THE DISTRIBUTION OF DEMERSAL FISHES OVER

HETEROGENOUS SEAFLOOR HABITATS: AN APPLICATION OF

LANDSCAPE ECOLOGY TO VIDEO IMAGERY COLLECTED IN A

CENTRAL CALIFORNIA STATE MARINE CONSERVATION AREA

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By

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THE DISTRIBUTION OF DEMERSAL FISHES OVER HETEROGENOUS

SEAFLOOR HABITATS: AN APPLICATION OF LANDSCAPE ECOLOGY

TO VIDEO IMAGERY COLLECTED IN A CENTRAL CALIFORNIA STATE

MARINE CONSERVATION AREA

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For all the sea has to teach us… and all the fun in learning it.

ABSTRACT

The distribution of demersal fishes over heterogeneous seafloor
habitats: An application of landscape ecology to video imagery
collected in a Central California State Marine Conservation Area
by
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Using landscape ecology approaches, this study investigated the importance of structural patterning in the seafloor landscape and the scales at which demersal fishes associate with different habitats. The following document describes the project in three parts: 1) The circumstances surrounding the management of the study site and the methodological approaches used; 2) The analytical framework and results; 3) Potential applications of these results in management.

By describing the landscapes across which demersal fish are distributed at the Piedras Blancas State Marine Conservation Area (PBSMCA), within the Monterey Bay National Marine Sanctuary, we evaluated fish-habitat associations in the context of other central California deepwater studies. Quantifying and monitoring the distribution of fishes over the habitats at this site is critical to understanding how this marine protected area (MPA) may function as a conservation measure.

Imagery surveys are ideal for collecting data on seafloor habitats and observing fishes in these habitats; these data are becoming an increasingly important contribution to marine conservation management. We examined imagery collected at the PBSMCA with a towed camera system. Surveys were conducted in 2007 and 2008 in water depths ranging from 30-120 m. Video imagery gathered with the sled was viewed as a set of non-overlapping video quadrats (frames). We compared generalized linear models to estimate the probability of response (detection) of selected demersal fish groups to a number of habitat variables, assuming a uniform probability of detection.

Results suggested that, for all fish groupings, there is evidence that seafloor substrate plays a very strong role in determining distributions. Depth also played an important role, while biogenic structure and soft-sediment bedforms were rarely of importance to the distributions. Our results are consistent for the most part with fish distribution studies conducted at other sites within the central California region.

These results highlight the importance of using imagery to collect monitoring data about marine landscapes. Use of a simple, low-cost camera system enabled us to address complex ecological questions about demersal fish-habitat associations across a heterogeneous landscape and provided useful results in the form of baseline data to MPA managers and site characterization to the Monterey Bay National Marine Sanctuary.

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CHAPTER 1

THE IMPORTANCE OF IMAGERY DATA AND LANDSCAPE MODELING IN ECOSYSTEM MONITORING AND MANAGEMENT

Challenges in marine resource conservation such as degraded ecosystems, declining resources (Worm 2009), and limited funding have increased the need for management in near-shore marine habitats. Traditionally, in an attempt to understand and prevent overexploitation of resources, managers have used single-species management approaches such as stock assessments and restrictions or quotas (NRC 2001; Preikshot and Pauly 2005). However, shortcomings in these methods have redirected management towards ecosystem-based approaches, which focus on monitoring relationships among populations, habitats, and human uses of the ecosystem (Pauly et al. 2002). Ecosystem management approaches such as marine protected areas (MPAs) and essential fish habitat closures have gained widespread recognition in coastal science and policy (NRC 2001) and have been implemented by federal, state, and local governments at a variety of scales.

MANAGEMENT BACKGROUND: STATE AND FEDERAL PROTECTED AREAS ON CALIFORNIA'S CENTRAL COAST

Along California's 1,350-km coastline, local, state, and federal managed areas are frequently overlapping. Although this overlap can sometimes cause ambiguity over governance and responsibility (Crowder et al. 2006) it can also foster collaboration among agencies and create a more effective management network (Airame et al. 2003). In California, the National Marine Sanctuary Program, under the National Oceanic and Atmospheric Administration, has designated four federal marine sanctuaries spanning over 600 km of California's coastline. A state-wide network of marine reserves, conservation areas, and parks are being implemented along the entire coast by the California Department of Fish and Game (CDFG). Also, county and city agencies have

established and managed local beaches, tidepools, and parks along their shores for decades (Brown 2001). Ecologically, there is a need to identify habitat-associated groups and guilds of fishes that persist along the entire coastline (Yoklavich et al. 2000). An understanding of these associations at various locations along the west coast of North America will be valuable for predicting community response to disturbances, for applications to resource surveys, and for identifying the components of essential fish habitats (Yoklavich et al. 2000).

Protection of fish habitats using ecosystem-based measures provides a number of conservation "insurance" benefits to allow for unforeseen natural and anthropogenic catastrophes, increases in biodiversity, and spillover of stocks into non-protected (fished) areas (NRC 2001; Palumbi 2001). Networks of protected areas provide additional ecological benefits for larval dispersal, genetic diversity, and for migratory species (Palumbi 2003). Understanding the degree to which fish stocks benefit from these ecosystem-based conservation measures requires monitoring of closed areas and comparison to actively fished areas.

The California Marine Life Protection Act of 1999 (MLPA) initiated a network of MPAs along the entire coast. After two failed implementation attempts, the Resources Legacy Fund stepped in to partner with the CDFG. This partnership facilitated the MLPA Initiative to involve stakeholders statewide and provided needed assistance to the CDFG. In September 2007, the MPAs in the Central Coast Region (CCR) of the network were implemented. This was the first of five regional networks to be implemented in the combined coast-wide network. Protected areas in the Central Coast Region include recreation-based marine parks, strict no-take marine reserves, and conservation areas, where limited take of particular, commercially-valuable species is allowed (CDFG 2007).

Obtaining baseline data for these MPAs upon establishment is a critical objective of the *MLPA Master Plan for MPAs* (CDFG 2007), a document guiding the designation, implementation, monitoring, and management of the CCR and future networks. These data are collected to describe the habitats and biota inside and adjacent to an MPA at the time of implementation. Comparison of baseline data with monitoring data gathered in subsequent years is fundamental to measuring the success of these protected areas. In the CCR, intertidal and shallow-subtidal (to 30 m) baseline and monitoring surveys are

primarily conducted by the Partnership for Interdisciplinary Study of Coastal Oceans (PISCO) using SCUBA and intertidal transecting techniques. Deepwater (30 - 365 m) data collection was conducted by a state-funded monitoring program using the human-occupied submersible *Delta* to collect video and photographic imagery. However, funding for monitoring was insufficient to collect data in each of the 29 MPAs. This left critical gaps in a data set to be used for future assessment of the efficacy of MPAs.

Many of the CCR MPAs fall within the boundaries of the Monterey Bay National Marine Sanctuary (MBNMS), a federally protected area designated in 1992. The MBNMS encompasses over 8,000 km^2 off the coast from San Francisco Bay to San Simeon and extends 48 km offshore. The large area of the MBNMS includes a variety of habitat types and ecosystems along the continental shelf as well as in deep submarine canyons. The area along the shelf - including California state waters - is an economically valuable area with regards to fisheries, and the "site characterization" of this area is a major objective of the *MBNMS Management Plan* (NOAA 2009). Site characterization includes an assessment of the diversity of habitats and biota within the sanctuary (NOAA 2009). Through this study, we have collected MBNMS characterization data to provide baseline MPA information at a study site encompassed by both state and federal management areas, filling one data gap in the CCR MPA network.

APPLIED RESEARCH: CONTRIBUTION OF IMAGERY DATA TO CONSERVATION MANAGEMENT

Imagery surveys of the seafloor are becoming an increasingly important contribution to marine conservation monitoring and management. Although projects directed at gathering seafloor imagery are often burdened by high operational costs and restricted to a narrow window of weather and sea conditions, the non-extractive nature of imagery collection (as opposed to the traditional trawl or hook-and-line sampling techniques) compliments well with monitoring for conservation and management goals.

