on those results, I conducted the full analysis using the locations at time of landing.

An issue that became evident during this analysis was the spatial imprecision of the sampling effort. Many fish were captured outside of the bounds of the sampling stations, to the extent that I added a 100m meter buffer around each station to the analysis to be able to retain the significant number of presence locations that would have been eliminated if the analysis was restricted to the sampling stations only. It's possible that this expansion contributed to the possible spatial bias observed in the canary rockfish model, as background points could have been extracted from areas that were not representative of the habitat surveyed, especially areas deeper than 50m. Future analysis of this data should include a more detailed examination of spatial error and bias, as well as the model's sensitivity to each.

CONCLUSION AND RECCOMENDATIONS

A success of this effort was replicating results from habitat studies undertaken using direct-observation by SCUBA, ROV, etc. This method, using relatively unsophisticated field methods, combined with open source data and software, was able to identify distinct niches occupied by the three study species. Proximity to some level of habitat complexity, captured by the distance to rough/smooth interface predictor, was important in predicting the relative suitability of habitat of all three species. Depth was perhaps the most important predictor in distinguishing the difference in niches occupied by the species; higher habitat suitability for black rockfish was predicted in waters shallower than about 30 meters, while relative suitability for canary rockfish was predicted to increase at greater depths. Lingcod distribution was not predicted to be strongly controlled by depth, and the response curve shows a flattened top—indicating higher predicted relative habitat suitability across a wider range of depths.

The methods used in this study added minimal workload during the sampling work itself, which was critical to the ability to collect location information with a small scientific crew. However, post-processing of the video was tedious and time consuming. A method to immediately record the time a fish is landed during sampling would reduce the time it takes to process the data, and would allow other fish attributes (e.g. fork length) to be related to its location. In this study, the field data taken on each fish was not linked to the exact location of capture extracted from the video because the fish were not always processed in the order of landing. During periods of high rates of capture, fish were placed in holding buckets to await identification and measuring, making it difficult to match the fish on video with data collected in the field. Further sampling where location and field data are connected, would significantly reduce the time needed for data processing, and allow exploration of the habitat associations of different life stages (if length or age data is collected), by different populations (if genetic information is collected), and whether habitat usage changes through time (if data collection is ongoing). Incorporating predictor variables of ocean condition (sea surface temperature, chlorophyll, etc.), when available, could also increase the usefulness of Maxent models as a tool for understanding the drivers of a spatial population structure in fishes.

As fisheries move towards ecosystem-based management, improved understanding of the drivers of habitat suitability, is needed to better inform models estimating stock abundance and biomass (Pirtle et al. 2017). Maxent modeling can inform the establishment of MPAs, designation of Essential Fish Habitat, and regional catch limits by identifying where habitat might support more productive populations, especially for stocks that have been poorly studied and where resources to conduct stock assessments are scant (Valavanis et al. 2008, Jones et al. 2012, Pirtle et al. 2017, Canty et al. 2018).

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