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# Predicting Spatial Distributions of Demersal Fishes off Central California

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PREDICTING SPATIAL DISTRIBUTIONS OF DEMERSAL FISHES OFF CENTRAL CALIFORNIA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Anne Tagini

December 2018

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The Designated Thesis Committee Approves the Thesis Titled

PREDICTING SPATIAL DISTRIBUTIONS OF DEMERSAL FISHES OFF CENTRAL CALIFORNIA

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## ABSTRACT

### PREDICTING SPATIAL DISTRIBUTIONS OF DEMERSAL FISHES OFF CENTRAL CALIFORNIA

Anne Tagini

Seafloor maps are often used in species distribution modeling (SDM), where maps are paired with fish observations to create models predicting habitat suitability, species density, or species biomass. Problems with the current use of SDM include limited understanding of species relationships with benthic morphology, lack of practical model testing, and deficiency of information on the effects of map resolution on population estimates. A drop camera was used to gather observations of fishes along Central California and paired with remotely sensed bathymetry to create predictive models and maps of species density and biomass. I found that relationships with remotely sensed habitat variables are strong enough to create robust models. However, predictive maps at 10m resolution only gave a broad-scale picture of density distributions. Predictive maps consistently overpredicted species density, but often underpredicted peaks in density. Map resolution had a large effect on biomass predictions, where total predicted biomass was found to increase with increasing resolution. In conclusion, predictive maps seem to capture general patterns of species distributions; however, often peaks or hot spots in density are not captured. Predictive maps are very useful for understanding general patterns of species distributions, but one should be cautious when using them to obtain density or biomass estimates, especially when using estimates to inform management.

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## LIST OF ABBREVIATIONS

AIC – Akaike’s Information Criterion  
ANOVA – Analysis of Variance  
BPI – Benthic Position Index  
CCA – Canonical Correspondence Analysis  
COPC – California Ocean Protection Council  
DEM – Digital Elevation Model  
EFH – Essential Fish Habitat  
GIS – Geographic Information System  
GLM – Generalized Linear Model  
MARE – Marine Applied Research & Exploration  
MBARI – Monterey Bay Aquarium Research Institute  
MBES – Multibeam echo sounder  
MGET – Marine Geospatial Ecology Toolbox  
MLML – Moss Landing Marine Laboratories  
MPA – Marine Protected Area  
MSA – Magnuson Stevens Fishery Conservation and Management Act  
NOAA – National Oceanic and Atmospheric Administration  
NCEI – National Center for Environmental Information  
NGDC – National Geophysical Data Center  
NRMSE – Normalized Root Mean Square Error  
PCA – Principal Component Analysis  
PC – Principal Component  
RMSE – Root Mean Square Error  
SDM – Species Distribution Modeling  
SFMP – California Seafloor Mapping Program  
SMCA – State Marine Conservation Area  
TPI – Topographic Position Index  
VIF – Variation Inflation Factor  
VRM – Vector Ruggedness Measure

## Introduction

### Background

In 1996, the Magnusson Stevens Fishery Conservation and Management Act (MSA) was amended to promote the protection of essential fish habitat (EFH) (*Sustainable Fisheries Act, 1996*). The MSA requires that regional fishery management councils describe EFH in their fishery management plans and minimize impacts on EFH from fishing activities. Since the passage of the MSA, state and federal fishery scientists have been working to define and map EFH. In California, to assist with mapping of EFH and to help in the planning and design of marine protected areas (MPAs), the California Ocean Protection Council (COPC) provided funding for a collaboration that created the California Seafloor Mapping Program (CSMP). The mission of the CSMP is to create high-resolution maps of benthic features on the seafloor that can be used as habitat base maps for demersal marine species.

Benthic features provide important habitat to many demersal fishes (Carr, 1991; Choat et al., 1988; Friedlander and Parrish, 1998; Sale, 1991). Relationships with benthic habitat are strong and predictable and are used to determine where we might find particular species. Large seafloor features such as the continental shelf and submarine canyons and general physical characteristics (i.e., substrate type-hard or soft) influence where fish can be found. However, within these broad-scale patterns are more detailed species distributions. Small-scale geomorphological features and seafloor sediment types such as mud, sand, cobbles, boulders, etc., influence mesoscale (10-100 m) and

macroscale (1-10 m) species distribution patterns (Gratwicke and Speight, 2005; Greene et al., 2000; Pearcy et al., 1989; Stein et al., 1992). Benthic habitat features have been used to obtain biomass estimates of fish species (Friedlander and Parrish 1998), and remotely-sensed benthic maps and derived habitat characteristics are being used more and more to describe and predict and map species distributions (Iampietro et al., 2008; Valavanis et al., 2008; Young et al., 2010) .

Using species distribution modeling (SDM) software, species observations can be overlaid onto benthic maps to predictively model species-specific distributions. SDM software incorporates the habitat characteristics of an area where there is a known occurrence of an organism to predict habitat suitability of other unsurveyed areas. Habitat suitability maps can be created using georeferenced environmental data layers and species observations. Species distribution modeling can be used to 1) estimate habitat suitability, 2) predict distributions in unsurveyed areas, 3) improve survey design, 4) inform management decisions regarding locations for area closures, and 5) obtain density and biomass estimates. Benthic habitat mapping has been used to predict the distribution of demersal fish both in tropical (Pittman and Brown, 2011) and temperate ecosystems (Young et al., 2010). In Alaska, habitat area and biomass estimates derived from SDMs have even been used in stock assessments (O'Connell et al., 2004).

There has been limited investigation into the effect of map resolution on estimates of predicted biomass or density (Kendall et al., 2011; Pittman and Brown, 2011).



Bathymetry resolution refers to the size of each cell, comprising the grid which is the bathymetry layer. A bathymetry layer, or digital elevation model (DEM), is made up of a grid of cells, like how a photo is made of a grid of pixels. The resolution, or cell size, determines how much detail is shown on a map. Bathymetry DEMs are available at different resolutions for different areas. Fine scale (high resolution) maps are more widely available for nearshore waters, but the resolution of bathymetry available usually decreases as depth increases due to difficulties associated with fine scale seafloor mapping at deeper depths. The resolution of a map used in predictive mapping could potentially affect resulting predictive estimates of organism density and/or biomass.

The first goal of this study was to understand benthic habitat associations of several demersal fish species along the California central coast. The second goal was to use spatial modeling of benthic habitat associations to predict demersal fish densities along the central California coast. Predictive species models and maps were created to help understand and visualize species density distributions. The final goal of this study was to understand the effect of map resolution on species biomass estimates. This information is important to understand when assessing biomass estimates derived from any predictive map, especially if fisheries managers are using biomass estimates to regulate a fishery.

## **California Groundfish**

More than 90 species of demersal fish species are managed by the Pacific Fishery Management Council (PFMC) in the federal Groundfish Fishery Management Plan (GFMC). These fish are important in commercial and recreational fisheries and provide an attraction for scuba divers. California groundfish include sharks, skates, roundfish (lingcod, cabezon, etc), rockfish, and flatfish.

Rockfish (*Sebastes spp.*) are a genus of fish characterized by long life spans, late maturity, and vivipary (Love et al., 2002; Love, 2011). There are over 65 species of rockfish in the Northeast Pacific (Lea et al., 1999), many of which are important in commercial and recreational fisheries (Starr et al., 2002). Rockfish dominate fish assemblages in California, making up 90.2% of species richness in depths of 20-365 m in southern California (Love et al., 2009). In Central California, rockfish encompass 77% of species richness in depths of 70-250 m and 93% of species richness in depths of 90-350 m (Anderson and Yoklavich, 2007; Yoklavich et al., 2000). The benthic habitats found at these depths include bedrock outcrops, boulder and cobble fields, and sand and mud flats. In addition, submarine canyons cut into the continental shelf and provide unique habitats for fish. Many rockfish live in deep waters (>30 m) and these features and characteristics provide habitat for a suite of species.

### **Species-Habitat Associations: Observed Habitat Features**

Associations with specific sediment types and other observed habitat features are known for many deep water demersal fish (Anderson and Yoklavich, 2007; Love et al.,

2009; Pearcy et al., 1989; Stein et al., 1992). Fish habitat is often described in terms of sediment or bottom type (i.e., rock, boulders, cobble, sand, mud), relief (height of substrate), and rugosity (complexity of substrate). This habitat information is observed using visual surveys either via scuba or underwater camera systems.

Many large demersal rockfish species, such as Yelloweye Rockfish (*S. ruberrimus*) and Bocaccio (*S. paucispinis*), occupy areas with rock ridge and boulders, often accompanied by smaller species such as Pygmy (*S. wilsonii*) and Squarespot rockfish (*S. hopkinsi*) (Anderson and Yoklavich, 2007; Love et al., 2009; Yoklavich et al., 2002). Combinations of cobble and mud are habitat for other species such as Greenspotted (*S. chlorostictus*), Greenstriped (*S. elongatus*), and Halfbanded Rockfish (*S. semicinctus*) (Anderson and Yoklavich, 2007; Pearcy et al., 1989). Many non-rockfish species such as poachers, zoarcids, and Spotted Ratfish are found in deep mud habitats (Stein et al., 1992; Yoklavich et al., 2000), along with Stripetail and Splitnose Rockfish (Anderson et al., 2009; Pearcy et al., 1989).

Habitat associations and spatial distributions of Canary Rockfish (*S. pinniger*), Copper Rockfish (*S. caurinus*), Greenspotted Rockfish (*S. chloristictus*), Greenstriped Rockfish (*S. elongatus*), Vermilion Rockfish (*S. miniatus*), and Pacific Sanddab (*C. sordidus*) are investigated in this study. These fish represent a group of demersal fish species that occur over a range of different habitat types. Pacific Sanddab are found in low structure soft bottom habitat (Anderson et al., 2009, Yoklavich et al., 2002). Greenstriped Rockfish are often observed over mixed and soft substrate and are grouped as cobble-mud

associates (Anderson and Yoklavich, 2007). Greenspotted Rockfish are often found in areas of mixed sediments (Anderson et al., 2009), consisting of a combination of mud, cobble, and rock (Anderson and Yoklavich, 2007). Canary Rockfish have been observed in high abundance over boulder habitat (Laidig et al., 2009), but also have been recorded on cobble fields and mud bottoms (Stein et al., 1992). Copper Rockfish have often been observed in areas with hard bottom and vegetative structure (kelp) (Johnson et al., 2003, Matthews, 1990a; Matthews, 1990b). Vermilion Rockfish associate with rock and boulder habitats (Anderson et al., 2009; Laidig et al., 2009; Yoklavich et al., 2002).

#### **Species-Habitat Associations: Remotely Sensed Habitat**

Multibeam echo sounders (MBES) are remote sensing tools used to collect seafloor data used in many SDMs because they collect both acoustic backscatter and bathymetry (depth) data (Brown et al., 2011). An MBES collects bottom data in swaths, which are mosaicked together, resulting in seafloor maps. Seafloor maps can be imported into a geographic information system (GIS) and paired with observations of species to create SDMs. Morphological characteristics derived from MBES bathymetry include slope, curvature, aspect, vector ruggedness measure (VRM), and topographic position index (TPI). Slope of the seafloor is thought to be a factor influencing fish distributions (Iampietro et al., 2008). Higher densities of deep water demersal fish have been found in areas of high slope (McClatchie, 1997; Young et al., 2010), and distributions of Rosy Rockfish have been reported to be influenced by slope (Young et al., 2010). Curvature is

the slope of the slope, or the rate of change of the seafloor slope. Aspect refers to the compass direction, or orientation of the seafloor. Currents transport suspended nutrients and zooplankton through the water column, which are important food for many fish species. In theory, fish should be found on rocks facing the oncoming current because these sides receive more nutrients. Aspect has been reported to be a significant predictor in determining the distributions of Rosy Rockfish at Cordell Bank (Iampietro et al., 2008). Rugosity is often referred to as a measure of the combination of two parameters, structural complexity and relief (Smith, 2014). Rugosity has been positively correlated with fish species richness and abundance (Kuffner et al., 2007; Luckhurst and Luckhurst, 1978). The vector ruggedness measure (VRM) in ArcGIS calculates rugosity through measurement of the dispersion of vectors. Previous studies have shown that this metric can influence the spatial distributions of Greenstriped Rockfish (*S. elongatus*) and Rosy Rockfish (*S. rosaceas*) (Young et al., 2010). Topographic position index (TPI) is the measure of the elevation of any given point relative to surrounding areas. TPI can be used to identify peaks, flat plains, and valleys on the seafloor. Greenstriped Rockfish (*S. elongatus*) have been found in areas with low broad-scale TPI values (large flat areas), while Yellowtail Rockfish (*S. flavidus*) have been found in high relief areas with high fine-scale TPI values (Young et al., 2010).

Additionally, there are larger scale features such as the shoreline or continental shelf edge which may affect fish distribution patterns. Distance to shoreline and distance to shelf edge were the most influential predictors in models predicting reef fish

distributions for four species in a study by Pittman et al. (2011). Submarine canyons are large features found along the central coast, which can provide unique habitat for demersal fish species (Yoklavich et al., 2000). Distance to canyon heads could be important in describing some species distributions.

### **Species Distribution Modeling**

Predictive modeling can be used to inform fisheries as well as fisheries management. SDMs can be used to estimate habitat suitability or likelihood of species occurrence over any given habitat. Predictive maps of habitat suitability can be used to physically locate areas where species occurrence is highly likely, which can be used by both fishers and fisheries managers to target specific species. Fishers might use this information to more precisely target their fishing efforts to catch desired species while avoiding non-desired species, whereas managers might use this information to inform their decisions regarding locations for area closures. This information can also be used by fisheries scientists to improve sampling design, by targeting survey efforts in areas of suitable habitat. Because it is quite difficult and expensive to do extensive deep-water visual surveys, these SDMs can be used to predict fish distributions and densities in unsurveyed areas, which can contribute to improving our understanding of the current status of fish populations over broader spatial scales. Models predicting population biomass can also be used to help understand stock size, and this information can be incorporated into stock assessments.

With the increased use of SDMs to predict fish distributions, it is important to empirically evaluate the species-habitat associations on which these predictive models are based. SDMs are based on relationships with remotely sensed habitat features. By quantitatively assessing species relationships with different categorizations of benthic habitat (i.e., observed habitat features vs. remotely sensed habitat features), we can evaluate how much of the spatial variability in fish distributions are explained by each set of habitat variables and look at the potential overlap in variation described by each set of variables. Additionally, it is important to understand the effect of map resolution on resulting predictions. Before these models are used to inform management, rigorous model testing is required. Testing the predictive capabilities of SDMs will help determine how useful these models are in estimating habitat suitability and predicting distributions outside of surveyed areas.

My first objective was to identify species relationships with observed habitat features and assess if my findings are consistent with the literature. The second objective was to identify species relationships with remotely sensed habitat features. The third objective was compare estimates of species relationships with observed and remotely sensed habitat features by comparing their collective ability to describe variation in species distributions. The fourth objective was to create predictive models and maps of species density in ArcGIS for Monterey Bay. The fifth objective was to test the predictive power of the models by comparing the densities observed in 2014 with

the densities predicted from a model using 2013 data. Finally, the last objective was to assess the effect of map resolution on predicted biomass estimates.



## **Materials and Methods**

### **Site Selection**

The study area spans 270 km of the central California coast from San Francisco to San Simeon (Figure 1). Visual surveys were conducted on the seafloor in depths of 70–250 m along the outer continental shelf and upper continental slope. The surveys were conducted over a large area and covered a large range of habitat types. The outer continental shelf is composed mostly of flat, soft-bottom habitats and sparsely scattered rocky outcrops and pinnacles. The shelf ends abruptly at depths of about 100–120 m and becomes a steep continental slope incised with submarine canyons such as Ascension Canyon, Monterey Bay Canyon, and Carmel Canyon. Many different habitat types occur on the continental slope, including soft sediments, rock outcrops, pinnacles, boulder fields, cobble fields, and brachiopod beds. Rocky bottoms were often targeted during visual surveys; however, all bottom types were sampled.

The study area was separated into three zones: North, Central, and South. This stratification was established based on spatial gaps in video observations within the study site. The North zone is situated offshore off San Francisco, the Central zone extends the entire Monterey Bay, and the South zone covers Big Sur, ranging from Cape San Martin to Lopez Point (Figure 1). Portuguese Ledge is a site used in this study to determine the effect of map resolution on biomass estimates. Portuguese Ledge is a State Marine Conservation Area (SMCA) in Monterey Bay (Central zone) lying in 80-100

feet deep, consisting of rock, boulders, cobble, and mud extending into the Monterey Bay Submarine Canyon.

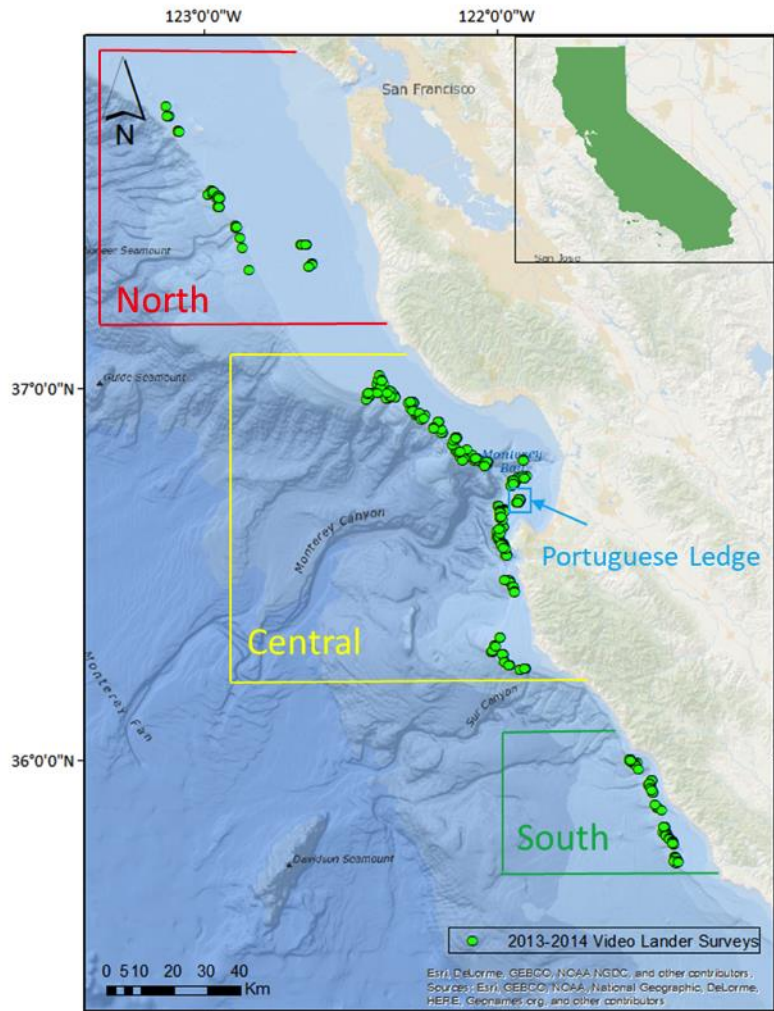
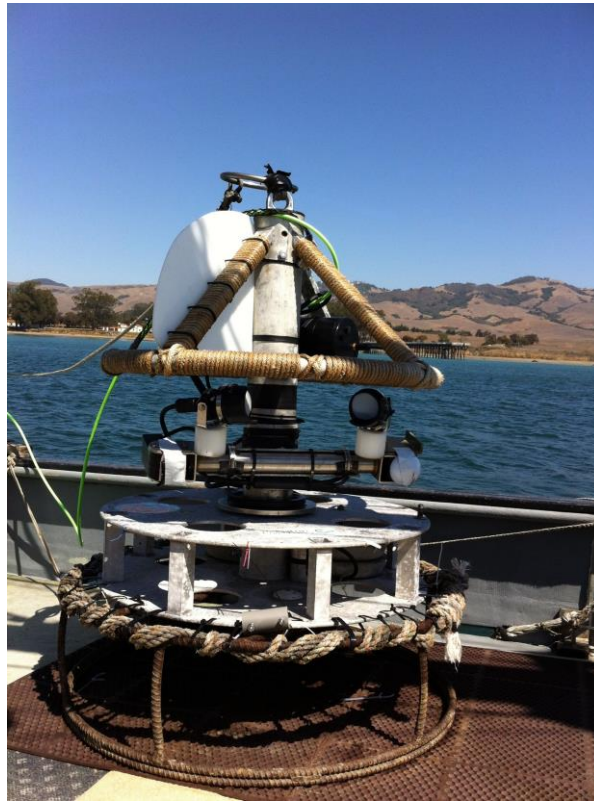


Figure 1. Map of study area and subdivisions of study area.

## Data Collection

The Video Lander (Figure 2) is a remote camera system used to observe fishes on the continental shelf and upper slope of central California. The Lander was built by Marine Applied Research & Exploration (MARE) and was utilized by The Nature Conservancy and Moss Landing Marine Laboratories (MLML) on a joint project aiming to locate and quantify overfished species. The Video Lander is a stationary camera system equipped with two stereo-video cameras rotating 360° on a motor.



*Figure 2.* The Video Lander.

The Video Lander was utilized from 2012-2016 to assess overfished rockfish populations in Central California. During that time, over 1500 underwater visual surveys were conducted. I used video observations collected from 2013-2014 for data analysis. The 700 visual surveys used for this thesis were collected aboard the F/V Donna Kathleen from May 2013 to October 2014. Data collection took place during spring, summer, and fall seasons, with rough seas preventing data collection during winter months (November - February). A live video feed came through an umbilical cable and was recorded onboard and watched by two science crew members while two others were on deck assisting in deploying, moving, and retrieving the Lander.

Once deployed, The Video Lander was slowly lowered to the bottom, taking 8-10 minutes to reach the seafloor depending on depth. Once securely on the bottom, lights were adjusted, and the motor was activated to begin rotation. We waited 1–3 minutes to allow sediment to settle before initiating data collection. During this interim period, the data recorders, captain, and crane operator communicated to ensure the Video Lander was sitting upright and secure and that there were no obstructions to camera rotation. Once this was complete and sediment had settled, video data recording and onboard data collection commenced.

The video cameras rotated a full 360°, and once they reach the end of the rotation, the motor switched direction and began the rotation in the opposite direction. Each full rotation lasted approximately one minute. Video was recorded for eight full rotations

(about eight minutes) based on species accumulation analyses showing a substantial decrease in the rate of influx of new fish after eight minutes (Denney 2017).

In each survey, the Video Lander was baited with two plastic jars containing about 450 g of chopped squid. Bait was used to bring fish closer to the camera for ease of identification. Often fish were disturbed when the Lander settled on the benthos, and bait helped to attract those fish back into the video frame. Many studies aiming to quantify demersal fish abundances have used baited video cameras (Brooks et al., 2011; Murphy and Jenkins, 2010; Stoner et al., 2008). Denney (2017) found no significant difference in the mean number of observed species or total mean number of fish observed between baited and un-baited Video Lander surveys in our study region.

### **Video Analysis**

All video files were exported daily from 64 GB Compact Flash cards on the Video Lander cameras to a hard drive after the completion of data collection. Video data were later analyzed in the lab using EventMeasure software in SeaGIS (SeaGIS Inc.). The video analyst referred to field datasheets for quality control to verify that all information matched between datasheets and videos by confirming data collection start and end times and reviewing notes.