In a collaborative partnership between the Institute for Applied Marine Ecology at CSU Monterey Bay (IfAME) and the MBNMS, a "towfish" camera sled system (Figure 1), owned and operated by the National Marine Sanctuary Program, was used to survey and characterize the continental shelf between depths of 20 and 250 m. The "sled" is a simple video camera system capable of collecting valuable imagery data. Its simple

design and operation gives it the potential to cover a considerably large area in a relatively short period of time. In comparison to other imagery platforms such as remotely operated vehicles (ROVs) and human-occupied submersibles, camera sleds are relatively inexpensive to operate and maintain.
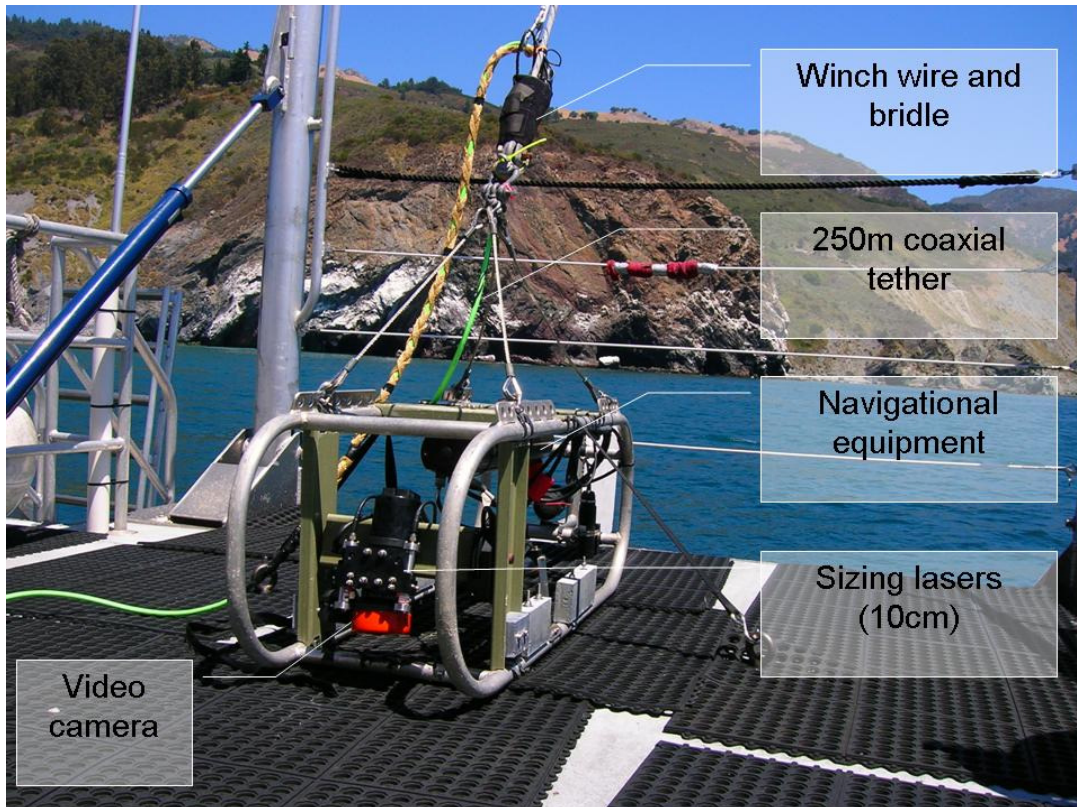
Figure 1. The "towfish" camera sled system consists of a single video camera, 10 cm sizing lasers, and navigational equipment (including depth and altitude sensors). The sled is tethered to the support vessel with a 250 m coaxial umbilical and winch wire.

To assist the state in monitoring MPAs, surveys conducted during partnership research cruises combined MBNMS site characterization efforts with MPA baseline data collection. These surveys were conducted from 2007-2011 and targeted areas of interest to the MBNMS as well as in overlapping, recently-designated state MPAs that were not included in California's state monitoring program. The goals of these surveys were to collect imagery on the seafloor habitats, demersal fishes, and invertebrate communities in these areas.

The Piedras Blancas State Marine Conservation Area is within the southernmost boundary of MBNMS and was surveyed with the sanctuary's camera sled in 2007, 2008, and 2011. These three benchmarks offer a significant contribution to the monitoring of the CCR Network and data from these surveys will be incorporated in the 2012 Five-Year Review of the CCR MPA Network.

Prior to these surveys at Piedras Blancas, there was little information available about the seafloor of the area. At implementation in 2007, seafloor mapping data were only available at 70 m resolution and the extent of hard- and soft-bottom seafloor habitats was largely unknown. However, as high resolution multibeam bathymetry (2 m resolution) became available from the Seafloor Mapping Lab at CSU Monterey Bay in 2010, the extent of these substrates became apparent. Since 2007, the video surveys conducted by the camera sled revealed complex, high-relief rocky habitats interspersed with low relief soft sediment patches including ripple-scour-depressions, a potentially important soft-sediment habitat for a variety of organisms (e.g., Hallenbeck 2010). An analysis of passenger fishing vessel surveys from 1988-2004 in the vicinity of Piedras Blancas describes the most frequently landed fish as rockfishes (most commonly blue, gopher, olive, vermillion, yellowtail, and copper) and lingcod (Reinicke et al. 2008).

The research encompassed by this project incorporated the imagery surveys from 2007 and 2008. We quantified the distribution of fish species and higher taxonomic groupings over the heterogeneous seafloor habitats encountered in the PBSMCA. We tested the response (detection) of fish with regards to several seafloor habitat variables: substrate classification, biogenic structure, soft-sediment bedforms, and depth. Since fish-habitat associations have been studied using a variety of scales of habitat classification, we examined the classification scale that best explained the distribution of each group. We then examined the particular categories of substrate, biogenic and bedform features, and depth that best explained the distribution of each group.

We employed an AIC model comparison approach using generalized linear models (GLMs, see Burnham and Anderson 2002) to estimate how the probability of detection of a fish group depended upon specific habitat variables. This approach assumes a uniform detection probability; that fish were detected equally in each habitat type. Although MacKenzie (2006) contends that inferences made in violation of this

assumption may result in an inaccurate estimation of habitat use by a species, given the difficulties of surveying the depths of the ocean floor with any tool, we must proceed with the assumption that we sampled an adequate amount of each habitat type to accurately represent distributions within each type. This modeling approach allowed us to investigate the evidence supporting the combinations of the variables that play the most important role in determining fish distribution as well as the habitat types with which each fish grouping demonstrated the strongest association. The model comparison approach allowed us to estimate the "best" combination of habitat variables, given all model possibilities. We were also able to test for spatial autocorrelation without having to eliminate large amounts of data, to address the possible violation of independence inherent in all spatially clustered data sets.

Our results indicated that there was very strong evidence suggesting that substrate is the most important variable (of the variables we examined in this study) in the distribution of demersal fishes. Although fish groups showed associations to the seafloor substrate at different classification scales (e.g., hard-bottom (general) vs. boulder (specific)), substrate was nonetheless the most influential variable on the response (detection) of fishes. Depth, followed by biogenic features and soft-sediment bedforms showed some importance in the distributions, but were not nearly as strong.

We divided observed fishes into groups based on species identifications, as well as morphological groups and broad taxonomic groups. Habitat associations of the broad taxonomic groupings of 'small' (<10 cm) and 'large' (>10cm) rockfish were identified as mixed low relief substrates (i.e. cobble-mud) and moderate relief rocky reefs, respectively. Habitat associations of flatfish were, not surprisingly, identified as soft sediments. Quantification of these distributions can be applied by managers when designating conservation areas based on broad management units such as rockfish bag limits and quotas.

An understanding of habitat associations even at a sub-genus scale can be valuable for species-specific regulations. This less-coarse sub-genus grouping used morphological similarities to group rockfish into clusters of two or more species. Rockfish within a sub-genus grouping were sometimes identifiable to species but often not. To assure consistency, whether species identification was possible or not, the fish

were grouped. Most of these groups showed similar habitat associations to low- to moderate-relief rocky reefs. This was consistent with the results of the broad "large rockfish" grouping (moderate-relief rocky reefs). However, distinction between some groups was seen. For example, detections of canary/vermillion/yelloweye rockfish complex were specifically associated with the occurrence of boulder habitats. Two of these three species are heavily managed (canary and yelloweye rockfish) but all three are often indistinguishable to recreational anglers (J. Watson, pers comm).

Ideally, imagery data would provide the ability to identify all individuals to the species level and up-grouping to the management units described above would be a simple bookkeeping procedure. However, even when using higher-resolution ROV and submersible imagery data, this level is not always attainable, thus understanding the application of these broad groups is important to management nonetheless.

Marine managers are faced with complex questions and insufficient data on the distribution of fishes (Airame et al. 2003). This paucity of knowledge was listed explicitly as a limitation in applying ecological criteria to the design of MPAs in the Channel Islands (Airame et al. 2003). The incremental scientific contributions of this study advance the body of knowledge surrounding these criteria. The sled may be an imperfect tool, but it is available, affordable, and has been used to answer complex questions and provide results that are useful to resolving management issues.

CHAPTER 2

A LANDSCAPE MODELING APPROACH TO
THE ANALYSIS OF SEAFLOOR IMAGERY
DATA

ABSTRACT

Landscape ecology is used to describe the distribution of species with respect to the spatial pattern of habitat patches. Application of this approach to seafloor landscapes, which are often heterogeneous in terms of substrate and structure, allows for a foundation upon which to study the distribution of fishes across patches and throughout the seafloor landscape. We used a towed video camera system to conduct surveys covering an area of approximately 40.5 km^2 of the seafloor over hard and soft bottom habitats at the Piedras Blancas State Marine Conservation Area offshore of central California. We evaluated the strength of observable fish-habitat associations at a variety of spatial scales, using a set of generalized linear models and compared them using Akaike's Information Criterion (AIC). Further, we evaluated the importance of secondary habitat variables such as depth, soft-sediment bedforms, and biogenic structure in the distributions of fishes. Model results suggested that the most important variable in the distribution of fishes was seafloor substrate, although different groups were associated with seafloor substrate at different scales (e.g., hard-bottom vs. boulders) and substrate categories (e.g., boulders vs. cobbles). Predictor variables of depth, biogenic structure, and soft-sediment bedforms showed importance for some fish groups, though to a lesser degree. Effective spatial management approaches to fisheries conservation must consider seafloor substrate at multiple scales to address the distribution of multiple fish groups.

INTRODUCTION

Landscape ecology describes how spatial heterogeneity (patterning) in an ecological landscape affects ecological processes, including the way organisms associate with their environment (Turner 1989). Although this approach to studying ecosystems

has emerged from observations in terrestrial systems, it has increasingly been applied to marine ecosystems in the past two decades (Robbins and Bell 1994; Hinchey et al. 2008). Application of the tenets of landscape ecology - structure, function, and change - can be used to identify the relationships between seafloor habitats and benthic ecosystem processes, specifically, the distribution of demersal fishes (Grober-Dunsmore et al. 2008; Hinchey et al. 2008; Zajac 2008).

Fish distributions are governed by broad-scale environmental and physical variables such as water temperature (Gilman et al. 2006), latitude (Witman et al. 2004), and water depth (e.g., Bergen et al. 2001; MacPherson 2003). At smaller scales, fish distributions have been described using structural attributes of seafloor habitat primarily related to substrate type (e.g., hard vs. soft, Anderson and Yoklavich 2007; Zajac 2008), macro-habitat scale (e.g., 10s of meters, Yoklavich et al. 2000; Auster and Lindholm 2005; Lindholm et al. 2007), and micro-habitat scale (e.g., centimeters, Auster et al. 2003a). Fish distributions in relation to biogenic (sessile invertebrate) structure have also been studied (Auster et al. 1991, 2003b; Brødeur 2001), though it has been challenging to demonstrate an association (Love and Yoklavich 2008). It is important to understand the variation in fish responses to these habitat variables, and the scale of response, in order to effectively assess conservation measures that manage certain habitats - or even landscapes of heterogeneous habitats - for protection (e.g., MPAs).

Traditionally, fish distribution studies have used trawl-sampling methods; however, these methods reduce seafloor structure, remove fish, and provide very little habitat data. Alternatively, collecting data with video (or photographic) imagery allows access to habitats inaccessible by bottom trawling (e.g., high relief rocks) and enables *in situ* observation of fish-habitat associations that are only available at these depths through remote imagery. Over the past decade, studies have increasingly used non-invasive fish observation methods with video imagery from submersibles (e.g., Anderson and Yoklavich 2007), remotely operated vehicles (e.g., Auster et al. 2003a), and towed camera systems (e.g., Auster et al. 2003b, Spencer et al. 2005).

Along California's central coast, several fish distribution studies using imagery data have been conducted in "deep" water (30 – 300 m). At Cordell Bank, fish distributions and assemblage structure were shown to differ based on different habitat

scales (Anderson and Yoklavich 2007). Further south, offshore of Davenport, Laidig et al. (2009) found that variability in the distribution of rockfishes over different habitat types may be attributable to life history stage. Within Monterey Bay, Yoklavich et al. (2000) identified guilds of fish species based on their distributions over various habitat types in Soquel Canyon. At the Big Creek Ecological Reserve, fishes were designated in assemblages based on their distributions over different seafloor habitats (Yoklavich et al. 2002). These studies describe, along a roughly 300 km latitudinal gradient, the way that fish are distributed across a variety of landscapes. We contribute to this body of knowledge with an evaluation of fish distributions further south, at Point Piedras Blancas, at a newly designated California State Marine Protected Area in the southern portion of the Monterey Bay National Marine Sanctuary (MBNMS). Understanding landscape variables that affect fish distributions at Piedras Blancas will contribute to the overall understanding of how fish use habitat throughout the central coast area.

Application of a model-comparison approach to fish distributions

In the studies discussed above and similar work in other areas, fish distributions have been evaluated using multivariate clustering representations and analytical approaches such as principal components analysis (PCA, Anderson and Yoklavich 2007; Anderson et al. 2009), canonical correlation analysis (CCA, Stein et al. 1992; Tissot et al. 2007), or with a combination of cluster analysis and null-hypothesis testing (Yoklavich et al. 2000; Tissot et al. 2007). These approaches provide qualitative diagrams that cluster species (or groups) with similar distributions close to one another on two axes and test correlation hypotheses against a null hypothesis.

Meanwhile, comparing fitted linear and logistic models using information-theoretical approaches, such as Akaike's Information Criterion (AIC), is gaining momentum in ecology (Anderson 2007). Terrestrial ecologists have frequently used the comparison of multiple working hypotheses in a model set to make inferences about the strengths of the different ecological landscape scenarios, such as those involving habitat type and elevation (e.g., Bruggeman et al. 2007). Here, we use a similar approach to describe the distributions of fishes over seafloor habitats, assuming a uniform detection probability. This approach, contrasted to the traditional method of comparing one null

hypothesis to all alternates, allows for improved interpretation of a more complicated and dynamic system (Burnham and Anderson 2002; Anderson 2007).

We used a set of generalized linear models (GLMs) to compare multiple working hypotheses (models) that represented different configurations of habitats in the landscape. By fitting a set of models with different combinations of possible explanatory variables, inferences about the system structure can be made from the model that best describes the distribution of each fish group. Further, the relative importance (RI) of each habitat variable can be inferred by examining more than just one model (Burnham and Anderson 2002).

In this study, we examined the distributions of several demersal fish groupings using a camera sled system near Point Piedras Blancas, California. We modeled the observed fish habitat associations using data collected on substrate type, substrate complexity (relief), soft-sediment bedforms, seafloor depth, and invertebrate structure of the habitat. We inferred the relative importance of each of these attributes, as well as the type of habitat with which each fish grouping demonstrated the strongest detectible association. By describing the landscapes across which these fish were distributed, we evaluate fish-habitat associations at Piedras Blancas in the context of other central California deepwater studies.

METHODS

Study site

We collected seafloor video imagery offshore of Point Piedras Blancas, California (35°39'N, 121°17'W) within and adjacent to the Piedras Blancas State Marine Conservation Area (PBSMCA). PBSMCA is one in a network of 29 MPAs implemented in 2007 off the coast of central California (Figure 2). PBSMCA encompasses an area of 22.8 km^2 near the southern boundary of the MBNMS, and is bordered eastward by a no-take Marine Reserve and westward by the California state waters (3 nautical mile) boundary. The PBSMCA is located approximately five kilometers north of San Simeon, California and is a limited-take, state MPA managed by the CDFG. Transects were conducted at depths ranging from 30-120 m and were within the MPA and 1.5 km to the north and west of the MPA boundary.
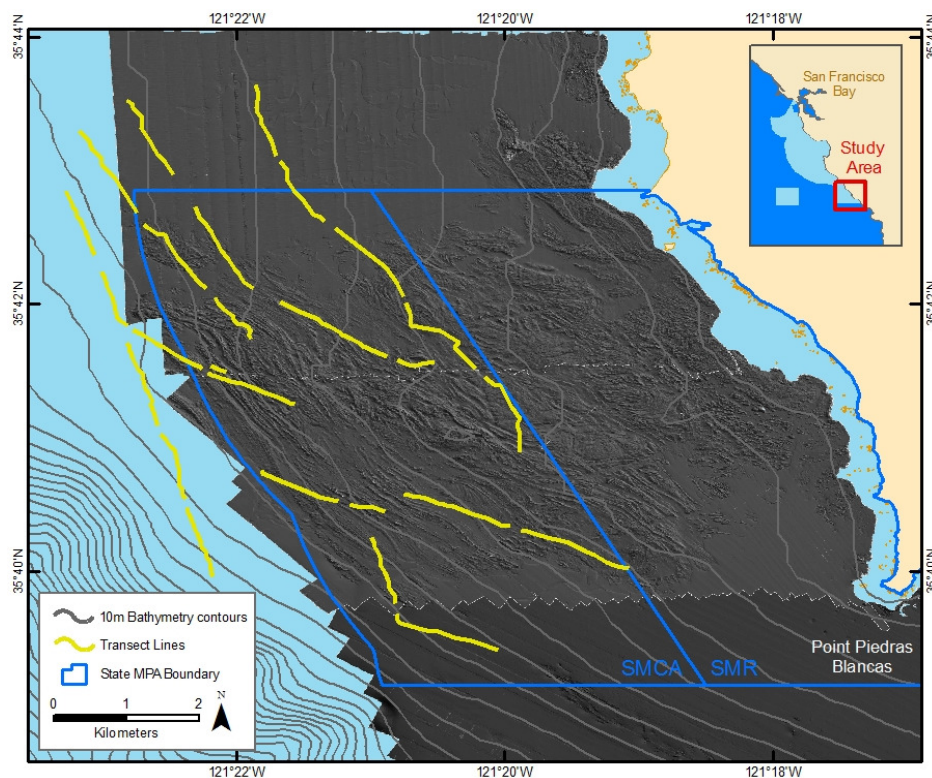
Figure 2. Study area at Piedras Blancas. Yellow lines indicate transects conducted in 2007 and 2008, the majority of which fall within the blue boundary encompassing the State Marine Conservation Area. Multibeam bathymetry (shaded area) shows areas of higher rugosity are concentrated in the MPAs. 10-m isobaths are represented by grey lines and show the rapid descent of the continental slope to the southwest.