Initially, all visible fish were counted and identified to the lowest taxonomic level by three people trained in west coast fish identification. Final fish counts were determined using the rotation in which the highest count of that species (MaxN) was recorded.

MaxN is defined as the maximum number of fish in a single frame during a video

recording. MaxN is a commonly used metric to count fish with stationary drop-cameras because it provides a conservative estimate by eliminating the possibility of counting a fish twice (Harvey et al., 2007). Here because we have a rotating camera system, we define MaxN as the maximum number of fish in a 360° rotation. With stationary cameras, fish situated next to and behind non-rotating drop cameras are not recorded because they are out of the field of view. Because the Video Lander has cameras on a rotating motor, using MaxN of the 360° rotation includes these fish that would have otherwise been excluded. Additionally, the number of identified fish would often differ from rotation to rotation, due to a fish having moved closer or farther away from the camera between rotations. Using MaxN of a rotation allows us to obtain the highest, most accurate count possible while still minimizing the chance of double-counting fish.

Paired calibrated stereo cameras determine precise 3D locations of fish, allowing for estimates of the distance of detection, area sampled, and thus density calculations. Paired calibrated cameras also provide accurate and precise fish length measurements (Harvey et al. 2004). We measured the total length (TL) of all fish to the nearest cm that were included in the MaxN statistic. Sometimes fish lengths could not be determined because either a) the entire fish was not captured by both cameras or b) the fish was too far from the cameras to get an accurate measurement. An annulus, or donut shaped area, was used to obtain density estimates. The inner radius was set by the closest point on the bottom that was recorded by the Lander cameras and the outer radius was set by

determining the distance that encompassed 95% of all observations for a given species (Figure 3).

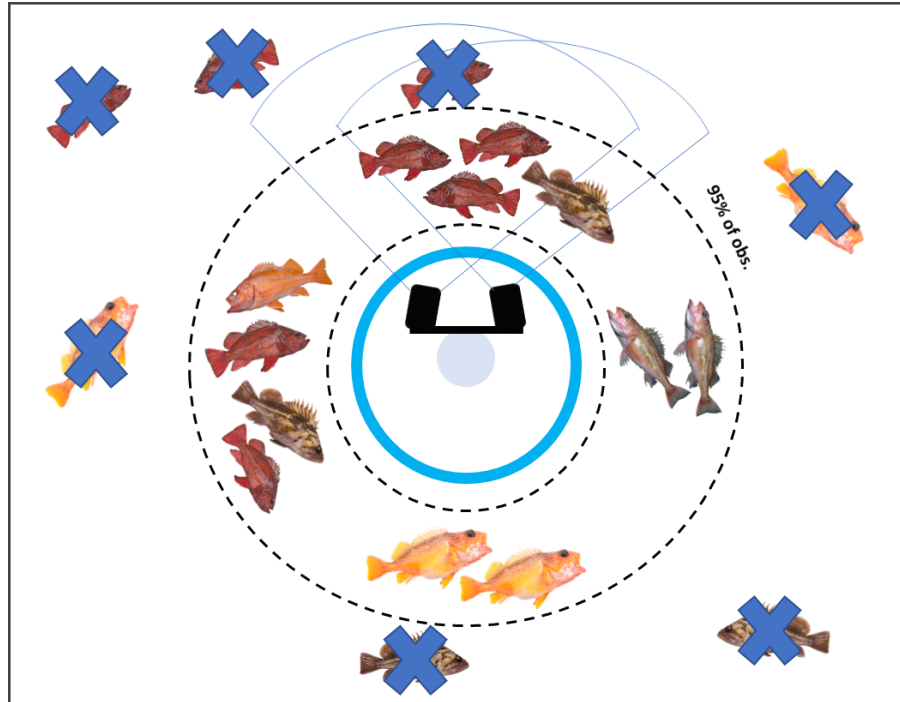


Figure 3. Diagram depicting how area figures were obtained for each species.

Observed habitat variables were recorded during video analysis using set protocols. Substrate was used to determine hard, mixed, and soft bottoms. Bottom type was classified as hard bottom if  $\geq 50\%$  of the bottom substrate was rock ridge or boulder, mixed bottom if it was  $\geq 50\%$  cobbles or pebbles, and soft bottom if it was  $\geq 50\%$  soft sediment (sand or mud). Relief categories included high, medium, and low, and were determined using measurements of local relief of substrates using EventMeasure. Relief was determined as low if substrate height was between 0-25 cm, medium if it was between 25-150 cm, and high if the substrate height was  $>150$  cm. Rugosity was

classified as low if the bottom was flat and had no structure that fish could use as a refuge. Rugosity was classified as medium if there were small depressions or holes in the substrate (< 25 cm at largest point of diameter) that small fish such as Pygmy Rockfish could use as refuge. Rugosity was classified as high if there were depressions or holes in the substrate that larger fish, such as Vermilion Rockfish or Lingcod, could use as refuge (>25 cm at largest point of diameter).

### **Data Preparation in ArcGIS**

Bathymetric data collected from multibeam echosounders were used to create precise Digital Elevation Models (DEMs) of the seafloor. The 1 m, 5 m, and 10 m resolution DEMs used for analyses were made available through the Monterey Bay Aquarium Research Institute (MBARI), California State University Monterey Bay Seafloor Mapping Lab (CSUMB SFML) and NOAA's National Centers for Environmental Information (NCEI, formerly National Geophysical Data Center [NGDC]). The DEMs for large regions of the central coast were obtained from NCEI at 10 m resolutions (<https://maps.ngdc.noaa.gov/viewers/bathymetry/>). The DEMs for Portuguese Ledge used in this research were created at 1 m, 5 m, and 10 m resolutions by MBARI, SFML (<https://walrus.wr.usgs.gov/mapping/csmp/gis.html>), and NOAA's NCEI, respectively. All data in ArcGIS were projected to WGS 84/UTM zone 10N with bounds at -126.0000, 34.4000, -120.0000, and 77.0000.

I used various tools within ArcGIS to create the slope, aspect, rugosity, and TPI DEMs from the base bathymetry DEMs. Slope was calculated with the "slope" tool, which gives



each cell a value by determining the steepest slope between the cell and its 8 nearest neighbors. Aspect was calculated with the “aspect” tool, which works by identifying the down-slope direction of the maximum rate of change between a cell and its neighbors. Rugosity was calculated using the Vector Ruggedness Measure (VRM) tool. VRM determines rugosity by measuring the variation in the three-dimensional (3D) orientation of a cell compared to its neighbors. VRM uses vector analysis and measures the dispersion of vectors to determine relative differences in 3D orientation. Values can range from 0 (no terrain variability) to 1 (complete terrain variability), however values typically fall between 0 - 0.4 for most terrain. Rugosity measurements are often calculated using the surface area to planar area ratio, however these estimates are strongly affected by slope. VRM does a good job at teasing out the effects of slope, and thus is a more accurate representation of terrain ruggedness (Sappington et al. 2007).

Topographic Position Index (TPI) and Benthic Position Index (BPI) both refer to the relative elevation of any given cell in comparison to its neighboring cells. BPI can be calculated at various scales, but I divided data into fine-scale and broad-scale BPIs. The fine-scale BPI was calculated by comparing the elevation of any given cell to nearby cells and determining differences in local elevation. Broad-scale BPI compares a cell's elevation to the elevation of cells farther away, using a larger neighborhood to determine relative elevation. In both cases, raw BPI at any given point was calculated as elevation – neighborhood mean elevation. High BPI values indicate higher elevation, low BPI values indicate low elevation, and a value of 0 means either the terrain is the same

elevation as the neighborhood, or that the cell in question is on a slope. Several large-scale seascape variables were also calculated. Distance to shoreline, distance to shelf edge, and distance to canyon heads were calculated using Euclidean Distance (i.e., straight-line distance).

Georeferenced 2013-2014 species observation data collected by the Video Lander were imported into ArcGIS. Species observations were overlaid onto the raster layers of the remotely sensed variables, and the value of each variable at each survey location was extracted onto the species observation file. In this way, remotely sensed variable information for each survey location could be obtained and used in analysis of species-habitat relationships.

### **Data Analysis**

**Species associations with observed habitat.** The Kruskal-Wallis Test was used to analyze the relationship between species density and bottom type, relief, and rugosity. The Kruskal-Wallis Test is a nonparametric test that can be used in lieu of an analysis of variance (ANOVA) when data do not meet the assumption of normal distribution. Additionally, Kruskal-Wallis tests can be used when determining differences in means of count and density data because these data are often skewed and contain many zeros.

The Wilcoxon-Mann-Whitney post hoc test was used to analyze differences in densities of each species over hard, mixed, and soft bottom habitats and areas of low, medium, and high relief and rugosity. The statistical software program JMP was used to run Kruskal-Wallis and Wilcoxon-Mann-Whitney post hoc tests.

**Species associations with remotely sensed habitat.** I used linear regressions to understand species associations with remotely sensed habitat variables. Simple linear regressions enabled an analysis of individual species relationships with each remotely sensed habitat variable. A principal component analysis (PCA) was also used to group remotely sensed variables based on the variation they describe. Additional linear regressions were performed using principal components as habitat variables. Data used in the PCA were log transformed. Linear regressions and PCA were performed using the statistical software program JMP.

**Comparison of species associations with observed vs. remotely sensed habitat.** To assess whether geomorphology is a good indicator of substrate type, I ran a canonical correspondence analysis (CCA) with both observed and remotely sensed variables. I conducted the CCA to visualize species relationships based on densities over both observed and remotely sensed habitat. The R statistical software package was used to run the CCA. Data used in the CCA were log transformed.

To evaluate each set of variables as a group, two sets of generalized linear models (GLMs) were run for each species: one using observed habitat variables as predictors and the other using remotely sensed habitat variables as predictors. GLMs are often used in predictive modeling of species distributions. GLMs do not force the data into unnatural scales, can handle data from several probability distributions (Guisan et al., 2002), and are recommended when abundance estimates are derived from counts (Guisan and Zimmerman, 2000). The amount of deviance explained by each model as

well as R-squared values can assist in understanding which habitat characteristics are better at explaining species density distributions.

Several metrics were used to compare model performance. Deviance is a direct measure of likelihood and a universal measure of a model's fit. The lower the deviance, the better the fit of the model. Akaike's information criterion (AIC) is another measure of deviance or model fit. AIC penalizes each additional predictor in the model, which helps discourage model overfitting. AIC is defined as deviance +  $2K$ , where  $K$  is the number of predictor variables. As with deviance, a lower AIC value indicates a better fit. R-squared values describe the proportion of the variance in the response variable that is explained by the predictor variables, which provides another indicator of model fit used to assess model performance. An R-squared value of 0 indicates that the regression line does not fit the data and an R-squared of 1 indicates that the regression line fits the data perfectly.

Model selection depends on several factors. The variance inflation factor (VIF) values indicate variable co-linearity. If VIF values were  $>7$ , the variable was removed to prevent co-linearity among predictors and the model was run again with the smaller set of variables. Stepwise backward selection was used in which all variables were included in each model to start with, and variables were removed until the best model with the lowest AIC was detected. Using model output summaries, I could assess which models explain more deviance in species densities, and which models had better model fit and lower error rates. In this way we can evaluate the strength of each predictor group.

**Creating predictive maps using MGET in ArcGIS 10.2.** The Marine Geospatial Ecology Toolbox (MGET) was used to create predictive models of species density and biomass. MGET is an open-source geoprocessing toolbox used in predictive modeling of species distributions. The statistical software package, R, is integrated within MGET and which allows it to be used in multivariate species distributions modeling (Roberts et al., 2010). MGET has been used in modeling leatherback turtle movements (Schick et al., 2013), Bluefin tuna larval distributions (Muhling et al., 2013), and albatross bycatch (Žydelis et al., 2011). MGET has also been used in predictive modeling studies to evaluate rockfish species distributions in central California (Bolton, 2014; Iampietro et al., 2008; Young et al., 2010). The MGET package allows for use of GLMs in predictive modeling. MGET is implemented on the ArcGIS platform to display species distribution models in the form of habitat suitability maps.

I ran Poisson GLMs to predict density for each species using the “Fit GLM” tool within MGET. Poisson GLMs assume the response variable has a Poisson distribution and are often used with count data, which are often zero-inflated. The stepwise backward function was used to determine which habitat variables were important, starting with all the predictor variables and taking them out one by one if non-significant ( $p$ -value  $>0.05$ ). Data were not transformed for preparation for the GLMs. The log-link function was used within the model.

I then used the “Predict GLM from Table” tool to test the model. This tool predicts the response variable for every survey point and uses statistics such as error rates and

R-squared values to assess how well the model's predictions match the actual observed values in those same locations. Twenty percent of the data were set aside to test the performance of the model. The rate at which predicted density values match the actual presence and absence values and the degree to which they differ determine model performance and accuracy.

The "Predict GLM from Rasters Predictive mapping of species biomass at 1 m, 5 m, and 10 m " tool is then used to create a habitat suitability layer indicating predicted density of each species. This habitat layer is based on the combined strength of the relationships between the density of fish and each predictor variable resulting from the GLM. This tool will output a continuous prediction map with a predicted density value for each pixel of the map.

**Model testing.** To conduct practical model testing, I created a model with species observations from one year and compared density predictions to actual densities observed the following year. A Poisson GLM predicting species density was created for each species using 2013 species observation data. Predictive maps of species density were made, and predictions were compared to 2014 observations at 2014 survey locations. If the models have high predictive power, the models I created from 2013 data should accurately predict 2014 fish densities.

**Influence of map resolution on predictions.** To test the effect of map resolution on species-habitat associations, I ran a biomass model for each species using data from the entire study area and created predictive maps of species biomass at Portuguese Ledge

using 1 m, 5 m, and 10 m resolution bathymetry maps. One model used for each species was applied to three levels of map resolution to assess the differences in predictions resulting from using maps of different cell size. Poisson GLMs were used in MGET predicting species biomass using 2013 and 2014 species biomass observations.

I used published length/weight relationship indices for each species (Arora, 1951; Keller et al., 2012; Lea et al., 1999) to calculate biomass of each species at Portuguese Ledge. First, I calculated the average length of each species over all drops. Then I calculated the weight of each individual at the average length using the length-weight indices for each species. Finally, species biomass of each video survey was calculated by multiplying the average fish weight by the number of fish seen in the video survey.

Using biomass estimates from the predictive maps, biomass was summed over the entire predictive map using 1 m, 5 m, and 10 m resolution predictor raster layers. Biomass estimates for each map were compared for each species to assess differences in total biomass estimates that are caused by map resolution changes. There is a larger area mapped at 5 m and 10 m resolutions, so these maps were scaled down to the size of the 1 m resolution map (~900 km<sup>2</sup>) so that biomass estimates could be compared over the same area. Total biomass over hard bottom was calculated for each species at each map resolution. Hard and soft bottom were delineated on the map, and species biomass was predicted over the area of hard bottom to produce an estimate of biomass over hard bottom.

## Results

### Field Sampling

Visual surveys occurred in May, July, September, and October of 2013 and 2014. The Video Lander was deployed 700 times from the FV Donna Kathleen, over a total of 91 days in 2013-2014. In total, 4,618 fish were identified from the visual surveys (Table 1). Vermilion Rockfish were the most abundant fish species observed in the visual surveys, making up 27% (1,261 fish) of all identified fishes, followed by Greenspotted Rockfish (1,101 fish) and Canary Rockfish (1,063 fish). Copper Rockfish were the least abundant species observed in the visual surveys (238 fish), comprising only 5% of observed fishes. Greenstriped Rockfish comprised ~8% of identified fish of the six species (364 fish) and Sanddab made up ~11% (495 fish) of identified fish.

Table 1

#### *Number of Study Species Identified in Visual Surveys*

<i>Scientific Name</i>	<i>Common name</i>	<i>Number seen</i>
<i>Sebastes pinniger</i>	Canary Rockfish	1,063
<i>Sebastes caurinus</i>	Copper Rockfish	238
<i>Sebastes chlorostictus</i>	Greenspotted Rockfish	1,101
<i>Sebastes elongatus</i>	Greenstriped Rockfish	364
<i>Sebastes miniatus</i>	Vermilion Rockfish	1,261
<i>Citharichthys sordidus</i>	Pacific Sanddab	495
<i>Total Fish</i>		4,618

Visual surveys with the Video Lander were conducted throughout the central coast. The northern end of the survey area was just north of San Francisco and the southern end was near Cape San Martin (Figure 1). Video surveys were distributed along the



length of the central coast but were concentrated on rocky habitats on the deeper continental shelf and around the shelf edge. Each video survey serves as an independent replicate.

Sampling effort was spread somewhat evenly over the categories of observed habitats (Figure 4). A total of 298 surveys were conducted over hard bottom, 168 over mixed bottom, and 233 over soft bottom habitats. Of the 699 video surveys, 194 surveys were conducted in areas of high relief, 212 in areas of intermediate relief, and 293 over low relief areas. Rugosity was the most unevenly sampled (given the current classification for high, medium, and low relief) observed habitat characteristic, with 62% of surveys (436 surveys) occurring in low rugosity habitat and only 10% (72 surveys) occurring in high rugosity habitat.

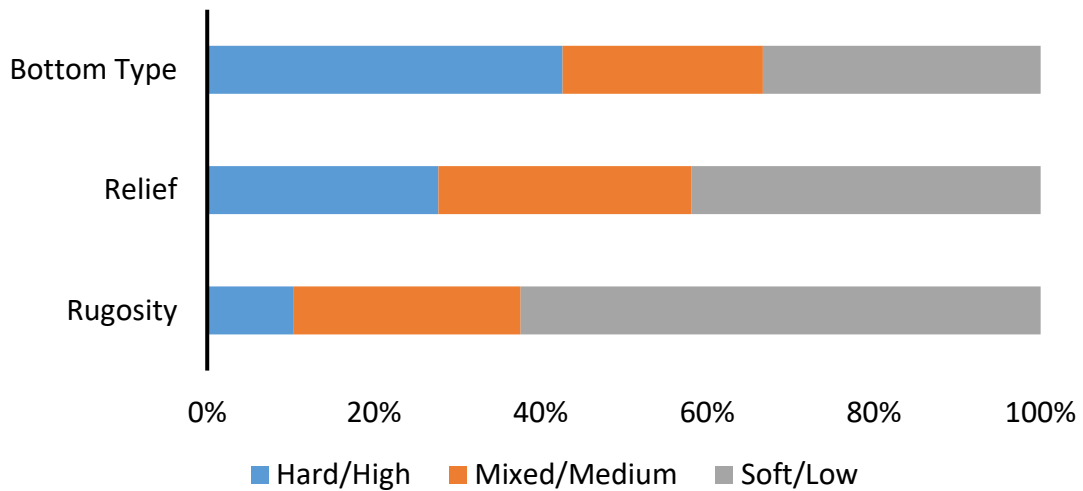


Figure 4. The distribution of sampling effort over observed habitat.

## Species Associations with Observed Habitat

**Kruskal-Wallis tests.** Data used in the Kruskal-Wallis tests were not transformed and zeros were not removed. P-values, R-squared values, and F-ratios were used to assess the strength of associations with each observed habitat variable and each species. Standard error was also calculated.

**Canary Rockfish.** The highest mean densities of Canary Rockfish occurred over hard bottom, low relief, and high rugosity habitats. Kruskal-Wallis tests found significant differences in Canary Rockfish densities with bottom type ( $X^2_2 = 31.2$ ,  $p < 0.0001$ ), relief ( $X^2_2 = 21.3$ ,  $p < 0.0001$ ), and rugosity ( $X^2_2 = 23.0$ ,  $p < 0.0001$ ). Canary Rockfish were seen in similar densities over hard (5.37 fish/100 m<sup>2</sup>, SE  $\pm$  0.65) and soft bottoms (5.35 fish/100 m<sup>2</sup>, SE  $\pm$  1.76), and in only slightly lower densities on mixed bottom habitats (3.88 fish/100 m<sup>2</sup>, SE  $\pm$  0.72). A Wilcoxon post hoc test found a significant difference in Canary densities between hard and mixed bottoms ( $p = 0.0151$ ), and mixed and soft bottoms ( $p = 0.0081$ ).

Canary Rockfish mean densities were similar over low (5.33 fish/100 m<sup>2</sup>, SE  $\pm$  0.80) and medium (5.27 fish/100 m<sup>2</sup>, SE  $\pm$  1.57) relief habitats, and only slightly lower over high relief habitats (4.23 fish/100 m<sup>2</sup>, SE  $\pm$  0.72) (Figure 5a). Significant differences were seen between Canary densities on high and low relief areas ( $p < 0.0001$ ) and medium and low relief areas ( $p < 0.0001$ ). There was a small difference in mean densities of Canary Rockfish over varying levels of rugosity. Mean density of Canary Rockfish was highest over high rugosity bottoms (6.15 fish/100 m<sup>2</sup>, SE  $\pm$  1.50), and slightly lower over medium

(4.99 fish/100 m<sup>2</sup>, SE ± 0.99) and low rugosity bottoms (4.82 fish/100 m<sup>2</sup>, SE ± 0.79) (Figure 5). Densities in high rugosity areas were significantly higher than those over low rugosity habitats (p<0.0001) and medium rugosity habitats (p=0.0003) based on a Kruskal-Wallis Wilcoxon post hoc test.

**Copper Rockfish.** The mean density of Copper Rockfish was high over hard and mixed bottoms, areas of high and medium relief, and high and medium rugosity habitats. Using Kruskal-Wallis tests, significant differences in Copper Rockfish densities were found with bottom type ( $X^2_2 = 20.6$ , p< 0.0001), relief ( $X^2_2 = 15.4$ , p= 0.0004), and rugosity ( $X^2_2 = 23.8$ , p< 0.0001). Copper Rockfish mean densities followed a linear trend with bottom type such that densities increased with bottom hardness. Highest mean density occurred over hard bottom (2.04 fish/100 m<sup>2</sup>, SE ± 0.27) and lowest mean density over soft bottoms (0.84 fish/100 m<sup>2</sup>, SE ± 0.19) (Figure 5b). Densities were found to be significantly higher over hard bottoms than over soft sediments (p< 0.0001) or mixed bottoms (p = 0.0237) based on the Wilcoxon post hoc test. Mean density of Copper Rockfish was highest over medium relief habitat (2.06 fish/100 m<sup>2</sup>, SE ± 0.19), slightly lower over high relief habitat (1.54 fish/100 m<sup>2</sup>, SE ± 0.26), and lowest over low relief habitat (0.96 fish/100 m<sup>2</sup>, SE ± 0.32). Densities were significantly higher over medium relief than over low relief habitats (p = 0.0002) and significantly higher over high relief than low relief habitats (p = 0.0020). Copper Rockfish densities followed a similar linear trend with rugosity as with bottom type, such that highest densities

occurred over highly rugose bottoms (2.55 fish/100 m<sup>2</sup>, SE ± 0.44) and lowest densities occurred over areas of low rugosity (1.22 fish/100 m<sup>2</sup>, SE ± 0.28) (Figure 5b).