The general geology of the study area shows a mixed-relief complex rocky seabed bordered by low-relief unconsolidated sediments to the north and south (Figure 2). Coastal outcrops bordering the area have been mapped as part of the Franciscan melange. These outcrops are composed of complexly-folded and sheared marine sedimentary rocks that were accreted during the subduction of the Farallon plate (e.g., Shervais et al. 2004). Multibeam imagery gathered by the Seafloor Mapping Lab at CSUMB shows that these structurally-complex features extend seaward from the coast to form the majority of the substrate within the MPA. The bedrock is divided by northwest-trending shear zones with well-expressed large- and small-scale, northwest-plunging folds. The generally planar bathymetry of the continental shelf and scattered boulder fields observed in video imagery indicate that the study area is a wave-cut platform eroded and drowned by Holocene sea level rise (Doug Smith, pers. comm.). Video imagery of the bedrock shows

that interstratified hard and soft sedimentary beds give rise to sharply-defined 1 m to 2 m tall ridges. Unconsolidated sediments border the rocky seabed to the north and the south, with rippled scour depressions present in the multibeam data and video imagery adjacent to the reef-sediment interface.

Field sampling

A camera sled was deployed from the National Marine Sanctuary Program's R/V *Fulmar* in July and August of 2007 and 2008. The sled consisted of an aluminum frame protecting an oblique-facing video camera, lights, sizing lasers (10 cm spacing), and navigational equipment; a 250 m armored coaxial cable (tether); and a topside viewing station for piloting the sled and making preliminary observations (Figure 1). The altitude of the sled was controlled by an operator using a dedicated winch that raised and lowered the sled above the seafloor by hauling in or letting out lengths of winch wire and tether. For optimal video quality, the vessel and sled drifted at a speed of one knot or less. Video imagery was recorded live and stored on miniature digital video tapes that were viewed later in the lab. Boat position, sled depth, and some temperature data were also collected.

Video post-processing

Each sample unit for extracting data from video imagery was a non-overlapping video quadrat (referred to here as a 'frame', Figure 3). Distance between the sizing lasers (10 cm) was used to calculate frame width for each sample. To standardize the area encompassed in each frame, we limited imagery to a consistent altitude above the seafloor. Samples in which the frame width was less than 1.0 m or greater than 2.0 m or where the angle was such that the seafloor encompassed less than 75% of the view were eliminated from analysis.

Three habitat variables were collected for each frame: substrate grain-size and corresponding relief, presence of soft sediment bedforms, and presence and morphology of biogenic structure. For the substrate grain-size variable, the primary grain size in a frame (encompassing $\geq 50\%$ of the area) and secondary grain size (encompassing $\geq 20\%$ of the area) were recorded using a modification of the microhabitat classification system of Greene et al. (1999) and as per Tissot et al. (2006). The relief of both the primary and secondary grain size was recorded using a categorical system (Table 1).
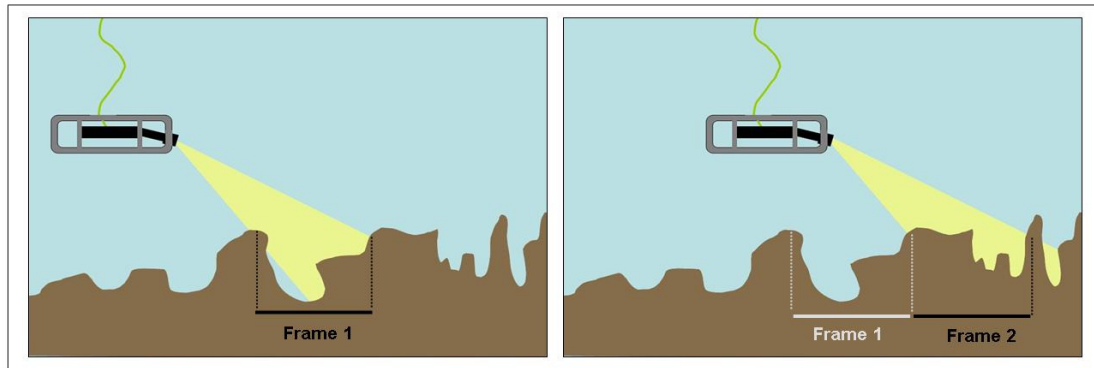
Figure 3. Camera sled frame delineation. Frames are non-overlapping segments of video as the sled moves over the seafloor and are treated as individual sample units

Soft-sediment bedforms were recorded as presence of mounds or depressions in mud or sand that were greater than 10 cm diameter. Biogenic structure was recorded as the presence of specific structure-forming, attached epifaunal invertebrates (sponges, gorgonians, sea whips, and sea pens) greater than 5 cm in height.

The depth of the camera was recorded approximately every minute, using the on-screen display when the camera was closest to the seafloor, and was used as a proxy for seafloor depth throughout that minute of sampling (change in depth rarely exceeded 5 m per 1 km of sampling).

Finally, the observation of any fishes, identified to the lowest taxonomic level possible, was recorded for each frame. Fishes were grouped at the species level (i.e. rosy rockfish, *Sebastes rosaceus*), at the "species complex" level using morphological similarities (i.e. olive or yellowtail rockfish, *Sebastes serranoides* or *S. flavidus*), at the genus level (i.e. large rockfish, *Sebastes* spp >10cm), and also at a more broad taxonomic level (i.e. flatfishes, Order Pleuronectiformes). The resulting dataset consisted of a matrix for each transect, where each sample unit (frame) had a primary and secondary grain-size with corresponding relief, detection/non-detection of bedforms, presence/absence and type of biogenic structure, a depth value, and detection/non-detection of each fish grouping. The occurrence of an individual fish could count in more than one grouping (i.e. a pygmy rockfish could be a species-level group "detection" and also a small

rockfish (<10cm) group "detection") because each grouping was tested with an independent model set.

Table 1. Model variables, categories, and definitions. Substrate, grain size, and relief categories (adapted from Greene et al (1999)); bedform categories; and biogenic structure categories

Substrate	Category	Description
Soft (S)	Mud (M)	Fine-grain soft sediment
	Sand (N)	Coarse-grain soft sediment
	Pebble/Gravel (P)	Loose rocks <2.5 cm
Hard (H)	Cobble (C)	Loose rocks 2.5-24 cm
	Boulder (B)	Loose rock >24 cm
	Rock (R)	Continuous rock (bed or ridge)

Relief	Category	Description
	Crested (CS)	Soft sediment with ripples or waves
	Low (LO)	<1 m above seafloor
	Moderate (MD)	1-2 m above seafloor
	High (HI)	>2 m above seafloor

Bedforms (Mounds/Depressions)	Category	Description
	Present (MODEP)	>10 cm in diameter
	Absent (NOMODEP)	<10 cm in diameter or no form whatsoever

Biogenic Structure	Category	Description
	Soft (BIO-S)	Sessile invertebrates >5 cm in height on soft substrate (sea whips e.g. *Halipteris* spp and *Stylatula* spp and sea pens e.g. *Ptilosarcus* spp)
	Hard (BIO-H)	Sessile invertebrates >5 cm on hard substrate (gorgonians, e.g. *Swiftia* spp; and sponges)
	None (BIO–NO)	No invertebrates >5 cm height

Statistical Analyses: Fitting Generalized Linear Models

To test the response (detection/non-detection) of a fish grouping as a function of the descriptive habitat variables and depth, we fit a set of generalized linear models (GLMs) to examine the response to each variable individually and as a combination of

variables. Our response, y_i, was binomial, where "1" is detection of a fish grouping and "0" is a non-detection.

We fit the models using the GLM function in the 'R' statistical package (R Development Core Team):

$$\ln(P_i/(1-P_i)) = \beta_0 + \beta_1\, x_{1,i} + \ldots + \beta_n\, x_{n,i}$$

where $P_i = \Pr(y_i = 1|\, x_i)$, β_o is a constant, $\beta_1 \ldots \beta_n$ are coefficients corresponding to the predictor variables $x_{1,i} \ldots x_{n,i}$, and y_i is the response variable (detection of a fish at location i).

We were primarily interested in fish occurrence, but our observation system (the towed camera system) only allowed us to quantify fish detection. Fish may have occurred within a frame but were either hidden from view (e.g. concealed in a crevice or hole) or may have fled the frame prior to arrival of the camera; both scenarios render the fish un-detectable. This non-uniform detection probability could potentially bias inferences about their true habitat associations (as in "Scenario 2" from MacKenzie 2006). We assumed that detection probability was essentially uniform, in order to achieve inference about actual fish occurrence; and we recognize that the validity of these inferences is conditional on the validity of that assumption.

The results from each GLM in a model set were compared using Akiake's Information Criterion (AIC). Specifically, the AIC weights (AIC_w) of each model were compared. AIC_w represents the probability that a model is the best-fit, given the other models in the set (Burnham and Anderson 2002). From the AIC_w, evidence ratios (ERs) for the best-fit models were calculated. ERs compare two models: for our results, ER_o compares the null model to the one with the highest AIC and ER_B compares the two highest AIC_w values to infer the degree to which one is the best fit. When any ER between the best-fit model and the next-best model in the set was $\leq \sqrt{10}$, both were considered (Jeffreys 1961).

We examined two sets of models. First, the Substrate Classification Model Set (MS1) used a number of substrate classification schemes that represented different scales of describing the same habitat (i.e. "hard-bottom" vs. "boulder"). Second, the Full Model

Set (MS2) incorporated additional habitat variables along with the resulting best-fit substrate classification scheme of MS1. The lists of all possible models for MS1 and MS2 are extensive and thus are listed in Appendix A.

Statistical Analyses: Substrate Classification Model Set (MS1)

The first model set (MS1) was constructed to determine the substrate classification scheme that best described the response of a given fish group. To investigate a fish grouping's response to different substrate classification schemes, the grain-size and relief data collected for each frame were re-categorized in several other ways. The resulting schemes included (1) substrate, where the seafloor is categorized as either homogenous hard-bottom or soft-bottom; (2) habitat complexity, where a grain-size and relief were combined (e.g., boulder-moderate or sand-low); (3) grain-size alone; and (4) relief alone. The combination of the primary and secondary coverage of each type (1, 2, 3, and 4, above) were also considered, resulting in a total of eight different habitat classification schemes: primary substrate, substrate combination, primary grain-size, grain-size combination, primary relief, relief combination, primary habitat complexity, and habitat complexity combination (Table 2). We used these eight habitat classification schemes as variables to fit a set of nine single-variable GLMs, where the ninth model was the null model, representing a random distribution.

We used ER_B values to determine which model was the best fit of the models in the set. The habitat classification scheme used in the best-fit model (highest AIC_w) from MS1 for each fish grouping was then used in the MS2 analysis. If the two highest AIC_w values held an $ER_B < \sqrt{10}$, both classification schemes were considered in MS2 because both were similarly well-fit. They occurred as alternate sets in MS2, never in the same model.

Statistical Analyses: Full Model Set (MS2)

The second model set (MS2) used the variable that represented the habitat classification scheme obtained from the best-fit model from MS1 as well as the other habitat variables: bedforms, biogenic structure, and depth. For the full model set, sixteen models total, one of every possible combination of all four variables were fit for each response (see Appendix A for the complete set). We inferred that the model (or models)

with the highest AIC_w values contained the predictors that best explain the detection of each fish grouping. ER_o values were used to compare the model with the highest AIC_w to the null model, to explain the combination of variables that best explained the habitat variables a fish was responding to.

Table 2. Habitat classification schemes used in MS1

SUBSTRATE (SUBS)		Categories
S=soft (mud, sand, pebble/gravel) H=hard (rock, boulder, cobble)		
Primary Substrate (**SUBS-primary**)	Describes the predominant substrate (>50% coverage) in a frame	H or S
Substrate Combination (**SUBS-combo**)	Combines the **SUBS-primary** with secondary substrate	HH or SS or HS or SH
		(SH and HS also called "mixed")
GRAIN SIZE (GS)		
M=Mud (fine-grain), N=Sand (coarse-grain), P=Pebble/Gravel (very coarse grain), C=Cobble (diameter 5-25cm), B=Boulder (diameter >25cm), R=Rock		
Primary Grain Size (**GS-primary**)	Describes the grain size (>50% coverage) in a frame	M, N, P, C, B, or R
Grain Size Combo (**GS-combo**)	Combines the **GS-primary** with seconday grain-size	e.g. CM, CN, CC, CB, CR
RELIEF (REL)		
LO=Low (flat and low, <1m), MD=Moderate (~1m), HI=High (>1m), CR=Crested (waves and/or ripples in M, N,		
Primary Relief (**REL-primary**)	Describes the relief of **GS-primary**	LO, MD, HI, or CR
Relief Combo (**REL-combo**)	Combines the **REL-primary** with secondary relief	e.g. MDLO, MDHI, MDCR
HABITAT COMPLEXITY (HABCOM)		
Primary Habitat (**HABCOM-primary**)	Combination of **GS-primary** and **REL-primary**	e.g. RLO, RMD, RHI, ~~RCR~~
Habitat Combination (**HABcombo**)	Combination of **HABCOM-primary** and secondary HABCOM	e.g. RLORMD, NLOCLO

*Note that some combinations are not physically possible. (These have been crossed out, above.) For example, R cannot be CR.

Statistical Analyses: Averaged Coefficients and Relative Importance (RI)

According to Anderson (2007), substantial information exists in the second, third, etc. best-fit models and that the averaged model coefficients and relative importance of the variables draw on this available evidence. Each model set from MS2, for each response, was averaged using the MuMIn (Multi-Model Inference) package for R (Barton 2011). This function averages all coefficients (β_n) across all models in the balanced set and returns an averaged value for each, relative to a user-set reference category. From these averaged coefficients, inference can be made about the categories of each variable that a fish is most strongly associated with.

For all habitat variables, the reference category was set at either mud (M), soft (S), low (LO), or the appropriate combination of these (e.g., MLOMLO for the habitat complexity combination scheme). This was done so that inference regarding the categories would be comparable across responses.

Coefficient values that were greater than the reference category values suggested a positive association with a given category and the magnitude of the association was inferred from its value relative to the reference category value. Coefficients less than the reference category would suggest a negative association with a given category. For averaged coefficients, setting the standard errors that were used for inference at a threshold <2.0 provided a level of certainty about each coefficient value.

The MuMIn package also quantifies the relative importance (RI) of each variable, providing the weight of importance that each plays in the model set. This gives an indication of the certainty that the response (detection) of a fish is associated with a given variable. RI values >0.50 suggest 'some' evidence that the variable plays a role, while values >0.75 suggest 'strong' or 'substantial' evidence.

Spatial Autocorrelation

Imagery data (non-overlapping "frames") were collected as sequential points along transect lines, potentially violating the assumption of independence in a random sample. To account for this, we tested for spatial autocorrelation in the residuals for each best-fit model using *Moran's I*. This correlation coefficient provided a value of the co-variation in responses within a defined spatial zone. We calculated *Moran's I* for each fish grouping at 50 m increments using custom R-code that is equivalent to the correlation function in the spatial package (Appendix C). Our code was modified to sum a weighted *Moran's I* for each transect, in order to preserve the independence of each transect from the others. These values were plotted as "correlograms" for increasing 50 m bins up to a maximum of 1000 m. For fish species that showed spatial autocorrelation (a decreasing *Moran's I* with increasing distance), the raw responses were culled to remove frames that were within 5 m of each other. Residuals from the culled data were then re-examined using the modified correlogram R-code. Fish species that did not have a decreasing *Moran's I* with increasing distance were assumed not to be spatially autocorrelated.

We used the residuals of the best-fit models to test for autocorrelation. This allows for the model variables to primarily account for the variability in the response and

then quantifies the remaining variation not explained by the variables in the original model fit.

RESULTS

A total of 25 video transects covering approximately 40.5 km^2 of seafloor were conducted with the camera sled system at the PBSMCA. Depths of the transects ranged from 30-120 m. Of the 15,116 frames observed, 10,540 frames were useable based on the criteria for standardizing frame size and used for analysis. The majority of frames were homogenous soft-sediment substrates (70% of frames), particularly fine-grain sandy-mud. Harder substrata were observed in 24% of frames and mixed hard-and-soft was observed in 6%. Homogenous mud substrates (MM) were the most commonly observed grain-size (64%) and rock (ridges and bedrock) was the next most common (17%).

The two other structural habitat variables, soft-sediment bedforms and biogenic structure were seen in 45.7% and 11.1% of the total frames, respectively. Biogenic structure comprised two classes; "hard substrate biogenic structure" (sponges and gorgonians) was observed in 1.5% of frames and "soft substrate biogenic structure" (sea whips and pens) was observed in 9.5% of frames. Although sponges are sometimes observed growing in soft substrates, this was not observed in imagery from this study.

A total count of 2,186 fish were observed within useable frames and identified to various taxonomic levels (Table 3). Hereafter, all fish counts discussed refer to counts of a fish grouping's detection in a frame, not the total number of individuals observed in a frame. The detection of fish in the frame-by-frame analysis totaled 1,403 fishes in 10,541 frames. Fish that were present in fewer than five frames and did not fit into a species, species-complex, or general group were not used in analysis.

Spatial Autocorrelation

Moran's I correlograms for the residuals of each response's best-fit model from MS2 demonstrated minimal to no spatial autocorrelation for all fishes except pygmy rockfish (Appendix B, Figure B6). The re-plotted correlogram for the culled data for this species showed no spatial autocorrelation (Appendix B, Figure B7), suggesting that the pygmy rockfish data are spatially autocorrelated at distances less than 5m. The culled data were used in the GLM sets.