**Greenspotted Rockfish.** Kruskal-Wallis tests showed significant differences in Greenspotted Rockfish densities for bottom type ( $X^2_2 = 18.0$ ,  $p < 0.0001$ ), relief ( $X^2_2 = 17.2$ ,  $p = 0.0002$ ), and rugosity ( $X^2_2 = 16.0$ ,  $p < 0.0003$ ). Mean density of Greenspotted Rockfish was highest over hard bottoms (7.31 fish/100 m<sup>2</sup>, SE ± 1.13) and only slightly lower over mixed bottoms (7.21 fish/100 m<sup>2</sup>, SE ± 1.24). Greenspotted Rockfish were observed in unusually high densities on a few occasions, over both hard and mixed bottoms (142.4 fish/100 m<sup>2</sup> and 138.7 fish/100 m<sup>2</sup>, respectively). In contrast, the mean density of Greenspotted Rockfish observed over soft bottoms was much lower (0.71 fish/100 m<sup>2</sup>, SE ± 0.67) (Figure 5c). Greenspotted Rockfish densities were significantly higher over hard bottom than soft bottom ( $p = 0.0046$ ) and significantly higher over mixed bottom and soft bottom ( $p < 0.0001$ ).

Highest mean density was observed over intermediate levels of relief (9.32 fish/100 m<sup>2</sup>, SE ± 0.87). Mean density over high and low relief areas (3.57 fish/100 m<sup>2</sup>, SE ± 0.82 and 4.97 fish/100 m<sup>2</sup>, SE ± 1.53, respectively) were about half of mean density over intermediate relief. Densities over medium relief areas were significantly higher than densities over high relief habitat ( $p = 0.0001$ ) and those over low relief habitat ( $p = 0.0015$ ) based on a Wilcoxon post hoc test. Patterns of density distribution of Greenspotted Rockfish were similar with rugosity as relief. Mean density of Greenspotted Rockfish was highest over intermediate levels of rugosity (8.41 fish/100

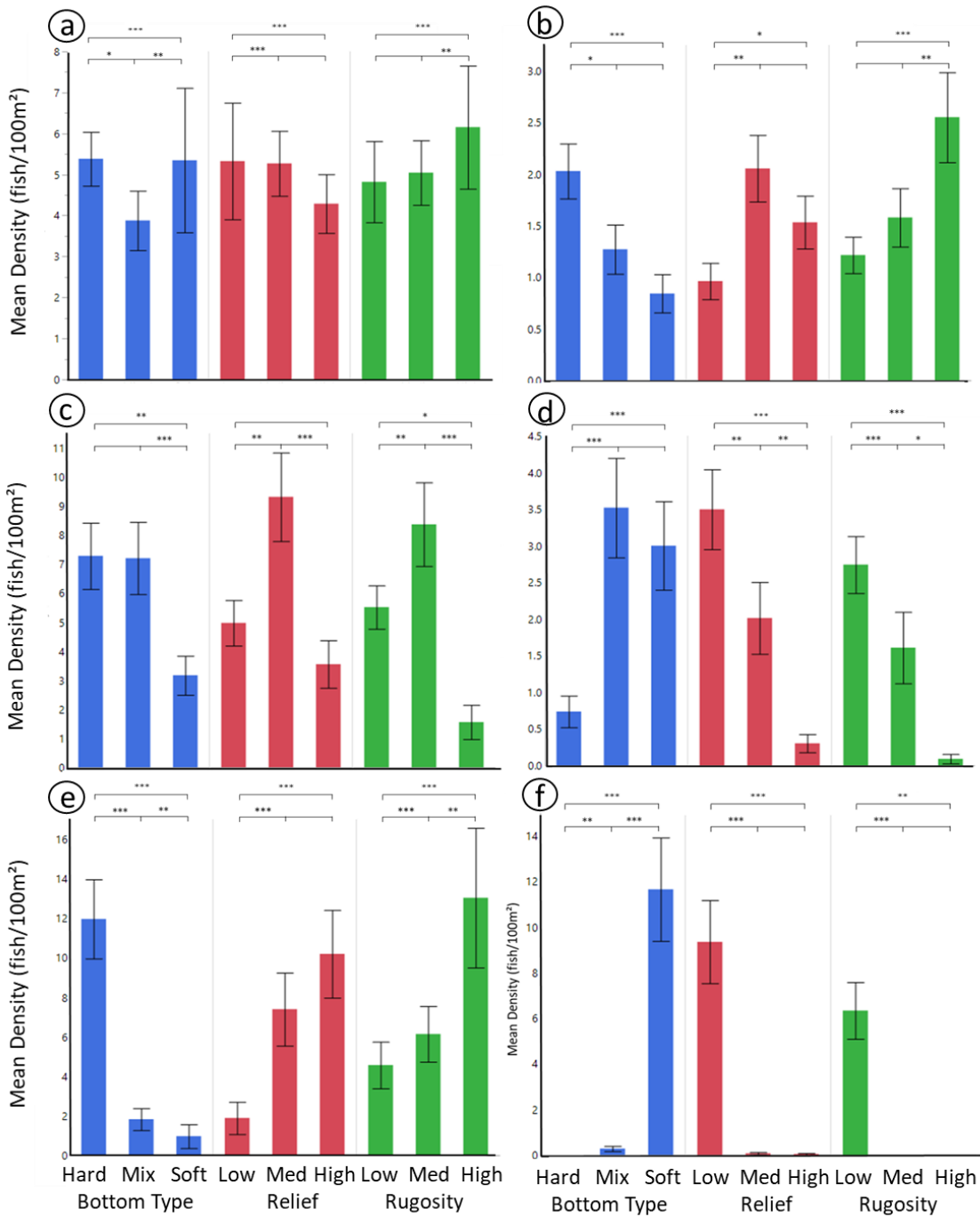
m<sup>2</sup>, SE ± 0.75), lower over low rugosity habitat (5.52 fish/100 m<sup>2</sup>, SE ± 1.44), and lowest in high rugosity habitat (1.5 fish/100 m<sup>2</sup>, SE ± 0.59) (Figure 5c). Densities were significantly higher with medium rugosity than with high rugosity (p = 0.0002) or low rugosity (p = 0.0065). Densities were also significantly higher over low relief areas than high relief areas (p= 0.0209).

***Greenstriped Rockfish.*** Using Kruskal-Wallis tests, significant differences in Greenstriped Rockfish densities were found for bottom type ( $X^2_2 = 57.5$ ,  $p < 0.0001$ ), relief ( $X^2_2 = 49.8$ ,  $p = 0.0001$ ), and rugosity ( $X^2_2 = 29.8$ ,  $p < 0.0001$ ). Greenstriped Rockfish mean densities were highest over mixed bottoms, low relief, and low rugosity. Mean density of Greenstriped Rockfish was highest over mixed bottoms (3.52 fish/100 m<sup>2</sup>, SE ± 0.68), and lower over soft (1.24 fish/100 m<sup>2</sup>, SE ± 0.61) and hard (0.74 fish/100 m<sup>2</sup>, SE ± 0.22) bottoms. Densities over mixed bottoms were significantly higher than densities over hard and soft bottom according to a Wilcoxon post hoc test ( $p < 0.0001$ ). A linear relationship was observed between Greenstriped densities and relief and rugosity such that densities increased with decreasing relief and rugosity. Mean density of Greenstriped Rockfish was highest over low relief, low rugosity habitat ((3.50 fish/100 m<sup>2</sup>, SE ± 0.49), (2.74 fish/100 m<sup>2</sup>, SE ± 0.48)), lower over medium relief, medium rugosity habitat ((2.01 fish/100 m<sup>2</sup>, SE ± 0.60), (1.62 fish/100 m<sup>2</sup>, SE ± 0.39)), and lowest over high relief, high rugosity habitat ((0.30 fish/100 m<sup>2</sup>, SE ± 0.12), (0.09 fish/100 m<sup>2</sup>, SE ± 0.06)) (Figure 5d). In both cases, Greenstriped Rockfish densities over low rugosity and

low relief were significantly higher than densities over high relief and high rugosity ( $p < 0.0001$ ) (Figure 5d).

**Vermilion Rockfish.** Vermilion Rockfish densities followed the expected trend of being higher in hard bottom, high relief and highly rugose habitats. Using Kruskal-Wallis tests, significant differences in Vermilion Rockfish densities were found with bottom type ( $X^2_2 = 100.6$ ,  $p < 0.0001$ ), relief ( $X^2_2 = 78.0$ ,  $p = 0.0001$ ), and rugosity ( $X^2_2 = 91.8$ ,  $p < 0.0001$ ). Mean density of Vermilion Rockfish was highest over hard bottom habitat (12.01 fish/100 m<sup>2</sup> SE  $\pm$  2.00) followed by soft bottom (6.13 fish/100 m<sup>2</sup>, SE  $\pm$  0.60) and was lowest over mixed bottom habitats (1.82 fish/100 m<sup>2</sup>, SE  $\pm$  0.55) (Figure 5e). There was a significant difference in densities between soft and mixed bottoms ( $p = 0.0002$ ), mixed and hard bottoms ( $p < 0.0001$ ), and soft and hard bottoms ( $p < 0.0001$ ) found using a Wilcoxon post hoc test. Mean density of Vermilion Rockfish was highest in high relief habitats (10.25 fish/100 m<sup>2</sup>, SE  $\pm$  2.22), slightly lower in mixed relief habitats (7.39 fish/100 m<sup>2</sup>, SE  $\pm$  0.90), and lowest in low relief habitats (1.89 fish/100 m<sup>2</sup>, SE  $\pm$  1.85). There was a significant difference in densities between high and low relief areas ( $p < 0.0001$ ) and medium and low relief areas. Mean density of Vermilion Rockfish was highest over high rugosity habitats (13.04 fish/100 m<sup>2</sup>, SE  $\pm$  3.53), followed by intermediate rugosity habitats (6.18 fish/100 m<sup>2</sup>, SE  $\pm$  1.18), and lowest over low rugosity habitats (4.57 fish/100 m<sup>2</sup>, SE  $\pm$  1.41) (Figure 5e). Significant differences in densities were found between high and low rugosity areas ( $p < 0.0001$ ), high and medium rugosity areas ( $p = 0.0018$ ) and medium and low rugosity areas ( $p < 0.0001$ ).

***Pacific Sanddab.*** Pacific Sanddab occurred almost solely on soft bottom, low relief, and low rugosity habitats. Using Kruskal-Wallis tests, significant differences in Pacific Sanddab densities were found with bottom type ( $X^2_2= 93.7$ ,  $p < 0.0001$ ), relief ( $X^2_2= 73.5$ ,  $p = 0.0001$ ), and rugosity ( $X^2_2= 38.1$ ,  $p < 0.0001$ ). No Sanddab were seen on hard bottom, and mean density was also very low over mixed bottoms (0.28 fish/100 m<sup>2</sup>, SE  $\pm$  0.11) (Figure 5). Densities on soft bottom habitat were significantly higher than those on hard bottom ( $p < 0.0001$ ) and mixed bottom ( $p < 0.0001$ ) using a Wilcoxon post hoc test. Mean Sanddab density was also very low in high (0.04 fish/100 m<sup>2</sup>, SE  $\pm$  0.04) and medium relief (0.08 fish/100 m<sup>2</sup>, SE  $\pm$  2.01) habitat and nonexistent in high and medium rugosity habitat (Figure 5f). Densities were significantly higher in low relief habitat than either medium or high relief habitat ( $p < 0.0001$ ), and significantly higher in low rugosity habitat than either medium or high rugosity habitat ( $p < 0.0001$  and  $p = 0.0011$ ).



Key: a) Canary Rockfish, b) Copper Rockfish, c) Greenspotted Rockfish, d) Greenstriped Rockfish, e) Vermilion Rockfish, f) Pacific Sanddab

Figure 5. Mean densities of all species over observed habitat with standard error.



## Species Associations with Remotely Sensed Habitat

**Linear regressions.** Data used in the linear regressions were not transformed. Surveys where the species did not occur (zeros) were removed to examine species-habitat relationships with remotely sensed habitat characteristics where species did occur. Metrics such as p-values were used to assess the significance of the linear relationship, while R-squared values were used to evaluate how well the data fit the linear model.

**Canary Rockfish.** Canary Rockfish densities showed little variation with respect to remotely sensed habitat variables. P-values showed that density distributions did not show dependence on fluctuations in these explanatory variables. All R-squared values were very low, showing that little variance in densities is explained by each of these variables individually (Table 2).

Table 2

*Linear regression analysis of Canary Rockfish Densities and Remotely Sensed Variables*

RS Variable	Relationship	p-value	R-squared	RMSE	F value ( $F_{1,699}$ )
Depth	N/A	0.153	0.010	0.298	2.052
Slope	N/A	0.262	0.006	0.298	1.268
Curvature	N/A	0.371	0.004	0.299	0.803
FS BPI	N/A	0.927	0.00004	0.299	0.009
BS BPI	N/A	0.595	0.001	0.299	0.284
VRM	N/A	0.810	0.0002	0.299	0.066
Dist. to Shore	N/A	0.120	0.012	0.298	2.435
Dist. to shelf edge	N/A	0.184	0.00002	0.298	1.780
Dist. to canyon	N/A	0.3018	0.00009	0.1777	3.1496

*Note.* RMSE is Root Mean Square Error. Values were rounded to three significant digits.

**Copper Rockfish.** Copper Rockfish densities did not show significant linear variation with most of the remotely sensed habitat variables. This is evidenced by high p-values and low R-squared and F-statistic values. The only remotely sensed habitat variable that was significant in determining Copper Rockfish densities was VRM (linear regression,  $F_{1,699} = 4.55$ ,  $R^2 = 0.03$ ,  $p = 0.035$ ). Although the p-value indicates significance, the R-squared value means that it only explains 3% of the variation in Copper Rockfish densities (Table 3).

Table 3

*Linear Regression Analysis of Copper Rockfish Densities and Remotely Sensed Variables*

RS Variable	Relationship	p-value	R-squared	RMSE	F value ( $F_{1,699}$ )
Depth	N/A	0.540	0.003	0.054	0.378
Slope	N/A	0.398	0.005	0.053	0.719
Curvature	N/A	0.207	0.012	0.053	1.612
FS BPI	N/A	0.325	0.007	0.053	0.975
BS BPI	N/A	0.125	0.017	0.053	2.384
VRM	Positive	0.035	0.032	0.053	4.559
Dist. to Shore	N/A	0.968	0.00001	0.054	0.002
Dist. to shelf edge	N/A	0.203	0.012	0.053	1.634
Dist. to canyon	N/A	0.559	0.003	0.054	0.342

*Note.* P-values indicating significant relationships are indicated in red. Values were rounded to three significant digits.

**Greenspotted Rockfish.** Greenspotted Rockfish densities showed significant variation with slope (linear regression,  $F_{1,699} = 15.28$ ,  $R^2 = 0.063$ ,  $p < 0.0001$ ), broad-scale BPI (linear regression,  $F_{1,699} = 6.36$ ,  $R^2 = 0.027$ ,  $p < 0.0123$ ), and distance to shoreline (linear regression,  $F_{1,699} = 50.86$ ,  $R^2 = 0.1$ ,  $p < 0.0001$ ) (Table 4). Although these

explanatory variables show significant influence on Greenspotted Rockfish density distributions, the R-squared values are very low. This shows that these variables each only explain a very small proportion of the variance in densities. High F-statistic values for slope and distance to shoreline support the low p-value and the rejection of the null hypothesis that these two variables are not related. Greenspotted Rockfish densities increased with distance to shoreline and decreased with increasing slope and broad-scale BPI.

Table 4

*Linear Regression Analysis of Greenspotted Rockfish Densities and Remotely Sensed Variables*

RS Variable	Relationship	p-value	R-squared	RMSE	F value ( $F_{1,699}$ )
Depth	N/A	0.832	0.0002	0.244	0.045
Slope	Negative	< 0.0001	0.063	0.236	15.288
Curvature	N/A	0.982	0.0001	0.244	0.0005
FS BPI	N/A	0.240	0.006	0.243	1.388
BS BPI	Negative	0.012	0.027	0.241	6.365
VRM	N/A	0.257	0.006	0.244	1.289
Dist. to shoreline	Positive	< 0.0001	0.182	0.221	50.866
Dist. to shelf edge	N/A	0.827	0.0002	0.244	0.048
Dist. to canyon	N/A	0.090	0.013	0.243	2.905

*Note.* P-values indicating significant relationships are indicated in red. Values were rounded to three significant digits.

**Greenstriped Rockfish.** Almost all the remotely sensed variables were not significant in describing Greenstriped Rockfish densities. The only variable which had a significant influence on Greenstriped densities is distance to shoreline, where densities increased with increasing distance from the shoreline (linear regression,  $F_{1,699} = 34.12$ ,  $R^2 = 0.21$ ,  $p <$

0.0001) (Table 5). A highly significant p-value, moderate R-squared value, and high F-statistic value indicate that fluctuations in densities are dependent on the distance to the shoreline.

Table 5

*Linear Regression Analysis of Greenstriped Rockfish Densities and Remotely Sensed Variables*

RS Variable	Relationship	p-value	R-squared	RMSE	F value ( $F_{1,699}$ )
Depth	N/A	0.301	0.008	0.073	1.079
Slope	N/A	0.228	0.011	0.135	1.466
Curvature	N/A	0.189	0.013	0.135	1.743
FS BPI	N/A	0.374	0.006	0.135	0.797
BS BPI	N/A	0.078	0.024	0.134	3.152
VRM	N/A	0.331	0.007	0.135	0.951
Dist. to Shore	Positive	< 0.0001	0.208	0.121	34.128
Dist. to shelf edge	N/A	0.698	0.001	0.135	0.151
Dist. to canyon	N/A	0.344	0.007	0.135	0.904

*Note.* P-values indicating significant relationships are indicated in red. Values were rounded to three significant digits.

**Vermilion Rockfish.** Vermilion Rockfish densities show significant variation with respect to distance to shelf edge (linear regression,  $F_{1,699} = 4.47$ ,  $R^2 = 0.026$ ,  $p = 0.036$ ) and distance to canyon heads (linear regression,  $F_{1,699} = 22.23$ ,  $R^2 = 0.12$ ,  $p < 0.0001$ ). Vermilion Rockfish densities were found to decrease with increasing distance from the shelf edge and increase with increasing distance from a canyon head. Although Vermilion density distributions were influenced by several of the explanatory variables, low R-squared values indicate that these variables explain a small proportion of the variance in

densities. Distance to shelf edge explained 2.6% of variation in densities and distance to canyon head explained 11.75% (Table 6).

Table 6

*Linear Regression Analysis of Vermilion Rockfish Densities and Remotely Sensed Variables*

RS Variable	Relationship	p-value	R-squared	RMSE	F value ( $F_{1,699}$ )
Depth	N/A	0.182	0.011	0.442	1.799
Slope	N/A	0.119	0.015	0.441	2.461
Curvature	N/A	0.774	0.0005	0.444	0.083
FS BPI	N/A	0.555	0.002	0.444	0.349
BS BPI	N/A	0.317	0.006	0.443	1.007
VRM	N/A	0.098	0.016	0.441	2.770
Dist. to Shore	N/A	0.210	0.009	0.442	1.583
Dist. to shelf edge	Negative	0.036	0.026	0.241	4.471
Dist. to canyon	Positive	<0.0001	0.118	0.418	22.238

Note. P-values indicating significant relationships are indicated in red. Values were rounded to three significant digits.

**Pacific Sanddab.** Pacific Sanddab densities did not show any significant linear variation with respect to any remotely sensed habitat variables. The variables showing slight, but insignificant influence on Sanddab densities were slope (linear regression,  $F_{1,699} = 2.57$ ,  $R^2 = 0.044$ ,  $p = 0.114$ ) and broad-scale BPI (linear regression,  $F_{1,699} = 2.75$ ,  $R^2 = 0.046$ ,  $p = 0.102$ ). Also, low R-squared values show the small amount of variability in Sanddab densities that each variable explained (Table 7).

Table 7

*Linear Regression Analysis of Pacific Sanddab Densities and Remotely Sensed Variables*

RS Variable	Relationship	p-value	R-squared	RMSE	F value $F_{1,699}$
Depth	N/A	0.963	0.0001	0.564	0.002
Slope	N/A	0.115	0.044	0.552	2.571
Curvature	N/A	0.720	0.002	0.563	0.130
FS BPI	N/A	0.732	0.002	0.563	0.119
BS BPI	N/A	0.103	0.047	0.551	2.751
VRM	N/A	0.882	0.0004	0.564	0.022
Dist. to Shore	N/A	0.757	0.002	0.564	0.757
Dist. to shelf edge	N/A	0.543	0.007	0.562	0.375
Dist. to canyon	N/A	0.254	0.023	0.557	1.326

*Note.* Values were rounded to three significant digits.

**Summary.** The results of the linear regressions show that, in general, individual remotely sensed habitat characteristics do a poor job of describing species densities. While individual species relationships with some of the remotely sensed habitat characteristics displayed significant p-values, low R-squared values indicate that only small proportions of the spatial variation in density are explained by remotely sensed habitat variables. Greenspotted Rockfish densities showed more significant dependent relationships with remotely sensed habitat variables than any of the other species (Table 8).

Table 8

*Summary of Linear Regression Analysis*

	<i>Canary</i>	<i>Copper</i>	<i>Greenspotted</i>	<i>Greenstriped</i>	<i>Vermilion</i>	<i>Sanddab</i>
<i>Depth</i>						
<i>Slope</i>			- ***			
<i>Curvature</i>						
<i>FS BPI</i>						
<i>BS BPI</i>			- *			
<i>VRM</i>		+ *				
<i>Dist. shoreline</i>			+ ***	+ ***		
<i>Dist. shelf</i>					- *	
<i>Dist. canyon</i>					+ ***	

Note. A “+” indicates a positive relationship and a “-” indicates a negative relationship. Significant relationships are determined by p-values indicated in asterisks. If  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*). If  $p \leq 0.0001$  (\*\*\*)).










**Principal component analysis.** PCA was used to group remotely sensed variables and assess the variation in the data described by these groupings. The PCA takes potentially correlated variables and assembles them into principal components based on the variability they describe. These principal components can be used as variables themselves to reduce the number of variables in a model and reduce them to the ones that explain the most variation. I used the principal components as new habitat variables in linear regressions. The principal component scores represented combinations of the remotely sensed habitat variables.

The first two principal components accounted for a large portion of the variability in the data (46.9%). Principal component 1 (PC 1) accounted for 25.2% of the variability in the remotely sensed variables while principal component 2 (PC 2) accounted for the

other 21.7% of the variability in the remotely sensed data (Table 9). The first four principal components cumulatively describe over 72% of variability. The remaining principal components each describe less than 10% of variability in remotely sensed data.

Table 9

*Table of Eigenvalues Associated with each Principal Component*

	Eigenvalue	Percent		Cum Percent
1	2.2686	25.206		25.206
	1.9529	21.699		46.905
3	1.3446	14.940		61.844
4	0.9372	10.414		72.258
5	0.7116	7.907		80.165
6	0.6301	7.001		87.166
7	0.4633	5.148		92.314
8	0.3885	4.317		96.631
9	0.3032	3.369		100.000

*Note.* Percent = the percent of variability explained by each principle component.  
 Cum Percent = cumulative percent of variability explained with each additional principle component.