Table 3. All fishes observed in the study area. The level indicates the taxonomic level fish were identified to, while the response grouping shows the groups as used in the GLMs. $n_{individuals}$ represents the total individuals observed for each group (total $n_{individuals}$ = 3,237) while n_{frames} represents the number of frames in which a given grouping occurs (total n_{frames} = 2,128).

Level	Response Grouping	Description	$n_{individuals}$	n_{frames}
Species Level	Painted greenling	*Oxylebius pictus*	12	12
	Blackeye goby	*Rhinogobiobs nicholsi*	314	236
	Pygmy rockfish	*Sebastes wilsoni* [2]	149	11
	Rosy rockfish	*Sebastes rosaceus* [1,3]	18	17
	Squarespot rockfish	*Sebastes hopkinsii* [3]	30	7
Species Complex	Blue and black rockfish (BLBK)	*Sebastes mystinus* and *S. melanops* [3]	46	22
	Copper/gopher rockfish (CPGP)	*Sebastes caurinus* and *S. carnatus* [3]	33	32
	Olive and yellowtail rockfish (OLYT)	*Sebastes serrinoides* and *S. flavidus* [3]	71	38
	Canary/vermillion/yelloweye (CVYE)	*Sebastes pinnager, S. miniatus, S. rubberimus* [3]	30	39
	Unidentified Sebastomus	Sebastomus complex [3]	363	321
Genus Level	Ronquils	*Rathbunella* sp	32	32
	Small rockfish (<10cm)	TOTAL	274	104
		Unidentified *Sebastes* spp <10cm [2]	225	93
	Large rockfish (>10cm)	TOTAL	925	584
		Unidentified *Sebastes* spp >10cm [3]	323	195
		Cowcod *Sebastes levis* [3]	1	1
		Boccacio *Sebastes paucispinus* [3]	1	1
		Flag rockfish *Sebastes rubrivinctus* [3]	3	3
		Greenspotted rockfish *Sebastes chlorostictus* [3]	1	1
		Halfbanded *Sebastes semicinctus* [3]	1	1
		Starry rockfish *Sebastes constellatus* [3]	4	4
Order/Family Level	Unidentified Flatfishes	Order Pleuronectiformes	289	283
	Combfish/lingcod (CMLG)	TOTAL	38	37
		Unidentified lingcod/combfish	15	15
		Lingcod *Ophoidon elongatus*	4	4
		Combfish *Zaniolepis* spp	19	19
Other species identified but not used in analysis (n<5)				
	Pacific hagfish	*Etaptretus stouti*	2	2
	Kelp greenling	*Hexagrammus decagrammus*	4	4
	Unidentified Poachers	Family Agonidae	2	2
	Unidentified Rays	Family Rajidae	4	4
	Pink surfperch	*Zacentrus rosaceus*	4	4

[1] Counted in Sebastomus complex

[2] Counted in small rockfish group

[3] Counted in large rockfish group

Overall Model Results

All best-fit models (highest AIC_w) in MS1 (Table 4) and MS2 (Table 5) had ER_o values above $\sqrt{10}$, demonstrating at least substantial association with the seafloor substrate, regardless of scale, for all groups (conditional on the assumption of uniform detection probability). In MS1, the most coarse-scale classification scheme, substrate (hard/soft/mixed), was the best predictor for nine fish groups, while the grain-size scheme (best predictor for two fish groups) and the habitat complexity scheme (grain-size plus relief, best predictor for four) described the rest (Table 4). The relief-only scheme was

not the best predictor for any fish group, although this scheme was considered in some MS2 sets because it was a next-best-fit model with an ER_B value $<\sqrt{10}$ for the combfish/lingcod group. Support for the best substrate scale within a set was often very clear. ER_B were greater than $> \sqrt{10}$ for all but four fish groups (details below). These responses had one or more habitat classifications from MS1 that were explored in MS2.

There was observable evidence for some form of habitat association by all fish groups considered because the ER_o between the best-fit model and the null model in MS2 was greater than 449, in all cases (assuming inconsequential detection bias, relative to the strength of the evidence ratios). Although the best-fit models varied in the number and type of variables, the best-fit for each response always included the substrate variable (Table 5). For all best-fit models that contained two or more variables, the depth variable was always present. ER_B values for all best-fit and second-best-fit models in MS2 were less than $\sqrt{10}$. This suggests that, while the models explain the distribution better than the null model (representing a random distribution) for all responses, the best-fit models within a set were similar. RI values and categories corresponding to averaged coefficients nonetheless allow us to infer which variables and categories of variables supported each response.

Table 6 represents the specific categories within each variable with which each fish was most strongly associated. For each fish grouping, we observed an association to at least one particular substrate category. For most fish groupings, we observed an association to more that one substrate category, such as large rockfish who demonstrated a positive association with 53 categories of habitat complexity classification scheme. For fish-habitat associations that were observed with more than two categories, the relative values of the coefficients are plotted in Figures B1A/B/C of Appendix B. Standard errors were > 2.0 for most coefficients in the bedform and biogenic structure variables, demonstrating that inference from these variables was often inconclusive. (Refer to Appendix B, Tables B3 and B5 for all coefficient values.)

Table 4. Results of MS1 AIC comparison. ER_o represents the ratio between the best-fit and null-model AIC_w values. ER_B represents the ratio between the best-fit and second-best-fit model. Multiple substrate classification schemes are reported for responses where ER_B values were < $\sqrt{10}$. The corresponding AIC_w value(s) ($AIC_w1/2/3$) for these fish groupings are also shown for the best-fit model (and the second and third best-fit models, where applicable).

	Best-supported Substrate Classification Scheme	$AIC_w1/2/3$	ER_o	ER_B
Single Species Level				
Painted greenling	SUBS-combo	0.91	3.51E+07	11.25
Blackeye goby	GS-combo	1.00	1.51E+175	9.74E+06
Pygmy rockfish	SUBS-primary	0.79	8.24E+05	7.40
Rosy rockfish	SUBS-combo	0.83	1.15E+08	5.94
Squarespot rockfish	SUBS-combo	0.75	449.62	5.48
Slecies Complex Level				
Blue/Black rockfish (BLBK)	GS-primary/SUBS-combo	0.63/0.26	6.07E+08	2.39
Copper/Gopher rockfish (CPGP)	SUBS-combo/SUBS-primary	0.66/0.24	7.08E+12	2.75
Olive/yellowtail rockfish (OLYT)	HABCOM-primary	0.99	2.81E+21	80.96
Canary/Vermillion/Yelloweye rockfish (CVYE)	GS-primary	0.88	1.60E+17	7.53
Sebastomus rockfish	HABCOM-primary	0.99	7.18E+166	78.09
Genus Level				
Ronquils	SUBS-primary/HABCOM-primary/GS-primary	0.47/0.28/0.17	4.98E+15	1.66
Small rockfishes (<10cm)	HABCOM-primary	0.91	8.99E+49	10.32
Large rockfishes (>10cm)	HABCOM-combo	1.00	7.53E+285	3.45E+03
Order/Multi-family Level				
Flatfishes (Pleuronectiformes)	SUBS-combo	0.82	1.96E+41	4.43
Combfish/Lingcod	SUBS-primary/REL-primary	0.41/0.33	6.10	1.24

Table 5. Results of MS2 AIC comparison and corresponding RI values for each variable. RI values >0.75 are bolded, indicating substantial evidence while RI values between 0.50 and 0.75 are italicized, indicating positive but not substantial evidence.

	Best Fit Model	AIC_w	ER_o	ER_B	Relative Importance (RI) Value			
					Substrate	Depth	Biogenic Struct	Bedforms
Single Species Level								
Painted greenling	SUBS-combo + DEPTH	0.60	4.15E+09	2.72	**1.00**	**0.99**	0.18	0.27
Blackeye goby	GS-combo + DEPTH + MODEPS	0.32	1.26E+177	2.18	**1.00**	**0.98**	0.39	0.54
Pygmy rockfish	SUBS-primary + DEPTH	0.54	1.32E+07	2.72	**1.00**	**0.94**	0.22	0.27
Rosy rockfish	SUBS-combo	0.41	1.15E+08	1.79	**1.00**	0.36	0.12	0.27
Squarespot rockfish	SUBS-combo	0.35	4.50E+02	1.44	**0.96**	0.41	0.17	0.29
Sub-genus Level								
Blue/Black rockfish (BLBK)	SUBS-combo + DEPTH	0.35	1.54E+11	1.37	**1.00**	**1.00**	0.26	0.42
Copper/Gopher rockfish (CPGP)	SUBS-combo + DEPTH + BIOGENIC	0.32	1.05E+14	1.76	**1.00**	**0.91**	*0.63*	0.28
Olive/yellowtail rockfish (OLYT)	HABCOM-primary	0.46	2.81E+21	2.70	**1.00**	0.27	0.14	0.27
Canary/Vermillion/Yelloweye rockfish (CVYE)	GS-primary	0.40	1.60E+17	1.62	**1.00**	0.38	0.12	0.27
Sebastomus rockfish (STOM)	HABCOM-primary	0.36	7.18E+166	2.18	**1.00**	0.27	0.28	0.31
Genus Level								
Ronquils	SUBS-primary + DEPTH + MODEPS	0.13	5.66E+15	1.05	**1.00**	*0.53*	0.18	*0.50*
Small rockfishes (<10cm)	HABCOM-primary + DEPTH	0.60	1.24E+56	2.63	**1.00**	**1.00**	0.17	0.28
Large rockfishes (>10cm)	HABCOM-combo + DEPTH + BIOGENIC	0.46	4.98E+287	1.71	**1.00**	**0.75**	**0.96**	0.37
Order/Multi-family Level								
Flatfishes (Pleuronectiformes)	SUBS-combo	0.35	1.96E+41	1.75	**1.00**	0.27	0.25	0.36
Combfish/Lingcod	REL-primary + DEPTH + MODEPS	0.29	1.12E+03	1.21	**0.84**	**1.00**	0.21	*0.58*

Table 6. Habitat categories with which each fish group was observed to have the strongest associations. The substrate column displays the category with the highest (and in most cases, second highest) coefficient value. Asterisks (*) indicates an association with multiple coefficients, see Appendix B for more information. Tilde (~) indicates that the standard errors for the coefficients were >2.0 and are not thus not reported.