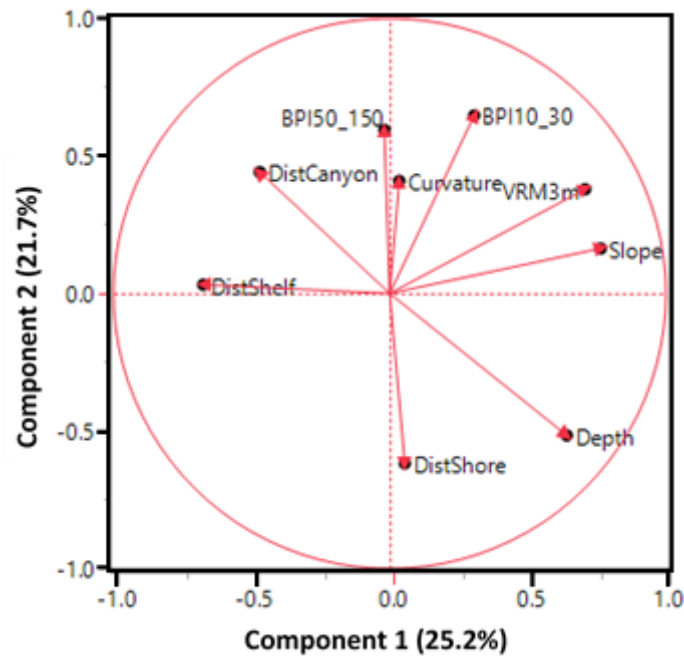


Figure 6. PCA plot.

A loading matrix and eigenvalue outputs were used to interpret the PCA plot (Figure 6). The loading values not only have directional eigenvector information but also combine magnitude and variance. PC 1 accounted for 25.2% of the variability in remotely sensed variables. Slope, depth, VRM, and distance to shelf edge, which loading values lie on the end of the range (either highest or lowest), described more variation than any other combinations of other variables (Table 10). PC 2 accounted for 21.7% of variability in the variables. The most important variables in PC 2 were fine and broad-scale BPI, distance to shoreline, depth, and distance to canyon heads. Distance to canyon head and depth appeared to be inversely related when looking at the plot (Figure 6), where drops further from canyon head were also shallower. Similarly, visual surveys conducted further from the shoreline had lower broad scale BPI values. This is

because as distance from the shoreline increases, the seafloor starts to slope down into submarine canyons, which would have low (negative) BPI values. Visual surveys conducted further away from the shelf edge had low slope values. These are probably areas along the continental shelf, which are flatter. Slope increases with proximity to the shelf edge and upper continental slope.

Table 10

*Table of Loadings (Eigenvectors \*  $\sqrt{\text{Eigenvalues}}$ ) for each Principal Component*

	P1	P2	P3	P4	P5	P6	P7	P8	P9
Depth	0.64	-0.52	0.20	0.07	0.25	0.09	-0.03	0.44	0.13
Slope	0.76	0.16	-0.28	0.13	0.21	-0.10	0.43	-0.07	-0.22
Curvature	0.03	0.41	0.41	0.15	0.004	-0.37	0.19	-0.05	0.21
BPI10_30	0.31	0.65	0.52	0.11	0.01	0.21	-0.26	0.07	-0.30
BPI50_150	-0.02	0.59	-0.01	-0.72	-0.05	0.23	0.21	0.15	0.09
VRM3m	0.71	0.38	-0.22	0.23	-0.04	0.32	-0.13	-0.23	0.29
Dist. Shore	0.05	-0.62	0.50	-0.30	0.31	0.26	0.05	-0.32	-0.04
Dist. Shelf	-0.67	0.03	0.11	0.47	-0.03	0.45	0.31	0.09	0.01
Dist. Canyon	-0.47	0.44	-0.23	0.05	0.71	-0.07	-0.11	0.01	0.06

*Note.* The value is the contribution of each variable to each principle component and includes variance and magnitude. Values were rounded to two significant digits.

Linear regressions conducted using principal components as habitat variables showed that the grouping of remotely sensed variables into principal components described more variation in densities and had stronger relationships with species densities than individual remotely sensed variables on their own. Canary Rockfish densities showed significant linear variation with principal component 4 (PC 4) (linear regression,  $F_{1,699} = 6.71$ ,  $R^2 = 0.01$ ,  $p = 0.0098$ ), PC 7 (linear regression,  $F_{1,699} = 4.13$ ,  $R^2 = 0.006$ ,  $p = 0.043$ ), and PC 8 (linear regression,  $F_{1,699} = 19.77$ ,  $R^2 = 0.027$ ,  $p < 0.0001$ ). The

strongest relationship occurred with PC 8, indicated by a large F statistic value, a higher R-square value, and a highly significant p-value. The low R-squared values are indicating that only a small amount of variation is being explained by these variables.

Copper Rockfish densities displayed significant variation with respect to PC 1 (linear regression,  $F_{1,699} = 17.53$ ,  $R^2 = 0.024$ ,  $p < 0.0001$ ), PC 2 (linear regression,  $F_{1,699} = 15.95$ ,  $R^2 = 0.022$ ,  $p < 0.0001$ ), and PC 8 (linear regression,  $F_{1,699} = 57.48$ ,  $R^2 = 0.076$ ,  $p < 0.0001$ ). P-values were all highly significant, however the F-statistic and R-squared value were highest in the linear regression with PC 8. This indicates that PC 8 explains more variation in Copper Rockfish densities than the other principal components.

Greenspotted Rockfish densities showed significant variation over PC 1 (linear regression,  $F_{1,699} = 35.79$ ,  $R^2 = 0.049$ ,  $p < 0.0001$ ), PC 2 (linear regression,  $F_{1,699} = 26.50$ ,  $R^2 = 0.037$ ,  $p < 0.0001$ ), PC 3 (linear regression,  $F_{1,699} = 31.96$ ,  $R^2 = 0.044$ ,  $p < 0.0001$ ), PC 4 (linear regression,  $F_{1,699} = 11.72$ ,  $R^2 = 0.017$ ,  $p = 0.0007$ ), and PC 6 (linear regression,  $F_{1,699} = 7.46$ ,  $R^2 = 0.01$ ,  $p = 0.0065$ ). PC 1 and PC 3 appeared to be the most influential variables for Greenspotted Rockfish. Although F values were high for many of these relationships and p-values indicated significant relationships, all R-squared values were low. Less than 5% of variation in densities was explained by any one principal component.

Greenstriped Rockfish densities showed significant variation over PC 2 (linear regression,  $F_{1,699} = 40.54$ ,  $R^2 = 0.055$ ,  $p < 0.0001$ ), PC 3 (linear regression,  $F_{1,699} = 25.75$ ,  $R^2 = 0.036$ ,  $p < 0.0001$ ), PC 4 (linear regression,  $F_{1,699} = 18.06$ ,  $R^2 = 0.025$ ,  $p < 0.0001$ ), PC 5

(linear regression,  $F_{1,699} = 11.02$ ,  $R^2 = 0.016$ ,  $p = 0.001$ ), and PC 6 (linear regression,  $F_{1,699} = 5.03$ ,  $R^2 = 0.007$ ,  $p = 0.025$ ). High F values and low p-values indicated significant dependent relationships. However, low R-squared values indicated that the variables did not explain much variation in Greenstriped Rockfish densities.

Vermilion Rockfish densities showed significant variation with PC 1 (linear regression,  $F_{1,699} = 10.28$ ,  $R^2 = 0.015$ ,  $p = 0.0014$ ), PC 2 (linear regression,  $F_{1,699} = 4.32$ ,  $R^2 = 0.006$ ,  $p = 0.038$ ), PC 5 (linear regression,  $F_{1,699} = 12.38$ ,  $R^2 = 0.017$ ,  $p = 0.0005$ ), PC 6 (linear regression,  $F_{1,699} = 7.64$ ,  $R^2 = 0.011$ ,  $p = 0.0059$ ), and PC 8 (linear regression,  $F_{1,699} = 5.38$ ,  $R^2 = 0.008$ ,  $p = 0.021$ ). Relationships between Vermilion Rockfish and principal components appeared weaker than those with other species, evidenced by lower F values and R-squared values and higher p-values.

Pacific Sanddab densities showed significant relationships with PC 2 (Linear regression,  $F_{1,699} = 6.56$ ,  $R^2 = 0.009$ ,  $p = 0.011$ ), PC 3 (linear regression,  $F_{1,699} = 5.53$ ,  $R^2 = 0.008$ ,  $p = 0.019$ ), PC 4 (linear regression,  $F_{1,699} = 4.32$ ,  $R^2 = 0.006$ ,  $p = 0.038$ ), and PC 7 (linear regression,  $F_{1,699} = 5.39$ ,  $R^2 = 0.007$ ,  $p = 0.021$ ). PC 2 was the most influential principal component in determining Sanddab density distributions.

Overall, linear regressions with remotely sensed habitat features did a better job at describing fish density distributions when grouped as principal components. Species densities showed significant variation with more variables when using principal components over individual remotely sensed features (Table 11). Generally, though, R-

squared values remained low, showing that the principal components still did a poor job or explaining variation in density distributions.

Table 11

*Summary of Species Relationships with Principal Components*

	<i>Canary</i>	<i>Copper</i>	<i>Greenspotted</i>	<i>Greenstriped</i>	<i>Vermilion</i>	<i>Sanddab</i>
<i>PC 1</i>		- ***	- ***		- *	
<i>PC 2</i>		+ ***	- ***	- ***	+ *	- *
<i>PC 3</i>			+ ***	+ ***		+ *
<i>PC 4</i>	- *		- ***	- ***		- *
<i>PC 5</i>				+ **	+ **	
<i>PC 6</i>			+ *	+ *	- *	
<i>PC 7</i>	- *					- *
<i>PC 8</i>	- ***	- ***			+ *	
<i>PC 9</i>						

Note. Significant relationships are determined by p-values indicated in asterisks. If  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*). If  $p \leq 0.0001$  (\*\*\*)

**Comparison of Species Associations with Observed vs. Remotely Sensed Habitat**

**Canonical correspondence analysis.** The CCA showed the relationships between species based on their densities over remotely sensed habitat variables. The vectors represent the directionality of the variables. Longer vectors signify a greater range of variability in values.

Pacific Sanddab and Greenstriped Rockfish fell in the upper left and lower left quadrants of the plot, in the direction of deep water that is further from shore and has low relief and soft bottoms. Copper and Vermilion Rockfish lay in the upper right and lower right of quadrat of the plot in the direction of high rugosity, high BPI areas (both fine-scale and broad-scale) that are further away from canyon heads. Based on the plot,

Copper and Canary Rockfish look to be in shallower areas of higher VRM and BPI that are far away from the continental shelf edge. Greenspotted Rockfish fell in the lower half of the plot and slightly into the bottom left quadrant, occurring further from the shoreline (Figure 7).

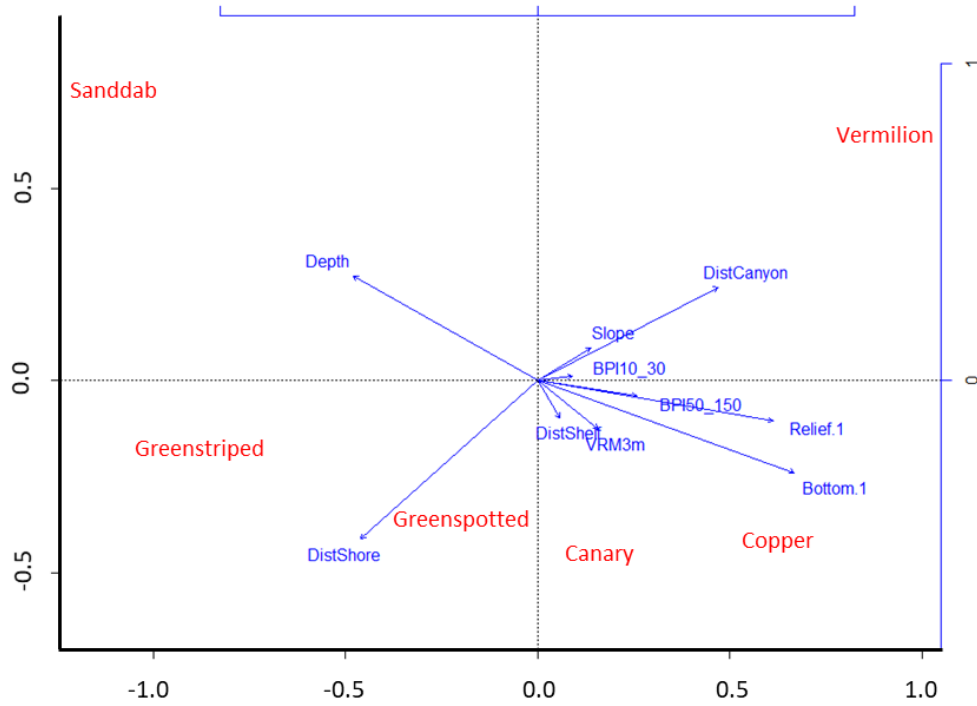


Figure 7. CCA plot.

Table 12

*Table of Canonical Correspondence Analysis Results*

	CCA1	CCA2	CCA3	CCA4	CCA5
Eigenvalue	0.516	0.266	0.23	0.029	0.016
Proportion Explained	0.488	0.252	0.217	0.027	0.015
Cumulative Proportion Explained	0.488	0.740	0.957	0.985	1

*Note.* Proportion explained is the proportion of variance explained by each axis in the CCA. Cumulative Proportion explained is the cumulative proportion of variance explained as axes are compiled.

About 35% of the variance in log-transformed species densities is explainable by the synthetic gradients created by the CCA. The first axis (CCA1) accounted for 48.8% of explained variance and the second axis (CCA2) accounted for 25.2% of the explained variance. The eigenvalue for CCA1 was fairly high (0.516), indicating that the first axis represents a strong gradient. The eigenvalues on the second and third axes indicated that these axes are much weaker, and the fourth and fifth axes much weaker still (Table 12).

**Generalized Linear Models.** To further understand similarities and differences between species relationships with observed versus remotely sensed habitat features, I ran GLMs to understand how using different habitat variables affected model outputs and measures of model fit. Models were run using observed habitat features as predictors and using remotely sensed habitat features as predictors. The best models using each set of predictors were selected for each species. Model summary outputs and test diagnostics provide metrics with which to compare model performance (e.g., percent deviance explained, AIC, R-squared values, and error rates)

**Canary Rockfish.** Bottom type, relief, and rugosity were all significant in the Canary Rockfish predictive model using observed habitat characteristics. Densities show positive relationships with low and medium relief habitat ( $p < 0.0001$ ), and negative relationships with low and medium rugosity habitats ( $p < 0.0001$ ) and soft and mixed bottoms ( $p = 0.018$  and  $p = 0.008$ , respectively). In the Canary Rockfish model using remotely sensed habitat characteristics, Canary Rockfish densities showed negative relationships with depth ( $p < 0.0001$ ), slope ( $p < 0.0001$ ), VRM ( $p = 0.058$ ), distance to shelf edge ( $p < 0.0001$ ), and distance to canyon heads ( $p < 0.0001$ ). Canary densities showed positive relationships with eastness ( $p < 0.0001$ ), northness ( $p < 0.0001$ ), broad-scale BPI ( $p < 0.0001$ ), and distance to shoreline ( $p < 0.0001$ ) (Table 13).



Table 13

*Variables Included in Final Models Predicting Canary Rockfish Densities*

Observed Habitat			Remotely Sensed Habitat		
<i>Relief (Low)</i>	+	***	<i>Depth</i>	-	***
<i>Relief (Med)</i>	+	***	<i>Slope</i>	-	***
<i>Rugosity (Low)</i>	-	***	<i>Eastness</i>	+	***
<i>Rugosity (Med)</i>	-	***	<i>Northness</i>	+	***
<i>Bottom (Soft)</i>	-	*	<i>BS BPI</i>	+	***
<i>Bottom (Mixed)</i>	-	*	<i>VRM</i>	-	.
			<i>Dist. to shoreline</i>	+	***
			<i>Dist. to shelf edge</i>	-	***
			<i>Dist. to canyon head</i>	-	***

*Note.* Plus and minus signs indicate the direction of the relationship and asterisks indicate p-values. If  $p \leq 0.1$  (.),  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*), if  $p \leq 0.0001$  (\*\*\*).

The Canary Rockfish model using observed habitat characteristics performed poorly, explaining 2.5% of deviance with a high AIC value (3095.5) and unbalanced deviance residuals. There was a low normalized root mean square error (NRMSE) (9.03%) in a model performance test but also a very low R-squared value of 0.002. The Canary Rockfish model using remotely sensed characteristics explained 25.5% deviance in densities (Figure 8). The R-squared value is slightly higher (0.027) than the R-squared value of the observed habitat model and the NRMSE remains low (9.08%) (Table 14).

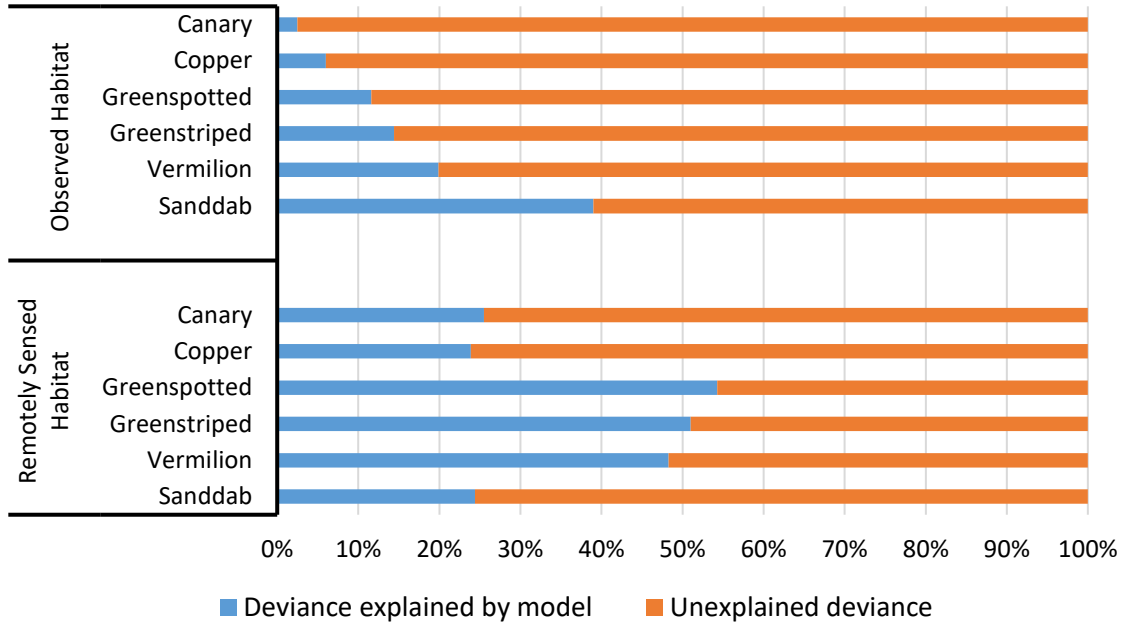


Figure 8. Proportion of deviance explained in the species' models using observed habitat characteristics (top) and remotely sensed habitat characteristics (bottom).

Table 14

*Model Performance Summary Statistics for Species Models*

	Deviance Explained		AIC		R-squared		NRMSE	
	OBS	RS	OBS	RS	OBS	RS	OBS	RS
Canary	2.5%	25.5%	3095.5	2491.6	0.002	0.001	9.03%	9.08%
Copper	6.0%	23.9%	884.14	508.22	0.016	0.100	13.98%	13.37%
Greenspotted	11.6%	54.3%	3429.3	2301	0.030	0.119	15.79%	19.61%
Greenstriped	14.4%	51.0%	1649.4	1080.9	0.040	0.121	12.83%	12.59%
Vermilion	19.9%	48.3%	3909.1	2665.8	0.045	0.074	11.66%	11.54%
Sanddab	39%	24.4%	1569.8	1915.3	0.067	0.002	9.42%	9.96%

Note. "OBS" stands for "observed models," or models made using observed habitat predictors. "RS" stands for "remotely sensed models."

**Copper Rockfish.** Relief, rugosity, and bottom type were all significant predictors in the Copper Rockfish predictive model using observed habitat features (Table 15).

Copper densities showed a positive relationship with areas of medium relief ( $p=0.0008$ ),

and negative relationships with medium and low rugosity areas ( $p= 0.0008$  and  $p= 0.015$ ), and soft and mixed bottoms ( $p= 0.004$  and  $p= 0.007$ ). In the predictive model using remotely sensed habitat characteristics, depth, eastness, northness, distance to shoreline and distance to canyon head were included in the final model. Copper Rockfish densities had negative relationships with depth and distance to shoreline ( $p< 0.0001$  and  $p= 0.058$ ) and positive relationships with eastness ( $p= 0.048$ ), northness ( $p= 0.003$ ), and distance to canyon head ( $p= 0.023$ ) (Table 15).

Table 15

*Variables Included in Final Models Predicting Copper Rockfish Densities*

Observed Habitat			Remotely Sensed Habitat		
<i>Relief (Med)</i>	+	**	<i>Depth</i>	-	***
	-	*	<i>Eastness</i>	+	*
<i>Rugosity (Med)</i>	-	**	<i>Northness</i>	+	*
<i>Bottom (Soft)</i>	-	*	<i>Dist. to shoreline</i>	-	.
<i>Bottom (Mixed)</i>	-	*	<i>Dist. to canyon head</i>	+	*

*Note.* Plus and minus signs indicate the direction of the relationship and asterisks indicate p-values. If  $p \leq 0.1$  (.),  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*), if  $p \leq 0.0001$  (\*\*\*)

The predictive model for Copper Rockfish using observed habitat characteristics performed relatively poorly, explaining 6.0% of the deviance in Copper Rockfish densities (Figure 8). A moderate AIC (884.14) and somewhat balanced deviance residuals indicate a moderate model fit and performance. In a model performance test

there was a low R-squared value (0.016) and a NRMSE of 13.98% (Table 14). The Copper Rockfish predictive model using remotely sensed habitat characteristics explained 23.9% of deviance (Figure 8). Deviance residuals were mostly balanced and the R-squared value was high ( $R^2 = 0.1$ ) in comparison to the Copper Rockfish model using observed habitat, as well as many of the other species models. NRMSE was 13.37% (Table 14).

***Greenspotted Rockfish.*** Relief, rugosity, and bottom type were all significant predictors in the Greenspotted Rockfish model using observed habitat characteristics (Table 16). Greenspotted Rockfish densities showed positive relationships with low and medium relief areas ( $p < 0.0001$ ) and low and medium rugosity areas ( $p < 0.0001$ ). Greenspotted Rockfish densities had negative relationships with soft and mixed bottoms ( $p < 0.0001$ ). In the Greenspotted Rockfish model using remotely sensed habitat features, Greenspotted Rockfish densities show positive relationships with curvature ( $p = 0.0001$ ), northness ( $p < 0.0001$ ), and distance to shoreline ( $p < 0.0001$ ). Greenspotted Rockfish densities exhibited negative relationships with depth ( $p < 0.0001$ ), slope ( $p < 0.0001$ ), eastness ( $p < 0.0001$ ), fine-scale BPI ( $p < 0.0001$ ), broad-scale BPI ( $p < 0.0001$ ), distance to shelf edge ( $p < 0.0001$ ), and distance to canyon heads ( $p < 0.0001$ ) (Table 16).