Single Species Level	Substrate	Depth	Biogenic Struct	Bedforms
Painted greenling	**HS, HH**	**shallow**	~	~
Blackeye goby	**MR, RC***	**shallow**	**Soft, Hard**[-]	**NO**
Pygmy rockfish	**H**	**deep**	~	~
Rosy rockfish	**HS, HH***	**deep**	**Hard**	~
Squarespot rockfish	**SH, HH**	**deep**	~	~
Sub-genus Level				
Blue/Black rockfish (BLBK)	**HS, SH***	**shallow**	~	~
Copper/Gopher rockfish (CPGP)	**HS, HH***	**deep**	**Soft, Hard**	**NO**
Olive/yellowtail rockfish (OLYT)	**RHI, RMD***		**Hard**	~
Canary/Vermillion/Yelloweye rockfish (CVYE)	**B, R***		~	~
Sebastomus rockfish (STOM)	**BHI, MCS***		**Hard, Soft**[-]	**NO**
Genus Level				
Ronquils	**H**	**deep**	**Hard**	~
Small rockfishes (<10cm)	**MCS, CLO***	**deep**	**Soft, Hard**[-]	~
Large rockfishes (>10cm)	**MLORMD***	**shallow**	**Soft, Hard**	**YES**
Order/Multi-family Level				
Flatfishes (Pleuronectiformes)	**SS, SH**[-]		**Soft**	**YES**
Combfish/Lingcod	**CS, LO**	**deep**	**Soft**[-]	**NO**

Species-level Model Results

We identified 428 fishes to one of five species levels: painted greenling *Oxylebius pictus* (n=12), blackeye goby *Rhinogobiops nicholsi* (n=381), rosy rockfish *Sebastes rosaceus* (n=17), pygmy rockfish *S. wilsoni* (n=11), and squarespot rockfish *S. hopkinsi* (n=7).

For MS1, the substrate classification scheme that best described the distribution of fish at the species-level was substrate (hard vs. soft). The substrate-combination (SUBS-combo) scheme described squarespot rockfish (AIC_w=0.75, ER_B=5.48), rosy rockfish (AIC_w=0.83, ER_B=5.94), and painted greenling (AIC_w=0.91, ER_B=11.25) while the primary-only substrate (SUBS-primary) best described pygmy rockfish (AIC_w=0.79, ER_B=7.40). Blackeye gobies, however, were shown to be distributed based on the grain-size combination scheme (GS-combo, AIC_w=1.00, ER_B=9.75x10^6) (Table 4).

For the averaged full model (MS2), the substrate variable had the highest RI for all species, followed by depth, bedforms, and biogenic structure (Table 5). For painted greenling, blackeye goby, and pygmy rockfish, depth showed strong evidence as an important variable (RI = 0.99, 0.98, and 0.94, respectively). Depth was also present in each of the best-fit models from MS2 for each of these groups. Bedforms demonstrated some evidence of importance in the distribution of blackeye gobies (RI=0.54).

From MS2, averaged coefficient values demonstrated that painted greenlings and pygmy rockfish were both observed to associate with primarily hard substrate categories, however painted greenlings were observed to be associated with shallow habitats while pygmies were observed to be associated with deeper areas (Table 6). Squarespot rockfish showed an observable association with mixed (soft-hard) and homogenous hard-bottom substrate categories. Blackeye gobies showed a strong observable association with a variety of grain-size combination categories, the strongest of which were mud-rock and rock-cobble (see Appendix B for a complete list) as well as a positive association with soft-substrate biogenic structure (though a negative association with hard-substrate biostructure) and to soft sediment without bedforms. Rosy rockfish showed an observable association with both mixed and homogenous hard substrate categories and hard-

substrate biogenic structure. (See Appendix B for a full list of averaged coefficient values for which the corresponding categories are described above.)

Species-complex-level Model Results

We identified 471 fishes to five multi-species groups (species complexes): blue/black rockfishes *Sebastes mystinus* and *S. melanops* (BLBK, n=22), copper/gopher rockfishes *S. caurinus* and *S. carnatus* (CPGP, n=32), olive/yellowtail rockfishes *S. serranoides* and *S. flavidus* (OLYT, n=38), canary/vermillion/yelloweye rockfish *S. pinnager, S. miniatus,* and *S. ruberrimus* (CVYE, n=39), and the *Sebastomus* complex within the *Sebastes* genus (STOM, n=340) which includes starry rockfish *S. constellatus,* greenspotted rockfish *S. chlorostictus*, rosy rockfish *S. rosaceus*, among others.

The species-complex-level revealed a broader spectrum of substrate classification schemes that best described the responses (Table 4). The SUBS-combo scheme was best only for CPGP (AIC_w=0.66) and due to the low ER_B (2.75) the SUBS-primary scheme was also considered in MS2 (AIC_w=0.24, ER_B=7.08). Primary grain-size (GS-primary) best described the distribution of both CVYE and BLBK (AIC_w=0.63 and 0.88, ER_B=2.39 and 7.53, respectively). Because of the low ER_B for BLBK, the second-highest classification scheme of SUBS-combo (AIC_w=0.26, ER_B=6.07) was also considered in MS2. For OLYT and STOM, the best classification scheme was the primary habitat-complexity scheme (HABCOM-primary, AIC_w=0.99 and 0.99, ER_B=80.96 and 78.09 respectively).

For the averaged full model (MS2, Table 5), the substrate variable had the strongest RI for all groupings, although depth also had a strong RI for BLBK and CPGP rockfish (1.00 and 0.91, respectively), suggesting that there is substantial evidence that substrate and depth play an important role in the distribution of these groups. CPGP also had a notable RI for the biogenic structure variable (0.64), suggesting some evidence that this variable is associated with CPGP distributions.

Averaged coefficients (Table 6) demonstrated that BLBK showed the strongest observable association with mixed substrates, while CPGP showed the strongest observable association with mixed and homogenous hard substrates. OLYT showed an observable association with high and moderate relief rock ridges and STOM with high

relief boulder grain sizes as well as crested mud. Both showed an observable association with hard-substrate biogenic structure and STOM showed an observable negative association to soft biostructure and bedforms. CVYE were observed to be associated with boulder and rock grain sizes. (See Appendix B for a full list of averaged coefficient values for which the corresponding categories are described above.)

Genus-level Model Results

Ronquils of the *Rathbunella* genus (*R. alleni* and *R. hypoplecta*) were indistinguishable and thus grouped together at the genus level (n=32). Additional genus-level responses were small rockfish (~ 5 – 10 cm) and large rockfish (> 10 cm). Small rockfish (n=104) included pygmy rockfish, halfbanded rockfish *Sebastes semicinctus*, and unidentifiable small rockfishes. Large rockfishes (n=584) included all other identifiable (see Table 3 for a complete list) and unidentifiable rockfishes.

For the substrate classification scheme (MS1; Table 4), both size classes of rockfish were observed to respond most strongly to habitat complexity (HABCOM) schemes; small rockfish responded to HABCOM-primary AIC_w=0.91, ER_B =10.32) and large rockfish responded to the HABCOM-combo scheme (AIC_w=1.00, ER_B =3445). Ronquils were observed to respond most strongly to the SUBS-primary scheme (AIC_w=0.47, ER_B =1.66). However due to the low ER_B of ronquils, two additional schemes were considered in MS2: HABCOM-primary (AIC_w=0.28, ER_B =2.81) and GS-primary (AIC_w=0.17, ER_B =5.96) (Table 5).

For the averaged full model (MS2; Table 5), the substrate variable again had the highest RI for each genus grouping. For small rockfish, depth had an equally strong RI (1.00). Large rockfish and ronquils showed some evidence of RI for the depth variable, though to a lesser degree (0.75 and 0.53, respectively). Large rockfish also showed a strong RI of 0.96 to biogenic structure, giving a substantial certainty that they are responding to biogenic structure. Biogenic structure was also present in the best-fit model (AIC_w=0.46, ER_o=4x10^{287}) for large rockfish.