Table 16

*Variables Included in Final Models Predicting Greenspotted Rockfish Densities*

Observed Habitat			Remotely Sensed Habitat		
<i>Relief (Low)</i>	+	***	<i>Depth</i>	-	***
<i>Relief (Med)</i>	+	***	<i>Slope</i>	-	***
<i>Rugosity (Low)</i>	+	***	<i>Curvature</i>	+	***
<i>Rugosity (Med)</i>	+	***	<i>Eastness</i>	-	***
<i>Bottom (Soft)</i>	-	***	<i>Northness</i>	+	***
<i>Bottom (Mixed)</i>	-	***	<i>FS BPI</i>	-	**
			<i>BS BPI</i>	-	*
			<i>Dist. to shoreline</i>	+	***
			<i>Dist. to shelf edge</i>	-	***
			<i>Dist. to canyon head</i>	-	***

*Note.* Plus and minus signs indicate the direction of the relationship and asterisks indicate p-values. If  $p \leq 0.1$  (.),  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*), if  $p \leq 0.0001$  (\*\*\*).

The Greenspotted Rockfish model using observed habitat characteristics as predictors explained 11.6% deviance in distributions (Figure 8). Residual deviance (2865.9) and AIC (3429.3) were high and deviance residuals were slightly unbalanced. The model performance summary reported a low R-squared value (0.03) and a NRMSE of 15.79% (Table 14). The Greenspotted Rockfish model using remotely sensed habitat characteristics as predictors did a better job at explaining deviance in densities. This

model explained over 50% deviance (54.3%), explaining more deviance than any of the other species models. While residual deviance was high (1729.6), indicating a poor fit, the deviance residuals were balanced. The R-squared value is ( $R^2 = 0.119$ ) and the NRMSE was 19.61% (Table 14).

***Greenstriped Rockfish.*** Relief, rugosity, and bottom type were all significant in the Greenstriped Rockfish predictive model using observed habitat features. Greenstriped Rockfish densities showed positive relationships with low and medium relief areas ( $p < 0.0001$ ), low and medium rugosity areas ( $p = 0.056$  and  $p = 0.01$ ) and soft and mixed bottoms ( $p = 0.0007$  and  $p < 0.0001$ ). There were also several significant relationships in the model using remotely sensed habitat features as predictors. Greenstriped Rockfish densities showed positive relationships with curvature ( $p = 0.02$ ), northness ( $p = 0.08$ ), VRM ( $p = 0.02$ ), and distance to shoreline ( $p < 0.0001$ ). Densities showed negative relationships with depth ( $p = 0.08$ ), slope ( $p = 0.001$ ), fine-scale BPI ( $p = 0.0009$ ), distance to shelf edge ( $p = 0.003$ ), and distance to canyon heads ( $p < 0.0001$ ) (Table 17).

Table 17

*Variables Included in Final Models Predicting Greenstriped Rockfish Densities*

Observed Habitat			Remotely Sensed Habitat		
<i>Relief (Low)</i>	+	***	<i>Depth</i>	–	.
<i>Relief (Med)</i>	+	***	<i>Slope</i>	–	**
<i>Rugosity (Low)</i>	+	.	<i>Curvature</i>	+	*
<i>Rugosity (Med)</i>	+	*	<i>Northness</i>	+	.
<i>Bottom (Soft)</i>	+	**	<i>FS BPI</i>	–	**
<i>Bottom (Mixed)</i>	+	***	<i>VRM</i>	+	*
			<i>Dist. to shoreline</i>	+	***
			<i>Dist. to shelf edge</i>	–	*
			<i>Dist. to canyon head</i>	–	***

*Note.* Plus and minus signs indicate the direction of the relationship and asterisks indicate p-values. If  $p \leq 0.1$  (.),  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*), if  $p \leq 0.0001$  (\*\*\*).

A GLM using observed habitat features as predictors explained 14.4% of the variance in Greenstriped Rockfish densities (Figure 8). Residual deviance was high (1341) and deviance residuals were slightly unbalanced. The R-squared value was low (0.038) and the NRMSE (12.59%) was comparable to error rates seen in the other models. The Greenstriped Rockfish model using remotely sensed habitat characteristics explained just over half (51%) of the deviance in densities. Residual deviance and AIC were moderately high (766.56 and 1080.9) and deviance residuals were somewhat balanced.

The model performance summary reported an R-square value of 0.121 and an NRMSE of 12.83% (Table 14).

**Vermilion Rockfish.** Relief, rugosity, and bottom type were all significant predictors in the Vermilion Rockfish predictive model using observed habitat features. Vermilion densities were higher in low relief areas ( $p= 0.02$ ), and lower in medium relief areas ( $p= 0.0001$ ), areas of medium rugosity ( $p< 0.0001$ ), and soft and mixed bottoms ( $p< 0.0001$ ). The final model predicting Vermilion Rockfish densities using remotely sensed habitat features includes depth, slope, northness, distance to shoreline, distance to shelf edge, and distance to canyon heads. Vermilion Rockfish densities have a positive relationship with distance to canyon heads ( $p< 0.0001$ ) and negative relationships with depth ( $p< 0.0001$ ), slope ( $p= 0.01$ ), northness ( $p< 0.0001$ ), distance to shoreline ( $p< 0.0001$ ), and distance to shelf edge ( $p< 0.0001$ ) (Table 18).



Table 18

*Variables Included in Final Models Predicting Vermilion Rockfish Densities*

Observed Habitat			Remotely Sensed Habitat		
<i>Relief (Low)</i>	+	*	<i>Depth</i>	-	***
<i>Relief (Med)</i>	-	***	<i>Slope</i>	-	*
<i>Rugosity (Med)</i>	-	***	<i>Northness</i>	-	***
<i>Bottom (Soft)</i>	-	***	<i>Dist. to shoreline</i>	-	***
<i>Bottom (Mixed)</i>	-	***	<i>Dist. to shelf edge</i>	-	***
			<i>Dist. to canyon head</i>	+	***

*Note.* Plus and minus signs indicate the direction of the relationship and asterisks indicate p-values. If  $p \leq 0.1$  (.),  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*), if  $p \leq 0.0001$  (\*\*\*).

The GLM using observed habitat features to predict Vermilion Rockfish densities explained 19.9% of the deviance in Vermilion densities (Figure 8). Deviance residuals were unbalanced, and AIC was high (3499.5). The R-square value was low (0.045) indicating poor model fit, and NRMSE was 11.6%. The GLM using remotely sensed habitat features to predict Vermilion Rockfish densities performed better on almost all metrics. The model explained a larger amount of deviance in densities (48.4%) and had a lower AIC (2671.8). Additionally, deviance residuals were more balanced. The model performance summary reported a similar R-squared value (0.073) and NRMSE (11.54%) as the model using observed habitat characteristics (Table 14).

**Pacific Sanddab.** Sanddab densities exhibited a significant positive relationship with areas of low relief ( $p= 0.008$ ). In the predictive model using remotely sensed habitat features, Sanddab densities had positive relationships with depth ( $p< 0.0001$ ), eastness ( $p= 0.03$ ), northness ( $p< 0.0001$ ), and fine-scale BPI ( $p= 0.0006$ ). Sanddab densities showed negative relationships with slope ( $p< 0.0001$ ), broad-scale BPI ( $p< 0.0001$ ), distance to shoreline ( $p= 0.008$ ), and distance to shelf edge ( $p< 0.0001$ ) (Table 19).

Table 19

*Variables Included in Final Models Predicting Pacific Sanddab Densities*

Observed Habitat			Remotely Sensed Habitat		
<i>Relief (Low)</i>	+	*	<i>Depth</i>	+	***
<i>Relief (Med)</i>	-		<i>Slope</i>	-	***
<i>Bottom (Soft)</i>	+		<i>Eastness</i>	+	*
<i>Bottom (Mixed)</i>	+		<i>Northness</i>	+	***
			<i>FS BPI</i>	+	**
			<i>BS BPI</i>	-	***
			<i>Dist. to shoreline</i>	-	*
			<i>Dist. to shelf edge</i>	-	***
			<i>Dist. to canyon head</i>	-	***

*Note.* Plus and minus signs indicate the direction of the relationship and asterisks indicate p-values. If  $p \leq 0.1$  (.),  $p \leq 0.05$  (\*), if  $p \leq 0.001$  (\*\*), if  $p \leq 0.0001$  (\*\*\*).

The GLM using relationships with observed habitat to predict Pacific Sanddab densities explained 39% of the deviance in Sanddab densities, explaining more deviance in distributions than any of the other species models using observed habitat features as predictors (Figure 8). Deviance residuals were unbalanced, and the AIC was moderately high (1569.8). The model performance summary reported a low R-squared value (0.067) and a low NRMSE (9.42%). The GLM predicting Sanddab densities using remotely sensed habitat characteristics was the only model using remotely sensed habitat characteristics to explain less deviance than its observed habitat model counterpart, explaining 24.4% of deviance. AIC was high (1915.3) and deviance residuals were not balanced. The R-squared value was very low (0.002) and NRMSE (9.96%) was similar to NRMSE of the observed habitat model (9.42%) (Table 14).

### **Creating Predictive Maps using MGET in ArcGIS 10.2**

**Maps predicting species density.** Predictive maps of species density were created with predictive models using species relationships with remotely sensed habitat features. Maps were made for each section of the study site: North, Central, and South. Using species densities observed in each survey, A Hot Spot Analysis (Getis-Ord  $G_i^*$ ) was performed to identify “hot” and “cold” spots of high or low densities. Statistically, these spots are determined hot or cold if the differences in densities to adjacent areas are larger than you would find by random chance. A z-score is reported which represents statistical significance based on the Randomization Null Hypothesis computation. A

visual comparison can be made of where actual hot spots occurred versus where high densities are predicted to occur on the predictive map.

**Canary Rockfish.** The Canary Rockfish predictive model showed that Canary Rockfish density distributions were dependent on several of the predictor variables. Canary Rockfish densities were seen to increase with predictor variables eastness, northness, broad-scale BPI, and distance to shoreline, and decrease with increasing depth, slope, distance to shelf edge and distance to canyon heads. Canary predictive maps showed higher predicted densities around canyon heads and the continental shelf edge. When looking at the predictive map, high density locations appeared to occur solely on the continental shelf, while the continental slope showed low predicted densities (Figure 9). The negative relationship with depth and slope could be driving this result. The positive relationship with northness and eastness causes higher predictive values on northeast facing facies. Many observed cold spots occurred in areas with low predicted densities, however predicted hot spots did not always coincide with observed hot spots (Figure 9).

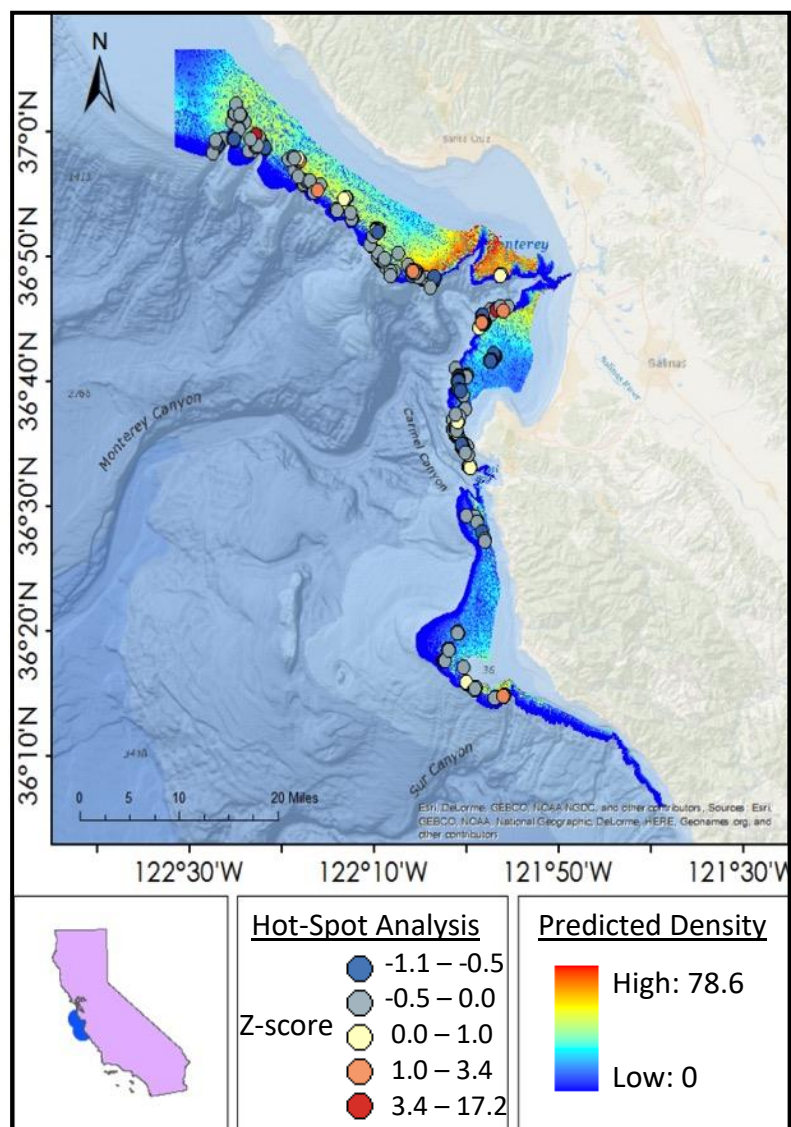


Figure 9. Map showing Canary Rockfish predicted densities in the Central location (Monterey Bay) from depths of 70-150 m overlaid with a hot spot analysis of observed densities. Predicted density is reported as fish/100 m<sup>2</sup>.

**Copper Rockfish.** The Copper Rockfish predictive model determined that Copper Rockfish densities displayed negative relationships with predictor variables depth and distance to shoreline, and positive relationships with northness, eastness, and distance to canyon heads. As depth and distance to shoreline increased, densities became smaller, and densities were greater further from canyon heads and on northeast facing facies. These results drove the distribution of predicted densities values on the predictive map. Highest predicted densities can be seen around the shoreline, in the shallower areas of the study sites. The predicted densities on the map appeared to fluctuate directly with depth. Depth explained a much larger proportion of the variance than any of the other predictors, which is probably driving this result (Figure 10). The hot spot analysis consistently matched up with locations of predicted densities. Low observed densities occurred in areas where densities were predicted to be low. Two hot spots indicating high densities can be seen on the predictive map. One hot spot occurred at Portuguese Ledge and the second occurred a little closer to the shelf edge. Densities are predicted to be higher at Portuguese Ledge (up to 1.6 fish/m<sup>2</sup>), which is consistent with the observed hotspot. However, model predicted densities predicted were low where the other hot spot occurred (Figure 10).

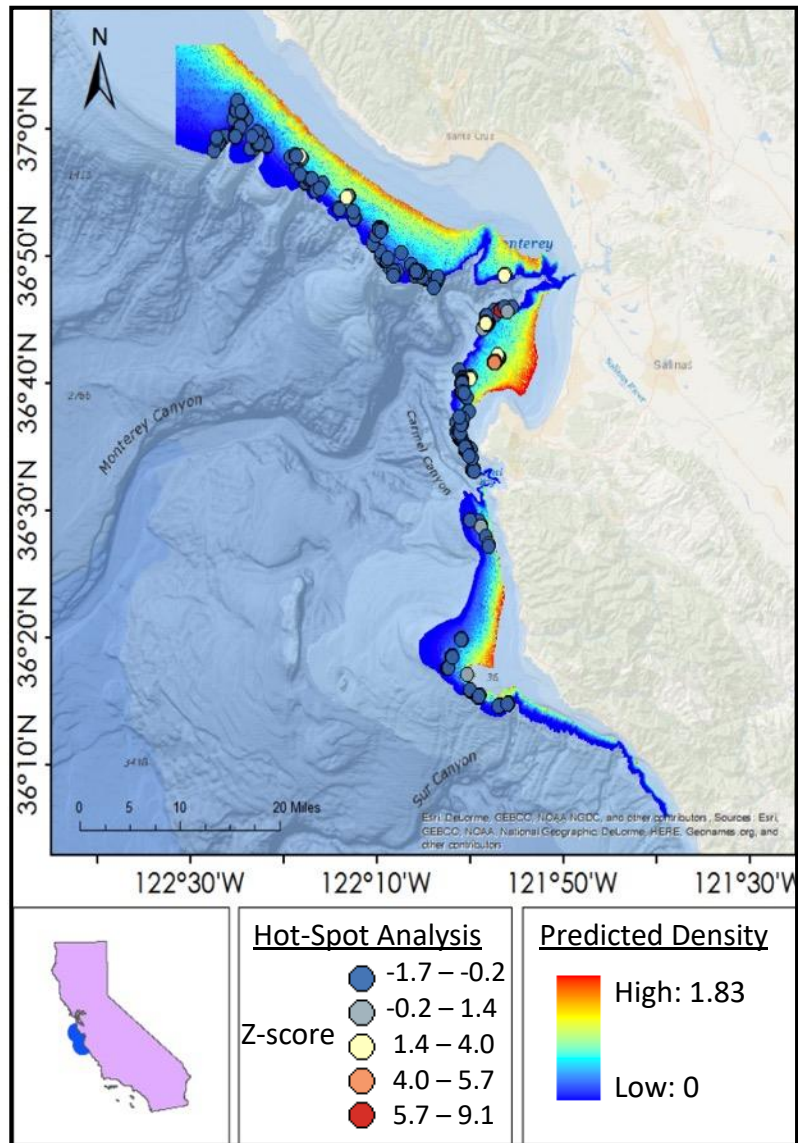


Figure 10. Map showing Copper Rockfish predicted densities in the Central location (Monterey Bay) overlaid with a hot spot analysis of observed densities. Predicted density is reported as fish/100 m<sup>2</sup>.

***Greenspotted Rockfish.*** The Greenspotted Rockfish predictive model showed that Greenspotted Rockfish density distributions were dependent on several of the predictor variables. Greenspotted Rockfish densities were seen to increase with incremental increases in predictor variables curvature, northness, and distance to shoreline and decrease with depth, slope, eastness, fine and broad scale TPI, distance to shelf edge and distance to shoreline. Most of the areas predicting higher densities occurred on the northern half of Monterey Bay. These high predicted densities fell north of the Monterey Canyon on the deeper areas of the continental shelf, the shelf edge, and upper slope (Figure 11). However, the negative relationship with slope was most likely preventing the model from predicting high densities at the boundary of the predicted map, where slope and depth start increasing rapidly.



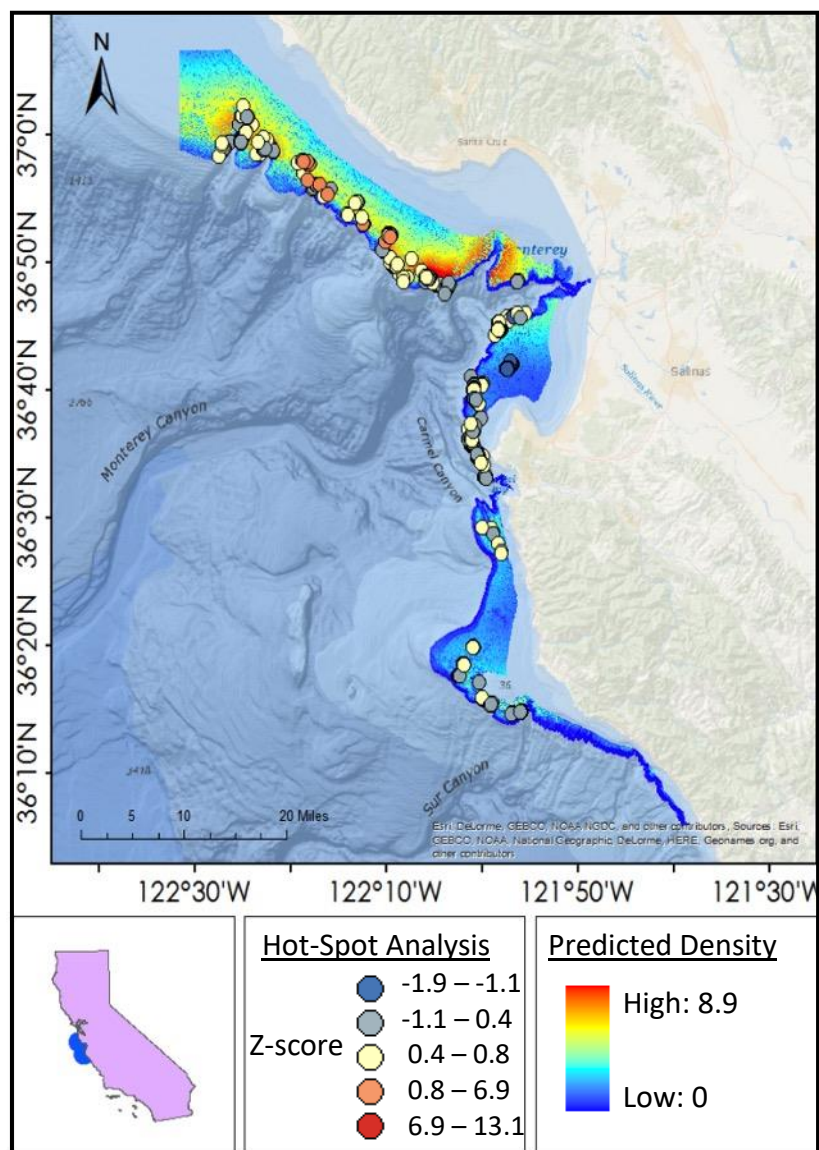


Figure 11. Map showing Greenspotted Rockfish predicted densities in the Central location (Monterey Bay) from depths of 70-150 m overlaid with a hot spot analysis of observed densities. Predicted density is reported as fish/100 m<sup>2</sup>.

***Greenstriped Rockfish.*** The Greenstriped Rockfish predictive model showed that Greenstriped Rockfish density distributions were dependent on several of the predictor variables. Greenstriped Rockfish densities showed positive relationships with predictor variables curvature, northness, VRM, and distance to shoreline, and negative relationships with depth, slope, broad scale BPI, distance to shelf edge, and distance to canyon heads. When looking at the map of predicted densities, highest densities of Greenstriped Rockfish were predicted to occur in the northern section of Monterey Bay along the continental shelf edge and upper continental slope (Figure 12). The positive relationship with distance to shoreline and negative relationships with distance to shelf edge and canyon heads could be driving this result on the predictive map, despite the negative relationships with depth and slope. The p-values reported from the relationships with the seascape ecology variables (distance to shoreline, shelf edge, and canyon heads) indicated higher significance than relationships with depth or slope. Additionally, distance to shoreline explained five times the amount of deviance than did slope, which was the factor explaining the second highest amount of deviance.

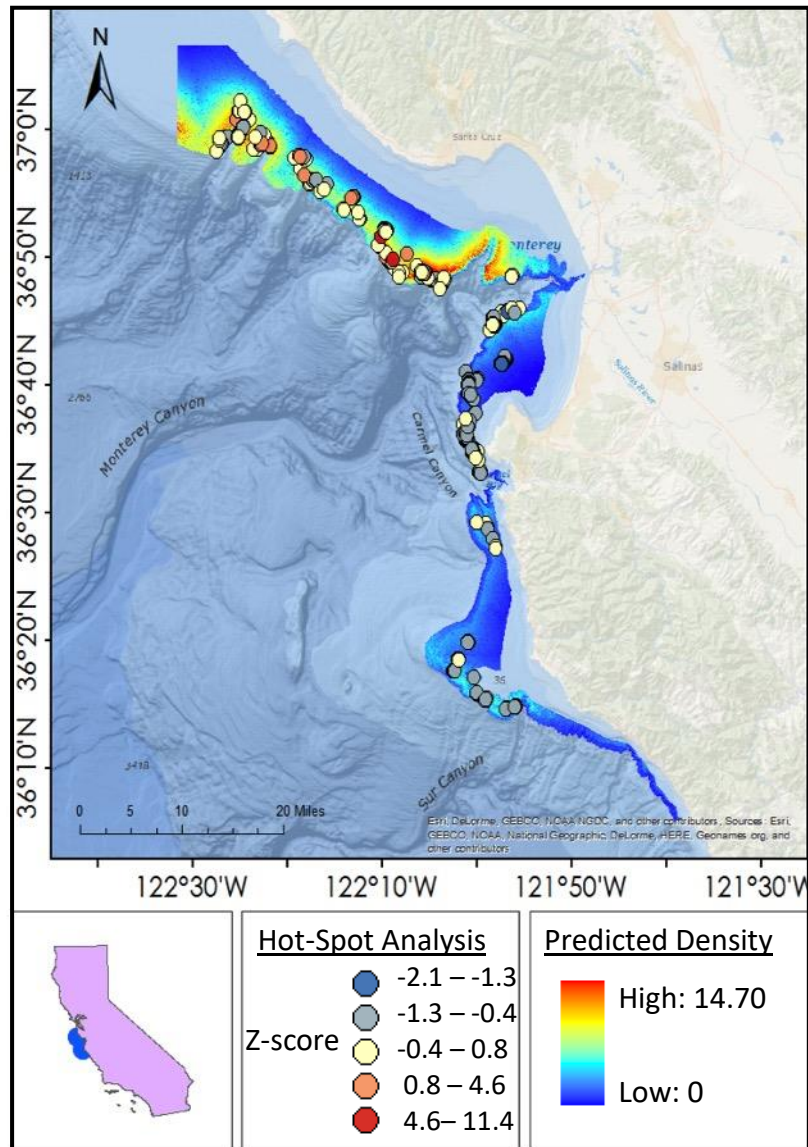


Figure 12. Map showing Greenstriped Rockfish predicted densities in the Central location (Monterey Bay) overlaid with a hot spot analysis of observed densities. Predicted density is reported as fish/100 m<sup>2</sup>.

**Vermilion Rockfish.** Vermilion Rockfish densities increased with distance to canyon heads and decreased with increasing depth, slope, northness, distance to shorelines, and distance to shelf edge. Almost all density predictions above zero occurred in the southern half of Monterey Bay, south of the Monterey Canyon. The light blue area corresponds to intermediate density predictions and is occurring along the deeper areas of the continental shelf. There is one area with high predicted density (7-9 fish/m<sup>2</sup>) occurring in the southern part of the predictive map closer to the shoreline. Hot spots of high density occurred relatively near the area of high predicted density and low densities occurred in areas of low predicted density (Figure 13).

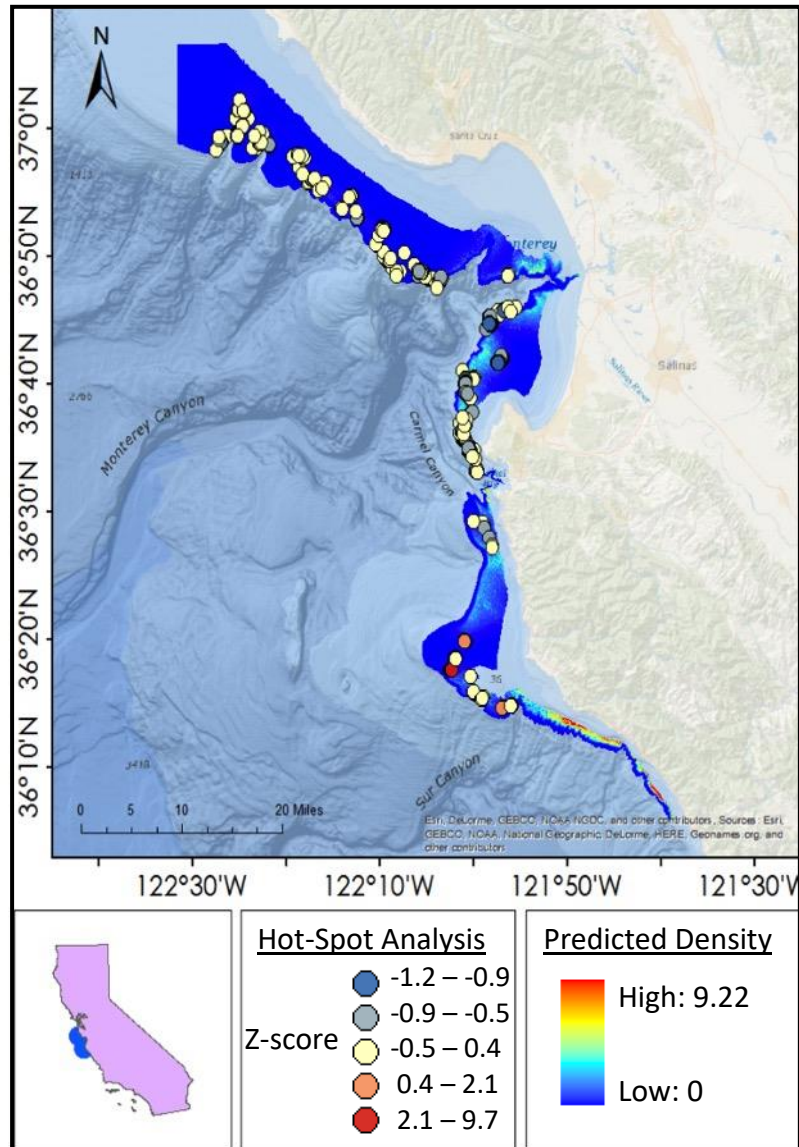


Figure 13. Map showing Vermilion Rockfish predicted densities in the Central location (Monterey Bay) overlaid with a hot spot analysis of observed densities. Predicted density is reported as fish/100 m<sup>2</sup>.

***Pacific Sanddab.*** The Pacific Sanddab predictive model showed that Sanddab had positive relationships with predictor variables depth, eastness, northness, fine-scale BPI, and negative relationships with slope, curvature, broad-scale BPI, VRM, distance to shoreline, distance to shelf edge, and distance to canyon heads. Most of the area on the Sanddab predictive map is dark blue, showing low predicted densities. Higher densities are predicted along the deepest edges of the predictive map, occurring in 150 m of water. These are the deeper areas of the continental shelf and shelf edge and descending into the upper continental slope. When looking at the predictive map, the hot spots of high density occurred mostly in these areas, however some occurred shallower on the continental shelf. All but one of the Sanddab hot spots occurred in the northern part of Monterey Bay, north of Monterey Canyon (Figure 14).

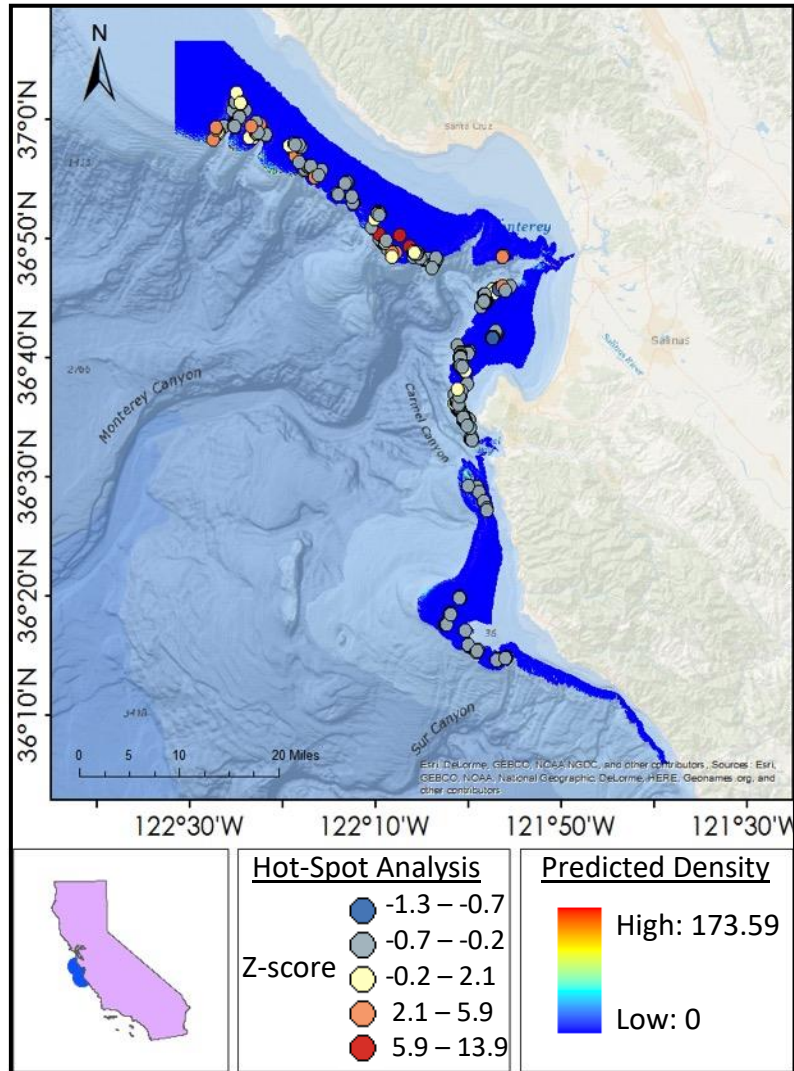


Figure 14. Map showing Pacific Sanddab predicted densities in the Central location (Monterey Bay) overlaid with a hot spot analysis of observed densities. Predicted density is reported as fish/100 m<sup>2</sup>.

## Model Testing

The data were separated by year and species models and maps were made predicting density using observations collected in 2013. I then overlaid the 2014 species observations onto the predictive map made with 2013 species observation data. In this way, 2013 predicted values could be compared with 2014 observed values. Predictive maps were not made for Greenstriped Rockfish and Pacific Sanddab. Due to the low number of observations of these species in 2013, the models were poor and output predictive maps were comprised solely of “No Data” values. Therefore, the model testing using comparisons of observed vs. predicted densities could not be done for Greenstriped Rockfish and Pacific Sanddab. For all other species, observed vs. predicted densities were plotted. A histogram was created of the proportion of 2014 observed density to 2013 predicted density for each species.

The relationship between observed and predicted densities of Canary Rockfish was nonsignificant with a weak fit (Linear regression,  $F_{1,x} = 0.1342$ ,  $R^2 = 0.0005$ ,  $p = 0.7$ ). The equation of the linear fit of Canary Rockfish observed vs. predicted densities is:

$$\text{Observed density} = 0.07 + 0.006 \times \text{Predicted densities.}$$

When assessing the equation of linear fit, densities predicted in 2013 are greater than densities observed in 2014. Additionally, by looking at the plot we can see the data points oriented along the x-axis. This shows that in most surveys, predicted densities were higher than observed densities. (Figure 15a).



Copper Rockfish observed densities displayed a significant positive linear relationship with predicted densities but a poor linear fit (Linear regression,  $F_{1,x} = 14.29$ ,  $p < 0.0002$ ,  $R^2 = 0.05$ ). The equation of the linear fit of Copper Rockfish observed vs. predicted densities is:

$$\text{Observed density} = 0.015 + 0.04 \times \text{Predicted densities.}$$

When assessing the equation of linear fit, 2013 predicted densities are greater than 2014 observed densities. The data points are oriented along the x-axis, further showing us that predicted densities were almost always higher than observed densities (Figure 15b).

Greenspotted Rockfish observed densities showed a significant positive linear relationship with predicted densities (Linear regression,  $F_{1,x} = 49.49$ ,  $R^2 = 0.15$ ,  $p < 0.0001$ ). The equation of the linear fit of Greenspotted Rockfish observed vs. predicted densities is:

$$\text{Observed density} = -0.02 + 0.08 \times \text{Predicted densities.}$$

When assessing the equation of linear fit, predicted densities are greater than observed densities. The slope of the line (0.08) shows us that there is not a 1:1 relationship between observed and predicted densities. The linear fit of this relationship was better than others seen in other models, as indicated by a higher R-squared value ( $R^2 = 0.16$ ) and the high F-statistic ( $F = 49.49$ ). This helps us further reject the null hypothesis that there is a strong relationship between observed and predicted fish densities (Figure 15c). Following the same pattern as Canary Rockfish and Copper Rockfish, we can see by

looking at the plot when Greenspotted Rockfish were observed to occur, they occurred in lower densities than were predicted. (Figure 15c).

Vermilion Rockfish observed densities showed a significant positive linear relationship with predicted densities, however a low R-squared value indicates poor linear fit (Linear regression,  $F_{1,x} = 3.97$ ,  $R^2 = 0.015$ ,  $p < 0.047$ ) (Figure 15d). The equation of the linear fit of Vermilion Rockfish observed vs. predicted densities is:

$$\text{Observed density} = 0.011 + 0.019 \times \text{Predicted densities.}$$

When assessing the equation of linear fit, predicted densities are greater than observed densities. Again, the points oriented along the x-axis indicate 2013 predicted values are higher than 2014 predicted values. However, there are several points that fall above the blue dotted line, showing that observed densities were higher than predicted densities in these surveys.

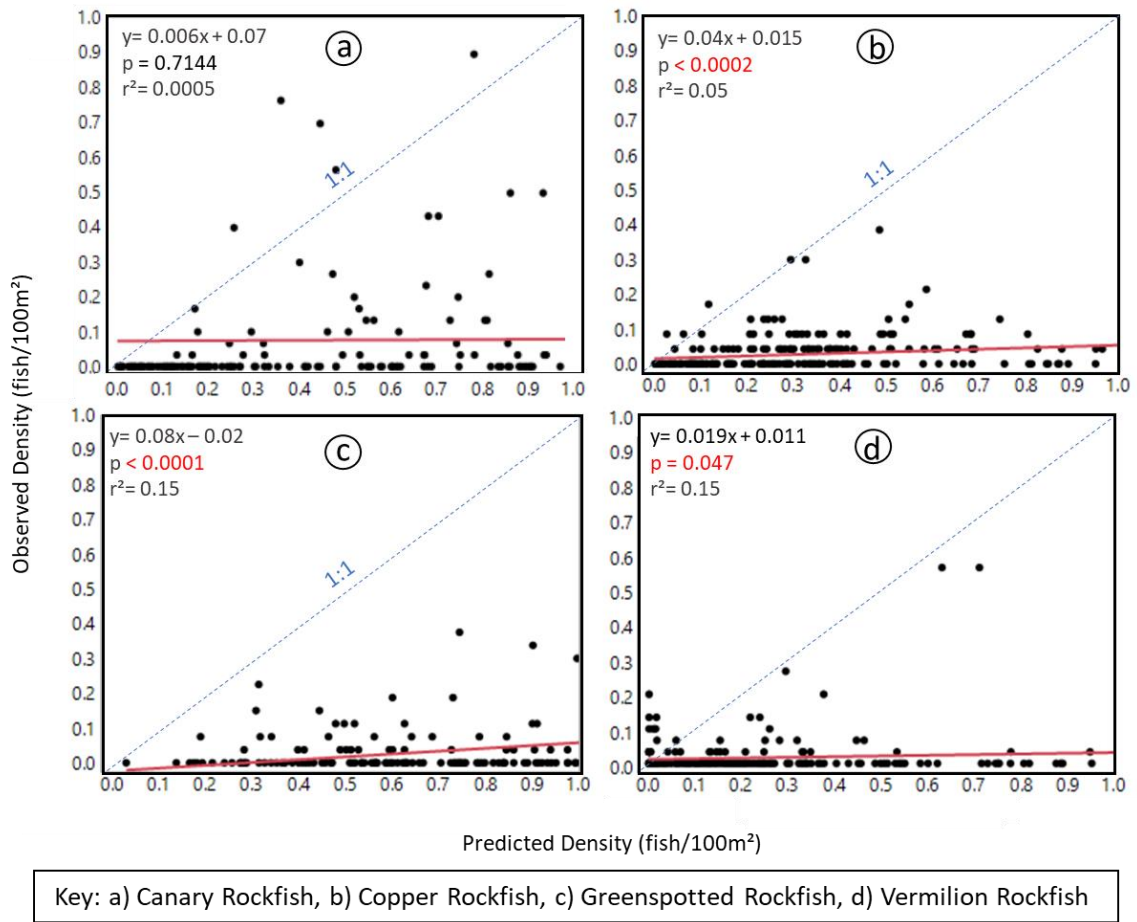
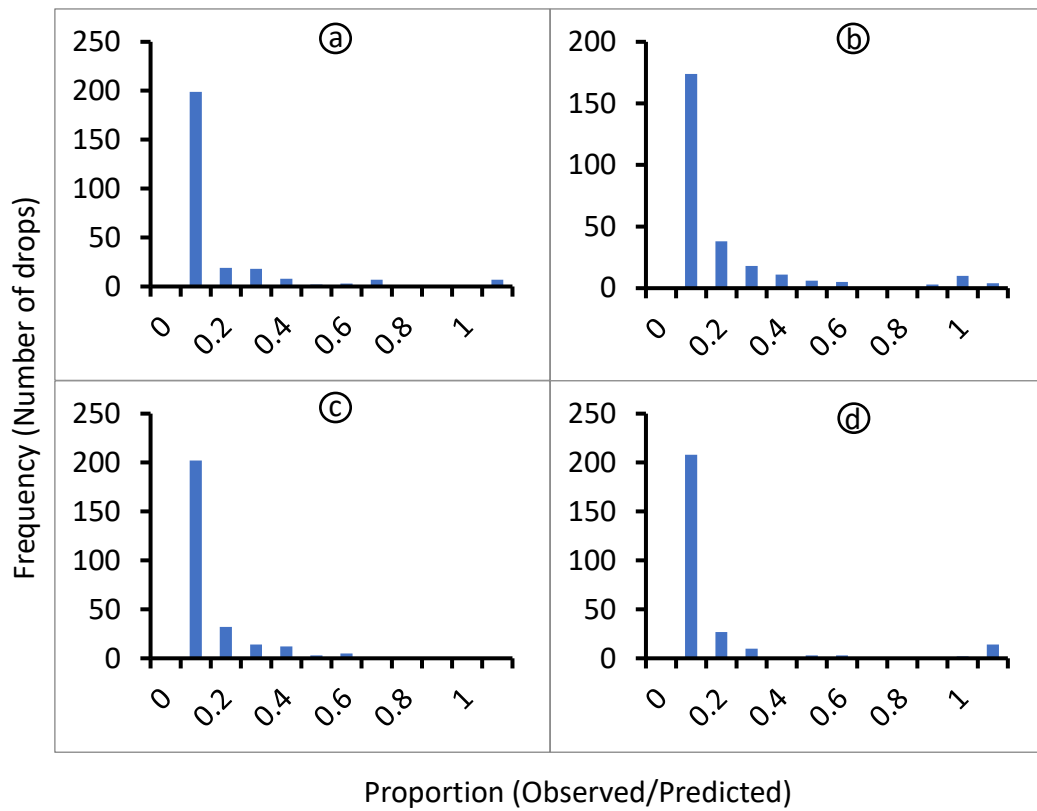


Figure 15. Multi-panel scatterplots of 2014 observed densities vs. 2013 predicted densities in each survey location.

Eighty seven percent of 2014 observations were within 10-20% of their predicted value (Figure 16). Predicted densities were often three to four times the observed value. Most of these instances occurred when the model predicted fish to occur when no fish were observed. A breakdown of the data showed that fish did not occur in 65 - 82% of video surveys. In the surveys which they did not occur, predicted densities were greater than zero 100% of the time. However, often when fish did occur, predicted densities were lower than observed densities. (Figure 16). These results indicate that the model is

consistently overpredicting or predicting higher densities than are occurring, especially when fish were not observed. However, there are instances where high densities of fish were observed but not predicted by the model. The models overall are overpredicting observed densities but also seem to be smoothing out peaks in densities by underpredicting peaks.



Key: a) Canary Rockfish, b) Copper Rockfish, c) Greenspotted Rockfish, d) Vermilion Rockfish

Figure 16. Multi-panel of histograms showing 2014 observed densities as a proportion of 2013 predicted densities.

## **Influence of Map Resolution on Predictions**

**Predictive mapping of species biomass at 1 m, 5 m, and 10 m resolutions.** Poisson GLMs predicting species biomass were run for every species using all data from the entire study site. Predictive maps were created at Portuguese Ledge for each species using maps of 1 m, 5 m, and 10 m resolution.

**Canary Rockfish.** The Canary Rockfish predictive model showed positive species associations with eastness, northness, broad-scale bpi, and distance to shoreline, and negative associations with depth, slope, distance to shelf edge and distance to canyon heads. On the 5 m and 10 m resolution maps at Portuguese Ledge, this translated to high biomass predictions on the high rocky points, and north-east facing facies and lower biomass predictions in the flatter areas surrounding the rock outcrop. However, the 1 m resolution map (Figure 17) displayed high biomass predictions over the flat areas surrounding the rocky outcrop as well. This may be due to artifacts in the bathymetry map that were being picked up as artificial bottom variation.

Although the maps were mostly similar in appearance, biomass predictions differed between predictive maps at 1 m, 5 m, and 10 m scales. The range of biomass values predicted at each point on the map differed slightly, but not too much between maps of different scale. The highest predicted biomass was predicted at Portuguese Ledge at the 5 m level of resolution, however total biomass predicted at Portuguese Ledge was much higher using 1 m resolution maps. Even without scaling down the 5 m

and 10 m biomass estimates to the smaller area, the total biomass estimates at 1 m resolution (279 tons, Figure 20) was more than double either of the biomass estimates at either the 5 m or 10 m resolutions, and the (102 and 35 tons, respectively). When the biomass estimates were all scaled to the same area (900 km<sup>2</sup>) the difference between the 1 m and the 5 and 10 m estimates increased. 279 tons of Canary Rockfish are predicted to occur when using the 1 m resolution map, 56 tons when using the 5 m resolution map, and 18 tons when using the 10 m resolution map. For Canary Rockfish, the biomass estimate decreased with increasing scale.

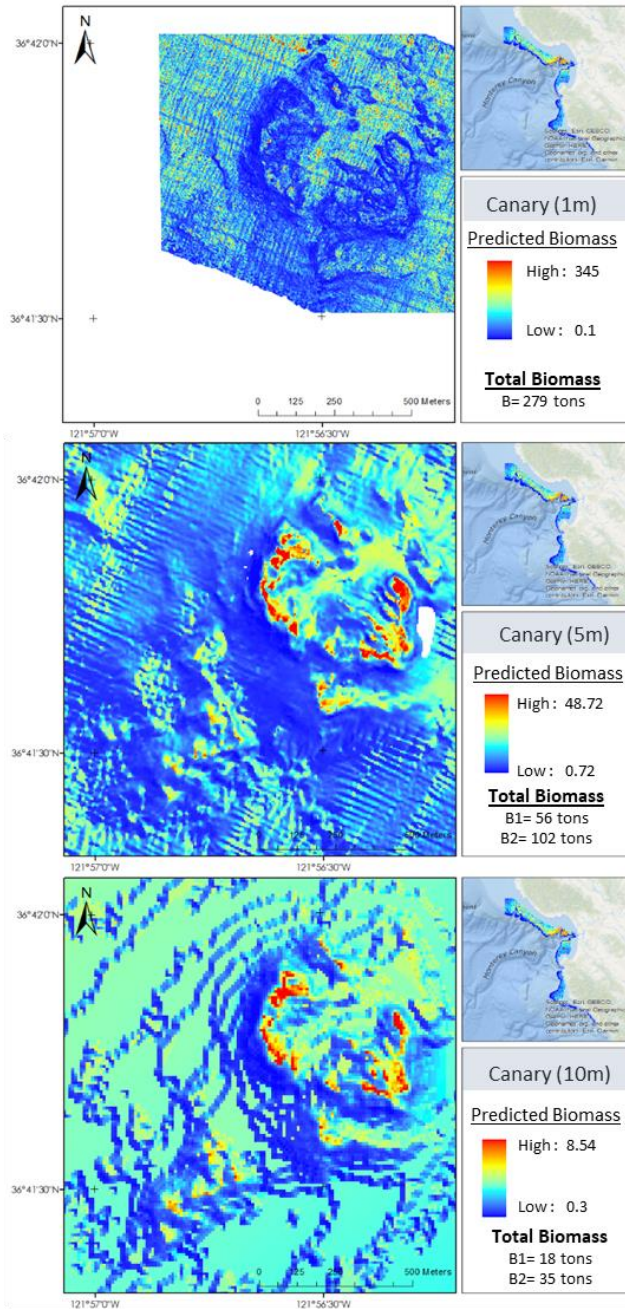
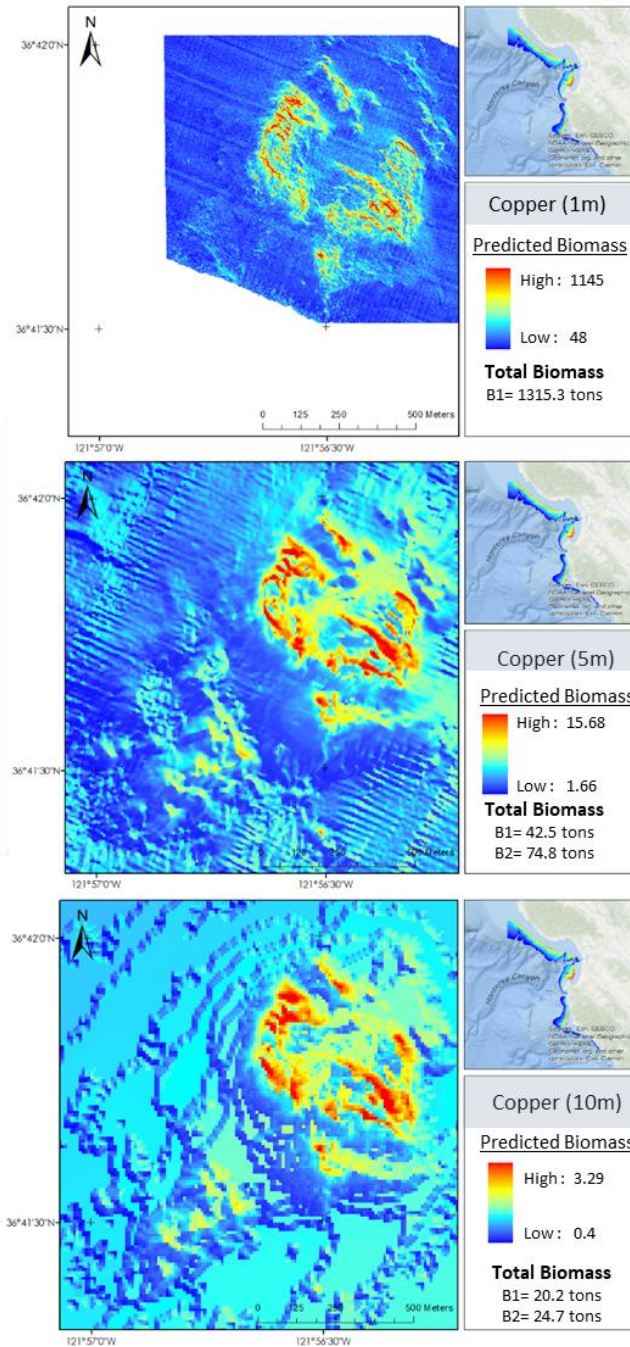


Figure 17. Predictive maps of Canary Rockfish biomass distribution at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolution. B1 is predicted biomass over the smaller area mapped at 1 m resolution bathymetry (~900 km<sup>2</sup>). B2 is biomass calculated over the larger area mapped at 5 m and 10 m resolutions (~2000 km<sup>2</sup>). Predicted biomass is scaled to kg/100 km<sup>2</sup> for all maps and total biomass is reported in tons.

***Copper Rockfish.*** The Copper Rockfish predictive model showed that Copper Rockfish biomass distributions were dependent on several of the predictor variables. Copper densities decreased with increasing depth and distance to shoreline, and increased with increasing northness, eastness, and distance to canyon heads. The rocky areas at Portuguese Ledge contained high predicted biomass, while the adjacent sandy areas showed low predicted densities.

The predictive maps at each scale displayed similar patterns in predicted biomass, but biomass estimates differed greatly depending on the resolution of the map. The 1 m resolution habitat map had the highest individual biomass prediction (1,145 kg/100 m<sup>2</sup> (~716 fish/100 m<sup>2</sup>)) and the highest total biomass predicted of the different maps (1315.3 tons). The highest individual biomass estimate on the 5 m resolution map was 15.68 kg/100 m<sup>2</sup> (~10 fish/100 m<sup>2</sup>) and the highest individual biomass estimate on the 10 m resolution map was 3.29 kg/100 m<sup>2</sup> (~2 fish/100 m<sup>2</sup>). When scaled over the same area, the total biomass estimate at the 1 m scale was over 30 times higher than the total biomass estimate of the same area at the 5 m or 10 m scales (42.5 tons and 20.2 tons respectively) (Figure 18).



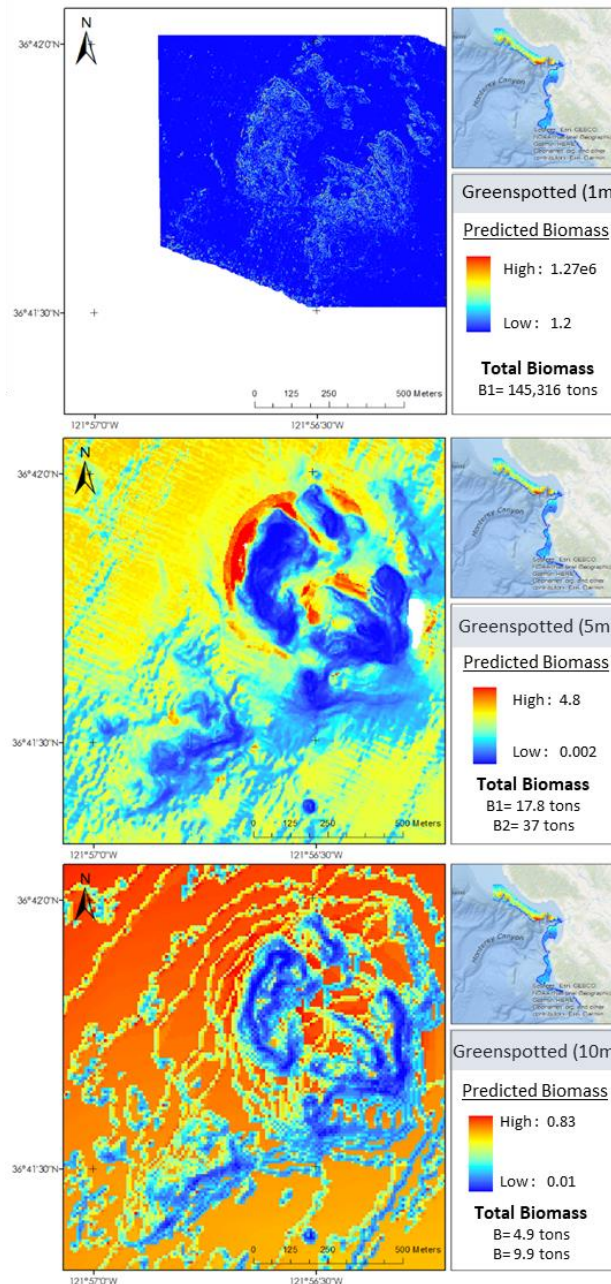


*Figure 18.* Predictive maps of Copper Rockfish biomass distribution at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolution. B1 is predicted biomass over the smaller area mapped at 1 m resolution bathymetry (~900 km<sup>2</sup>). B2 is biomass calculated over the larger area mapped at 5 m and 10 m resolutions (~2000 km<sup>2</sup>). Predicted biomass is scaled to kg/100 km<sup>2</sup> for all maps and total biomass is reported in tons.

***Greenspotted Rockfish.*** The Greenspotted Rockfish predictive model showed that Greenspotted Rockfish biomass distributions were dependent on several of the predictor variables. Greenspotted Rockfish densities showed positive relationships with curvature, northness, and distance to shoreline and negative relationships with depth, slope, eastness, fine and broad scale TPI, distance to shelf edge and distance to shoreline. The higher elevation areas have lower predicted values, while the adjacent flat areas adjacent display high predicted densities on the 5 m and 10 m maps. This result could be due to the negative relationship with TPI. However, while the predictive maps made at 5 m and 10 m scales both have intermediate biomass predictions over the larger, flatter portion of Portuguese Ledge, while the 1 m map shows very low predicted densities in this same area (Figure 19). Additionally, the whole rock outcrop appears to have high biomass predictions on the 1 m resolution map, while on the 5 m resolution map the areas immediately around the base of the rock have the highest predicted biomass. This detail cannot be distinguished on the 10 m resolution map; we can only see low predicted biomass on the rock outcrop and higher predicted biomass in the flatter areas.

The high biomass predictions were higher on the 1 m scale map than the other maps in the same areas. The 1 m resolution habitat map contained the highest biomass individual biomass prediction ( $1.27E+06$  kg/100 m<sup>2</sup> (~3 million fish/100 m<sup>2</sup>)) and the highest total biomass (145,316 tons). These estimates are orders of magnitude higher than total biomass estimates from either the 5 m or 10 m predictive maps (17.8 and 4.9

tons, respectfully). The highest individual biomass predictions are also much lower on the 5 m resolution map (4.8 kg/m<sup>2</sup> (~11.5 fish/100 m<sup>2</sup>)) and the 10 m resolution map (0.83 kg/m<sup>2</sup> (~2 fish/100 m<sup>2</sup>)). Greenspotted Rockfish predicted biomass followed the pattern of decreasing with increasing resolution (Figure 19).

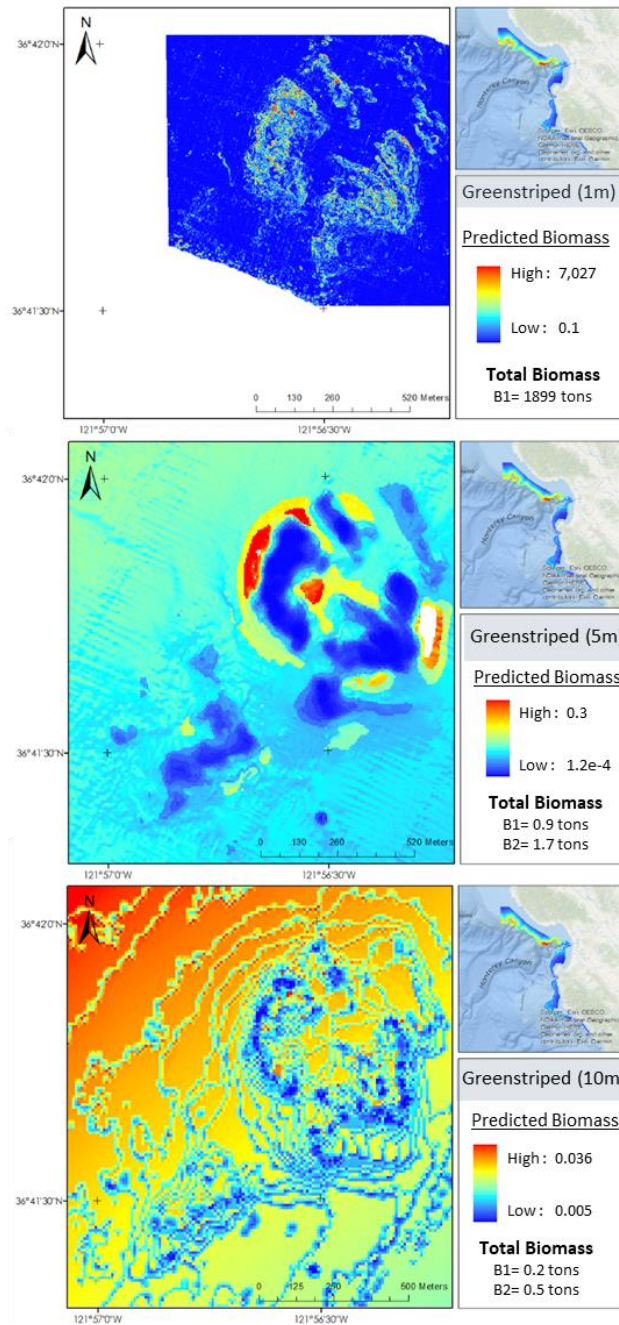


*Figure 19.* Predictive maps of Greenspotted Rockfish biomass distribution at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolution. B1 is predicted biomass over the smaller area mapped at 1 m resolution bathymetry (~900 km<sup>2</sup>). B2 is biomass calculated over the larger area mapped at 5 m and 10 m resolutions (~2000 km<sup>2</sup>). Predicted biomass is scaled to kg/100 km<sup>2</sup> for all maps and total biomass is reported in tons.

***Greenstriped Rockfish.*** The Greenstriped Rockfish predictive model showed that Greenstriped Rockfish biomass distributions were dependent on several of the predictor variables. Greenstriped Rockfish densities showed positive relationships with curvature, northness, VRM, and distance to shoreline, and negative relationships with depth, slope, broad scale BPI, distance to shelf edge, and distance to canyon heads. Greenstriped Rockfish are predicted to occur in lower densities than the other species at Portuguese Ledge. Greenstriped Rockfish relationships are similar to those of Greenspotted Rockfish, and the resulting predictive maps at 5 m and 10 m resolutions also show similar patterns in predicted biomass. The areas of rock have low predicted biomass. This could be because these areas have high elevation in comparison to adjacent areas, and so the negative relationship with TPI could be driving this result. Higher predicted biomass occurs immediately adjacent to these high elevation spots on the 5 m resolution map (Figure 20). Again, the 10 m resolution predictive map does not capture this, however the pattern of high predicted biomass on lower lying areas and lower predicted biomass on areas over areas of high elevation can be seen. The 1 m map shows almost the opposite predictions, where the areas of rock have high predicted biomass values and the lower lying areas have very low predicted biomass.

As with the other species, differences in biomass estimates were most marked between the 1 m resolution maps and the 5 m and 10 m resolution maps. Total predicted biomass at Portuguese Ledge using the 1 m resolution map was almost 2000 tons (1899 tons), while total predicted biomass for that same area on both the 5 m and

10 m resolution maps was less than 1 ton. Individual predictions using 1 m resolution are also higher, with the highest predicted biomass being 7,027 kg/100 m<sup>2</sup> for an individual cell. In comparison, the highest biomass estimate at the 5 m resolution scale was 0.3 kg/100 m<sup>2</sup>, and the highest biomass estimate for individual cell at the 10 m resolution scale was 0.036 kg/100 m<sup>2</sup>. Biomass predictions increased with decreasing resolution (Figure 20).



*Figure 20.* Predictive maps of Greenstriped Rockfish biomass distribution at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolution. B1 is predicted biomass over the smaller area mapped at 1 m resolution bathymetry (~900 km<sup>2</sup>). B2 is biomass calculated over the larger area mapped at 5 m and 10 m resolutions (~2000 km<sup>2</sup>). Predicted biomass is scaled to kg/100 km<sup>2</sup> for all maps and total biomass is reported in tons.

**Vermilion Rockfish.** The Vermilion Rockfish predictive model showed that Vermilion Rockfish biomass distributions were dependent on some of the predictor variables. Vermilion Rockfish densities increased with distance to canyon heads and decreased with increasing depth, slope, northness, distance to shorelines, and distance to shelf edge. The hard bottom, southern facing facies contained the high predicted biomass values, while lower lying flat areas and northern facing facies displayed lower predicted biomass. The patterns of predicted biomass are consistent among all maps.

Again, the highest individual biomass estimate was found at the 1 m resolution and this estimate decreases with decreasing resolution. The highest individual biomass estimate on the 1 m resolution map was 269 kg/m<sup>2</sup> (~140 fish/100m<sup>2</sup>), 15.3 kg/25 m<sup>2</sup> (~8 fish/100m<sup>2</sup>) on the 5 m resolution map, and 3.58 kg/100 m<sup>2</sup> (~0.3 fish/100m<sup>2</sup>) on the 10 m resolution map. Biomass predicted for the entire area are 7x higher when using the 1 m resolution map than they are over the same area on the 5 m or 10 m resolution map (Figure 21).



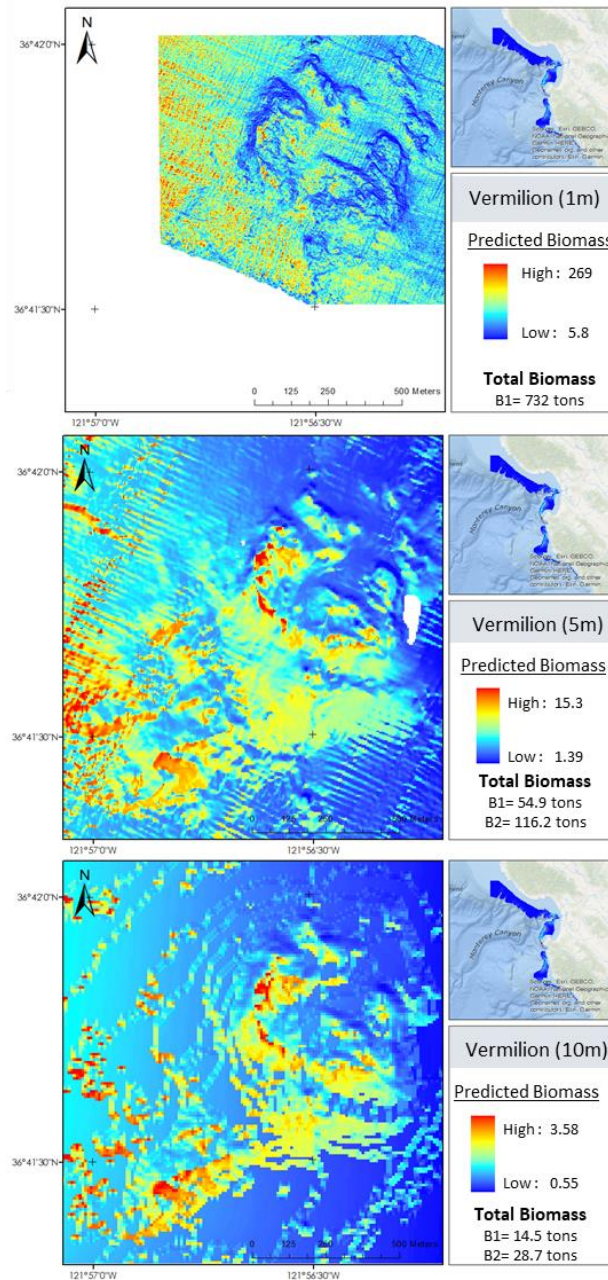
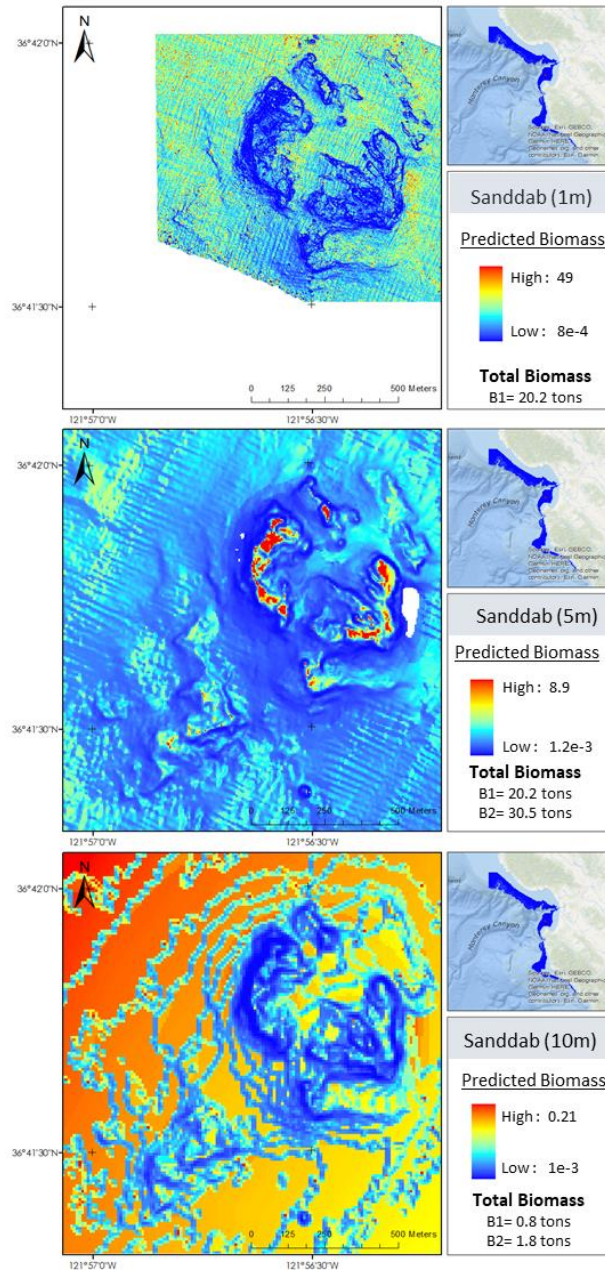


Figure 21. Predictive maps of Vermilion Rockfish biomass distribution at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolution. B1 is predicted biomass over the smaller area mapped at 1 m resolution bathymetry (~900 km<sup>2</sup>). B2 is biomass calculated over the larger area mapped at 5 m and 10 m resolutions (~2000 km<sup>2</sup>). Predicted biomass is scaled to kg/100 km<sup>2</sup> for all maps and total biomass is reported in tons.

***Pacific Sanddab.*** The Pacific Sanddab predictive model showed that Sanddab densities had positive relationships with depth, eastness, northness, fine-scale BPI, and negative relationships with slope, curvature, broad-scale BPI, VRM, distance to shoreline, distance to shelf edge, and distance to canyon heads. Low to intermediate predicted biomass values occur over most of the area. The rocky areas displayed low predicted biomass on all maps except for the 5 m resolution map. There were high predicted values on the top of the rocks on the 5 m resolution map (Figure 22). This could be a result of map scale. There can be only one value per pixel, and even if the top parts of the rock are not 5 m wide, there will be one value to represent that area. It could be that at the 5 m scale these rocks may appear to have a flat surface while the 1 m resolution will pick up more detail and it will not appear flat. Conversely the 10 m surface may pick up the high value as it averages everything in the 100 m<sup>2</sup> cell.

Biomass predictions were lower for Sanddab than for many of the other species at Portuguese Ledge. Total Sanddab biomass predicted at Portuguese Ledge at the 1 m resolution (83.7 tons) was much higher than biomass predicted for the same area using either the 5 m or 10 m resolution maps (3.1 and 0.8 tons, respectively) (Figure 22).



*Figure 22.* Predictive maps of Pacific Sanddab biomass distribution at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolution. B1 is predicted biomass over the smaller area mapped at 1 m resolution bathymetry (~900 km<sup>2</sup>). B2 is biomass calculated over the larger area mapped at 5 m and 10 m resolutions (~2000 km<sup>2</sup>). Predicted biomass is scaled to kg/100 km<sup>2</sup> for all maps and total biomass is reported in tons.

**Total biomass predicted at Portuguese Ledge.** Total predicted biomass at Portuguese Ledge increased with decreasing pixel size. In general, unrealistically high biomass estimates were calculated using the 1 m map. However, biomass values were much smaller and more in range of what we might expect when using the 5 m and 10 m bathymetry maps. For example, the model predicted over 145,000 tons of Greenspotted Rockfish to occur on Portuguese Ledge when plotted on the 1 m resolution maps while the same model predicted just over 17 tons when using 5 m resolution bathymetry, and less than 5 tons when using 10 m bathymetry for the same area. The closest estimate of biomass between the 1 m and 5 m resolution occurred for Canary Rockfish. The estimate for Canary Rockfish biomass was 5 times larger using a 1 m resolution map than a 5 m resolution map. The largest difference in the biomass estimates between 1 m and 5 m bathymetric maps was for Greenspotted Rockfish. The biomass estimate using a 1 m map was 8,500 times the biomass estimate using a 5 m map. Biomass estimates using 1 m bathymetry were consistently much higher than estimates using 5 m bathymetry, and estimates using 5 m bathymetry were usually about 3 times larger than those using 10 m bathymetry (Table 20).

Table 20

*Total Biomass Predicted for Portuguese Ledge at 1 m, 5 m, and 10 m Resolutions*

	<i>1 m (900km<sup>2</sup>)</i>	<i>5 m (900km<sup>2</sup>)</i>	<i>10 m (900km<sup>2</sup>)</i>
<i>Canary Rockfish</i>	279	56	18
<i>Copper Rockfish</i>	1,315	43	14
<i>Greenspotted RF</i>	145,316	18	5
<i>Greenstriped RF</i>	1,899	1	0.2
<i>Vermilion Rockfish</i>	732	55	14
<i>Pacific Sanddab</i>	84	3	0.8

*Note.* Total biomass is reported in tons and rounded to the nearest whole number.

**Total biomass over hard bottom habitat at Portuguese Ledge.** Estimates of the area of hard bottom differed with map size and map resolution. To make biomass estimates over hard bottoms comparable, the 5 m and 10 m maps were scaled down to the size of the 1 m map. In this way, we can compare estimates of hard bottom over the same area. However, even scaled to size, the amount of area designated as hard bottom area was different using maps of different resolution. The area designated as hard bottom was a smaller when using the 1 m map than using the other maps. For each species, highest predicted biomass occurred on the 1 m resolution maps. These estimates were larger despite being predicted over a smaller area (Table 21).

The difference between total biomass estimates between maps of different resolution decreased when scaled down to hard bottom only (Table 21). For example, 23 tons of Canary Rockfish were predicted over hard bottom habitat at Portuguese Ledge using a 1 m resolution map and 18 tons were predicted using a 5 m map (5-ton difference).

Mean observed biomass was calculated for all species over all resolutions and multiplied over the area of hard bottom on each map, which gave an estimate of total observed biomass over hard bottom. For all species, the largest differences between total observed biomass and total predicted biomass occurred on the 1 m resolution map. For example, no Greenspotted or Greenstriped Rockfish were seen on the area of hard bottom covered by the 1 m resolution map, and therefore total observed biomass was zero for both species. However, total predicted biomass for Greenspotted Rockfish was over 81,000 tons and for Greenstriped Rockfish was over 1000 tons. At the 5 m resolution, total predicted biomass and total observed biomass were similar for some species. Observed and predicted total biomass were very similar for Greenspotted Rockfish; 2.1 tons of Greenspotted were observed for hard bottom area at Portuguese Ledge and 2 tons were predicted over the same area. Total predicted biomass exceeded total observed biomass for all species except Copper Rockfish and Greenspotted Rockfish. Total predicted biomass was closest to total observed biomass at the 10 m resolution for all species except for Copper Rockfish and Greenspotted Rockfish. At the 10 m resolution, total observed biomass exceeded total predicted biomass for all species except Greenstriped Rockfish and Pacific Sanddab (Table 21).

Table 21

*Total Observed Biomass and Total Predicted Biomass over Hard Bottom Area on 1 m, 5 m, and 10 m Resolution Predictive Maps*

	1 m (180km <sup>2</sup> )		5 m (300km <sup>2</sup> )		10 m (300km <sup>2</sup> )	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
<i>Canary Rockfish</i>	10	23	11.4	18	11.5	6
<i>Copper Rockfish</i>	18	446	23.5	16	23.6	5
<i>Greenspotted RF</i>	0	81,084	2.1	2	2.1	1
<i>Greenstriped RF</i>	0	1,160	0.03	0.2	0.03	0.06
<i>Vermilion RF</i>	4	103	9	18	9.1	5
<i>Pacific Sanddab</i>	1	9	0.003	1	0.003	0.1

Note. Total biomass sums are over slightly different sized areas. Total biomass is reported in tons. Rockfish is abbreviated to “RF” for some species

**Total predicted biomass over North, Central, and South zones of the study site.**

Biomass was summed over the whole area to get an idea of the biomass estimations of these six species in 70-150 m depth along the central coast at the 10 m resolution (Table 22). Canary biomass estimates were high for the North and Central regions (20,000 and 18,000 tons) but were much lower for the South region (1200 tons). The area for which biomass predicted differs for each region. We could be seeing lower predicted biomass in the southern region because the area of the southern predicted region is much smaller than the north or central regions. Conversely though, the highest biomass estimates for Vermilion occur in the southern region (20,000 tons). These results show there is some spatial variation in predicted distributions across regions. In total, Vermilion had the highest predicted biomass on the Central coast between 70-150 m of water. More than 47,000 tons of Vermilion were predicted in this area, with half of this

biomass predicted in the small southern region between Cape San Martin and Lopez Point.

Table 22

*Biomass Summations over Larger Areas Using a 10 m Resolution Map*

	<i>North</i>	<i>Central</i>	<i>South</i>	<b><i>TOTAL</i></b>
<i>Canary Rockfish</i>	20,512	18,342	1,214	<b>40,068</b>
<i>Copper Rockfish</i>	9,341	7,331	1,653	<b>18,325</b>
<i>Greenspotted RF</i>	22,520	10,651	291	<b>33,462</b>
<i>Greenstriped RF</i>	2,071	673	20	<b>2,764</b>
<i>Vermilion Rockfish</i>	19,519	6,740	20,194	<b>46,453</b>
<i>Pacific Sanddab</i>	951	2,184	159	<b>3,294</b>

Note. Biomass is reported in tons.



## Discussion

### Species Relationships with Observed Habitat

Using a video lander, I described species-habitat relationships with observed habitat features (bottom type, relief, and rugosity) for six fish species off central California. My results showed relationships consistent with results described by other U.S. West Coast researchers (e.g., Stein et al., 1992; Tissot et al., 2007; Yoklavich et al., 2002). Vermilion and Copper Rockfish were observed more frequently in hard bottom habitats, and areas with medium-high relief and rugosity. Greenstriped Rockfish were observed mostly over soft and mixed bottoms of low relief and rugosity. Greenspotted Rockfish distributions overlapped with the hard bottom species but are also observed on mixed bottoms of medium and low relief and rugosity. Pacific Sanddab were encountered almost exclusively in soft bottoms of low relief and rugosity. Canary Rockfish distributions followed less of a pattern than the other species with respect to observed habitat characteristics; they were found in similar densities over all bottom types, relief, and rugosity.

Species-habitat relationships were strong for all species and observed habitat variables that I evaluated. There were significant differences in densities for every species and every observed habitat variable. I expected this to occur because I chose to study species that are known to occur on a variety of habitats, from soft to hard bottoms. For example, Pacific Sanddabs were found almost exclusively on soft bottom, low relief, low rugosity habitats. Pacific Sanddab displayed the strongest relationship

with observed habitat features, and no Sanddabs were observed over hard bottom habitat, or high and medium rugosity habitats. Conversely, Vermilion Rockfish showed a clear, strong relationship with hard bottom, high relief, and high rugosity habitats and were rarely seen over soft sediments.

Although the relationships among species densities and observed habitat features were strong for most species, they were not always clearly defined. Preferences of observed habitats were shown by almost all species, yet often the difference in mean densities among different types of habitat was small. Many species occupied a variety of observed habitat types, with an affinity to a particular type. Greenspotted Rockfish were observed in similar densities over hard and mixed bottoms and appeared to prefer seafloors of mixed relief and rugosity but were also found in areas of both low and high relief and rugosity. Canary Rockfish density distributions did not follow clear patterns regarding bottom type, relief, or rugosity. Mean density of Canary Rockfish was almost identical over both hard and soft habitats. This might be an indication of utilization of ecotones, as Canary Rockfish are known to use the interface between habitats (Hunter-Thompson, 2011).

My work suggests that relationships with observed habitat alone do not perfectly describe species density distributions. While observed habitat features provide insight into preferred habitat types, these habitat features alone do not describe the variation in species distributions. Alternate classification systems of benthic habitat may be useful in explaining distributions of species whose distributions are not tightly tied to sediment

type. For example, seascape patterns might be useful in describing the variation in benthic fish distributions. Densities of rockfish have been found to be disproportionately higher at the edge of rock patches. Hunter-Thompson (2011) found densities of Vermilion, Canary, and Bocaccio Rockfish were positively correlated with proximity to rocky patches. Hunter-Thompson (2011) also reported positive effects on population size with increased patch size.

### **Species Relationships with Remotely Sensed Habitat**

After the State of California invested heavily in mapping nearshore habitats, there has been interest in using remotely sensed variables instead of observed bottom types to evaluate species distributions. This is partly because a) species such as Canary Rockfish might be less tied to a particular bottom type and more to a habitat patch or seafloor feature (e.g., reef), and b) using remotely sensed variables allows for broad scale mapping of seafloor characteristics. Because observed habitat data are only available at surveyed locations, they cannot be used to create maps of habitat suitability in other locations. However, remotely sensed data are available for large swaths of the seafloor, and thus can be used to create maps predicting habitat suitability and to obtain density and biomass estimates for larger areas.

My results showed that many of the individual remotely sensed habitat variables had little to no influence on species density distribution. R-squared values showed that individually these variables explain little variation in species distributions. Canary Rockfish and Pacific Sanddab density distributions showed no significant dependence on

variation of the remotely sensed variables. Linear regression analyses for all the other species provided significant relationships with one to three of the nine remotely sensed variables. When remotely sensed variables were grouped as principal components, all species density distributions showed dependence on fluctuations in the explanatory variables. Even so, R-squared values remained low.

Copper Rockfish densities were found to increase with VRM. I did not find any studies that have described the relationship between Copper Rockfish and VRM, but VRM has been reported to be a significant predictor in Rosy Rockfish and Greenstriped Rockfish predictive models (Young et al., 2010). In my work, Greenspotted Rockfish displayed a negative significant relationship with broad-scale BPI in the predictive GLMs. These results are consistent with results from Young et al. (2010) who also found broad-scale TPI to be a significant predictor in a GLM predicting Greenstriped Rockfish distributions.

Distance to shoreline has not been widely used as a variable in habitat association studies. The results from my research suggest distance to shoreline is an important predictor in determining fish density distribution patterns. My results were similar to Pittman et al. (2011), who reported distance to shoreline to be the most influential predictor in spatial models for two coral reef fish species and important for other species as well.

The positions of samples on the seafloor relative to the distance to shoreline and distance to canyon head are often inversely related. This could be why we always saw a

positive relationship with one and a negative relationship with the other. Pitman et al. (2011) observed distance to shelf edge to be a powerful predictor in spatial models predicting reef fish distributions. Similarly, I found distance to shelf edge to influence Vermilion Rockfish densities.

### **Comparison of Species Associations with Observed vs. Remotely Sensed Habitat**

The CCA results indicated that a) the remotely sensed variables as a group explain more variance in species densities than did relationships between species and observed habitats, and b) the variation explained by the observed habitat variables was generally also explained by a number of the remotely sensed habitat variables. Species locations on the plot also corresponded with remotely sensed variable vectors.

To complete the assessment of observed and remotely sensed habitat characteristics as variables to describe species distribution patterns, I compared the collective power of each group of variables to describe the variation in species densities. Two models predicting species densities were created for all species. One model was created using observed habitat variables as predictors, and another was made using remotely sensed habitat characteristics as predictors.

The models using remotely sensed variables did a better job at explaining species distributions than observed habitat variables. Some remotely sensed model predictors were significant in the model even though they were not significant in linear regressions. Models using remotely sensed habitat variables described a higher proportion of deviance in species densities than models using observed habitat

characteristics for all species except Pacific Sanddab. Additionally, model fits were better using remotely sensed habitat variables for all species except Pacific Sanddab.

In summary, the variation explained by observed habitat characteristics was also explained by the remotely sensed habitat characteristics and seascape variables that were included in this study. Additionally, predictive models using remotely sensed data explained more deviance and performed better for almost all species. These results indicate that remotely sensed variables might be more appropriate to use when modeling species distributions. Also, it is a good idea to use a large array of predictors to describe fish distributions. As more variables are included, more variation is explained even when penalizing for each variable using measures like AIC. This indicates that it is not just one or two benthic features driving distributions but rather the collective influence of a large number of smaller drivers.

### **Creating Predictive Maps using MGET in ArcGIS 10.2**

I created maps of predicted species densities using the models of species relationships with remotely sensed habitat features. The maps created in Monterey Bay using 10 m resolution bathymetry provided a broad indication of where to find fish in the area. The resulting maps offer reasonable descriptions of species density distributions. However, patterns in species densities followed broad scale patterns and appeared to be primarily driven by relationships with one or two variables.

There are several potential causes of the broad scale density patterns seen on the maps and the poor predictive power of models. One explanation is that there could be

important environmental drivers missing in the model. Oceanographic variables such as temperature, salinity, chlorophyll level, etc. can also influence fish distributions and were not included in the models. Although some seascape variables were included in these models, perhaps integration of variables such as habitat patch size and distance to patch edge would have described more variation in densities and could have yielded maps with more detailed patterns and higher predictive power.

Investigators studying seascape ecology in California have noted effects on fish distributions. Stripetail Rockfish (*S. saxicola*) and Splitnose Rockfish (*S. diploproa*) have been found to occur more often in larger habitat patches (Anderson et al. 2009), whereas the biomass of Squarespot Rockfish (*S. semicinctus*) and Starry Rockfish (*S. constellatus*) were found to be positively correlated with habitat patch size (Hunter-Thompson, 2011). Also, Blackeye Goby (*Rhinogobiops nicholsii*) density and biomass were found to be correlated with distance to the ecotone boundary (Hunter-Thompson, 2011). Acoustic tracking of Ocean Whitefish (*Caulolatilus princeps*) showed movement along a rock-sand ecotone, where the Ocean Whitefish utilized the sand side during the day and the rock side at night (Bellquist et al., 2008).

I originally wanted to include additional seascape variables such as patch size and distance to patch edge in the models. To understand how habitat patch size and distance to patch edge affected the density distributions of each species, I planned to subdivide the study area into patches of hard and soft substrate. However, I was unable to delineate habitat patches of hard and soft substrate for the entire study area due to

the limitations of using 10 m resolution data. Substrate was going to be calculated by reclassifying the VRM raster to distinguish between hard and soft substrate. Several cut-off values were evaluated and the substrate map which best-represented reality would have been chosen. However, the coarse data did not provide enough variation in VRM to enable a demarcation of hard and soft substrate. Attempts were made to delineate habitat patches using NOAA Habitat Maps and observed habitat at each survey location, but often these data contradicted each other and therefore this strategy was abandoned. Because habitat patches could not be delineated for the study area, distance to patch edge could not be calculated.

Using the fine-scale data at Portuguese Ledge, I was able to delineate habitat patches. A substrate DEM at 5 m resolution was available for Portuguese from CSUMB SFML ([http://seafloor.otterlabs.org/SFMLwebDATA\\_mb.htm#CMB](http://seafloor.otterlabs.org/SFMLwebDATA_mb.htm#CMB)) and I was able to create a substrate layer for the 1 m resolution map. These data were used to delineate habitat patches, where patch boundaries were set at hard and soft substrate interfaces. The issue with using habitat patch size as a predictor was that the sandy areas were all interconnected and appeared as one large “soft” patch instead of several small patches. There was no way to separate the patches without being arbitrary, and the large sand patch would affect the results if trying to determine relationship to patch size. I was able to create layers showing distance to patch edge and distance to rock which I could be more confident represented reality. Unfortunately, these variables could only be



created for a small area (Portuguese Ledge) and therefore were not included in the model.

### **Model Testing**

The bivariate fitting of 2014 observed densities vs. 2013 predicted densities showed that the model consistently predicted higher densities than were observed and most of observed densities were ~ 10-20% of the predicted densities. One explanation for the discrepancy between 2013 predicted values and 2014 observed values could be that there was a large decline in the populations of these fish between the two years. But when looking at 2013 observed densities in comparison to 2014 observed densities, we see this is not the case. Another possible explanation is that we failed to capture fish in our surveys in 2014 due to small-scale temporal changes in spatial distributions. Peaks in Copper Rockfish densities in fall and winter seasons and significant decline in summer months have been observed by Matthews (1986). However, visual surveys used in my study occurred over many months and throughout different seasons. Because of this, I think it is unlikely we missed peaks in densities for all species because of temporal variation in spatial distributions.

These results indicate that the predictive maps are not capturing peaks or hotspots in species densities using remotely sensed features alone. While the predictive maps capture general patterns in density distribution patterns, they are greatly overpredicting densities at a large scale and underpredicting observed peaks. This suggests that there are other factors that have not been included in the model that might make one benthic

habitat more likely to harbor fishes than another. Fish are not homogeneously distributed, even over habitats that are structurally similar. Not all rock is created equal, and there are other factors such as oceanographic variation which can make one rock outcrop favorable than the next. These results might suggest that predictive maps of species density may be more useful when gathering information on general areas where there is a higher chance of encountering species, which can help when targeting a species either for commercial reasons, for sampling, or to protect habitat in specific areas. However, based on the consistent discrepancy between observed and predicted values, I would be cautious when using these maps to obtain estimates of fish abundance, density, or biomass.

### **Influence of Map Resolution on Predictions**

The effect of map resolution on model estimates is another reason to be cautious about using predictive maps to estimate biomass of a species. To evaluate the influence of map resolution on predicted biomass estimates, I calculated biomass of each study species at Portuguese Ledge using maps of 1 m, 5 m, and 10 m resolutions. One model was used to evaluate the difference in biomass estimates when map resolution was the only variable to change. This is an important question because the map resolution of available bathymetry varies along different parts of the California coast. For example, there are 2 m resolution data for the nearshore central coast, but only within state waters. Outside of that, 10 m resolution data are available for some areas, and 30m resolution data for others. Along the entire state, the resolution of bathymetry maps

can be somewhat arbitrary, and people making species distribution maps must make do with what is available. Fish density estimates have been multiplied over rocky habitat to estimate regional population abundance for stock assessments (O'Connell and Carlile, 1993). It is important to understand the effect of map resolution on these estimates and the range of biomass estimates that might be generated for each map resolution.

Biomass estimates were found to decrease with map resolution. Predictive maps using 10 m resolution maps had the lowest biomass estimates, followed by 5 m maps, with 1 m resolution maps predicting the highest biomass. The 1 m resolution maps resulted in biomass estimates that were unrealistically high. The 5 m and 10 m resolution maps provide more realistic estimations of biomass over Portuguese Ledge, however, they still appeared to overestimate biomass. When looking at biomass estimates over hard bottom alone, the same pattern was seen of large differences between biomass estimates. The 1 m resolution maps predicted higher biomass estimates than either the 5 m or 10 m resolution maps. However, the difference in biomass estimates between the 1 m and the 5 and 10 m maps for some species decreased.

There could be a couple reasons for this. First, there were a large number of artifacts in the 1 m bathymetry. Artifacts are artificial variations in bathymetric maps caused by rolling of the ship during seafloor mapping. Although artifacts can be minimized by mapping on calm days, they cannot be avoided altogether. There were many more artifacts in the fine-scale data, showing up as ribbing along the sandy areas, which add

false variation in the seafloor topography. There were high predicted densities in these areas caused by this false variation. The reduction in the discrepancy between biomass estimates made using 1 m maps and those using 5 m and 10 m maps over hard bottom is probably due to the removal of the artifacts occurring over the soft bottom areas.

Another reason for the higher biomass estimates in the 1 m resolution maps is the increased extrapolation of data over many pixels. The finer scale the map, the more pixels are in it. The observed vs. predicted densities plots show us that when fish do occur, the model is generally predicting lower densities than observed. However, the species used in this study did not occur in 67-91% of surveys, and in these instances when a fish did not occur, the models predicted values higher than those observed 68-99% of the time. If the models are consistently over-predicting at each pixel or cell where no fish are observed, when total biomass is summed over all pixels, the biomass prediction will be greater for maps with more pixels. These small overestimations in aggregate can lead to a large overestimation in biomass summations over a larger area.

Total predicted biomass estimates over hard bottom at Portuguese Ledge were most similar to total observed biomass using the 10 m resolution map. The last stock assessment of Vermilion in 2005 (MacCall, A.D., 2005) estimated abundances of age 1+ Vermilion Rockfish to be between 2,584- 5,423 tons in Northern California and between 2,237-12,205 tons in Southern California. In comparison, the models (using a 10 m resolution map) predicted over 47,000 tons in Central California. It is worth noting that map predictions and stock assessment estimates are for slightly different locations in

California. However, the difference between my model estimates and stock assessment estimates is quite large and not likely due to real differences in biomass between these areas. While there is error and uncertainty in stock assessments, the discrepancy between the model estimates and stock assessment estimates is not likely due to uncertainty in stock assessments. Furthermore, biomass sums from my predictive models over the larger regions of the study site were made with 10 m resolution bathymetry. When comparing biomass estimates obtained using maps of 1 m, 5 m, and 10 m resolutions, 10 m resolution maps were seen to garner the lowest biomass estimates. If biomass estimates were obtained from predictive maps using 5 m or 1 m resolution bathymetry, there would be a larger discrepancy between my map predictions and stock assessment estimates. Additionally, the large biomass predictions from the model are only over the small area between 70-150 m in Northern, Central, and Southern California regions. If biomass was predicted across these entire regions using the predictive models, the discrepancy between stock assessment biomass estimates and predictive spatial model biomass estimates would be even larger.

My results show that map resolution has a large influence on resulting biomass estimates. These results indicate that one should be cautious when mapping to obtain biomass estimates and be cognizant that map resolution can have a large effect on resulting biomass summations. Predictive modelling and mapping are great tools to help better understand species distribution patterns. They can give us a better idea of where

we can find certain species and predict distributions onto unsurveyed areas. However, density or biomass estimates derived from the maps might be less reliable.

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