Averaged coefficient values from MS2 (Table 6) demonstrated that ronquils were observed to be associated with deeper hard substrates as well as with hard-substrate biogenic structure. Large rockfish showed an observable association with shallow depth

and many habitat complexity categories, but the strongest was flat-mud-moderate-rock (see Appendix B for all categories). Large rockfish also showed an observable association with biogenic structure in both hard and soft substrates and, curiously, bedforms in soft substrates. Small rockfish showed an observable association with deeper depths, soft-substrate biogenic structure, and an association with a variety of habitat types (see Appendix B for the complete list). The strongest observable association was with crested mud and low-relief cobble. (See Appendix B for a full list of averaged coefficient values for which the corresponding categories are described above.)

Order-level and Multi-family-level Model Results

All flatfishes (Order Pleuronectiformes, n=283) were grouped together. This included right-eye and left-eye flatfishes, whether or not the eye-side was distinguishable. It is likely that a large portion of these flatfish were sanddabs (*Citharichthys* spp.); however, to maintain accuracy in identifications they were all grouped at the order level. A second group consisting of combfish (*Zaniolepis* spp.) and lingcod (*Ophiodon elongatus*) was created because of the often indistinguishable occurrence of both fishes over soft sediments ("CMLG", n=37). Most of the smaller (younger) lingcod fell into this "indistinguishable" category and were observed over soft substrates. Most of the larger (older) lingcod occurred over hard-bottom substrates.

In the habitat classification scheme model (MS1; Table 4), flatfish were observed to respond most strongly to the SUBS-combo scheme (AIC_w=0.82, ER_B=4.43) while CMLG were observed to respond most strongly strongest to the SUBS-primary scheme (AIC_w=0.41, ER_B=1.24) but also to the primary relief scheme (AIC_w=0.33, ER_B=3.80).

For the averaged full model set (MS2; Table 5), substrate demonstrated substantial evidence as an important variable for flatfishes (RI=1.00) while both depth and substrate demonstrated substantial evidence for CMLG (RI=0.84, 1.00 respectively). There is some evidence that bedforms may also play a role for CMLG, but to a lesser degree (RI=0.58).

Averaged coefficients from MS2 (Table 6) demonstrated an observable positive association of flatfishes to homogenous soft substrates and an observable negative association with mixed substrates. Additionally, flatfishes showed an observable

association to soft-sediment biogenic structure and bedforms. Standard errors were too high to report the relief category with which CMLG were most strongly associated with however they showed an observable negative association with soft-sediment biogenic structure and bedforms. (See Appendix B for a full list of averaged coefficient values for which the corresponding categories are described above.)

DISCUSSION

These results demonstrate that there is strong evidence suggesting that seafloor substrate is an important indicator of demersal fish distributions. Distributions vary across different fish species (and genera, family, etc.) and morphologies, both in the scales at which fish respond to the seafloor and in the importance of certain substrate or grain size categories. For the most part, fish-habitat association data derived from imagery collected with the camera sled are consistent with other studies conducted along the California central coast using imagery from a human-occupied submersible (Yoklavich et al. 2000; Laidig et al. 2009). The fish-habitat associations reported here were quantifiable using an AIC comparison of generalized linear models. This demonstrates the value of this approach both in obtaining results consistent with other literature and for exploring the use of a new analytical method that eliminates very few data from the set – an important consideration amidst the challenges of collecting data in deep ocean ecosystems. Given the widespread use of substrate and depth in describing demersal fish distributions (Miller and Lea 1976; Eschmeyer et al. 1983; Love et al. 2002), these results validate the use of these variables, particularly at this site and for the substrates observed. Additional structural variables of biogenic structure and soft-sediment bedforms demonstrated little importance in fish distributions.

By modeling the response of each fish grouping to a variety of equivalent habitat classification schemes, we showed that some schemes describe fish-habitat associations better than others. While these single-variable classification-scheme models (MS1) explained the specificity of the scale that best describes the distribution of each grouping, inference from the averaged coefficients in MS2 suggested the particular substrate, grain-size, or relief categories a given fish was observed to associate with.

Primary substrate (SUBS-primary) and substrate combination (SUBS-combo) most commonly described the scales at which multiple groups were distributed. This suggests that characterizing the seafloor in terms of substrate (soft, hard, or mixed) is important, perhaps essential when describing fish habitats. This is true across different fish grouping levels; all four showed at least one best-fit model to this type of classification. This scale is a straightforward classification and can easily be obtained and applied using moderate-resolution (10-20 m) multi-beam maps or simple imagery surveys.

The grain-size and the habitat-complexity (grain size plus relief) microhabitat scales were also important in describing fish distributions, suggesting that not only the basic substrate types, but micro-habitats within substrates are important. Some groupings, such as blackeye gobies (which responded most strongly to grain-size) showed an association with more specific habitats (i.e. mud-rock) within an area that was categorized as "mixed" by another, simpler scheme. Two observed color morphs of gobies may further describe the distribution of this small species. Green- or yellow-shaded gobies are often seen over higher-relief homogenous hard substrates while white or tan gobies were observed primarily over mixed sand and cobble substrates. Further investigations of sub-species-level distributions may explain variability within grain-size category associations.

Two rockfish-complex groups (OLYT and *Sebastomus*) also responded to the grain-size scale, but with the added component of relief, suggesting an even more specific habitat association. Indeed, these two groups were frequently seen in moderate-relief patches of varying grain-sizes. Olive/yellowtail rockfish are known to occur over boulders and rock walls (Love et al. 2002). The *Sebastomus* complex contains too many species to infer associations about each, though rosy rockfish probably composed a significant amount. Rosy rockfish have been described to inhabit a variety of rock substrates including boulders, high-relief rock, and sometimes low-lying cobbles (Love et al. 2002).

Our analytical approach assumed a uniform detection probability; that individuals of each species were equally detectable in each habitat type. Cryptic or well-disguised species in concealing habitats and species or groups that may be more easily startled by

the oncoming sled and remain out of view – occurrences which both may be present in these data – can violate this assumption when they are undetected in observations. Although MacKenzie (2006) contends that inferences made in violation of this assumption may result in an inaccurate estimation of habitat use by a species, given the difficulties of surveying the depths of the ocean floor with any tool, we must proceed with the assumption that we sampled an adequate amount of each habitat type to accurately represent distributions within each type. With this assumption acknowledged, the results presented here represent our understanding of the distributions as they were observed with the camera sled.

The taxonomic level to which an individual fish can be identified (often a factor of the image quality) can influence the applicability of these associations and, ultimately, their role in management. For many fishes, especially rockfishes (Genus *Sebastes*) and flatfishes (Order Pleuronectiformes) the ability to identify to species proved difficult, given the continuous movement of the sled (and often of the fish). While grouping at the genus or species-complex level prevents us from making inferences about some individual species, broad grouping of fishes are important groups for management considerations. These more general groupings represent regulatory units, such as recreational bag limits of 10 "rockfish" per person per day (CDFG 2011) on recreational vessels. Commercial fisheries also operate under "rockfish" quotas. In both cases, take of fish is not managed at the species scale, with the exception of a few protected species (i.e. cowcod and boccacio).

The RI scores provided support for the role that each of the variables play within a model set. Clearly, for each taxonomic-level grouping, substrate was the most strongly supported variable for nearly all groups (depth, the one exception, was the strongest for combfish/lingcod). In many cases, depth was the second-most supported variable. The disparate importance of bedforms and biogenic structure variables for most groupings suggests that these have little to no effect on distributions; minimally, we can say that they received considerably less support than substrate and depth. Variables from models with high RI values across many groups, for example substrate (hard vs. soft), may be considered good global monitoring attributes for monitoring many groups simultaneously. Variables that demonstrated high relative importance for certain groups,

such as biogenic structure for large rockfishes, can be considered important attributes to study for monitoring a given group of interest.

Ideally, a multiple-variable landscape description for each fish grouping would be the outcome resulting from these models. The high ER_o scores for MS2 suggest that, the best-fit model(s) are quite good at describing distributions compared to a random model (the null) while the low ER_B values suggests that the combination of variables does not affect the fit of the model as much. It is possible that other variables not collected in this study would better describe the distribution. Such variables worth considering include distance to an ecotone (e.g., Hunter-Thompson 2011), a measure of rugosity obtained from multibeam data (e.g.,Young et al. 2010), and the co-occurrence of conspecifics and other fishes (Williams and Ralston 2002). Other distribution literature suggests that demersal fish distributions are not simple but are contingent on many other variables (Anderson et al. 2007). Continuing incorporation of additional environmental and structural variables will eventually lead to the ability to converge upon a model that includes the multitude of predictors of fish distributions.

The high standard error values for some of the averaged model coefficients prevented us from making statements with certainty about those specific categories. These standard error values may be due to data collection methods used with the camera sled. It is difficult to "fly" the sled at a constant altitude over stretches of moderate- and high-relief hard substrates. Thus, useable frames within the study area were often representative of lower-relief and soft-bottom substrates. Regardless, these lower-relief habitats contained different taxonomic groups, fewer fish, less diversity, and mostly flatfish, which are difficult to identify to species with camera sled imagery. Low sample sizes of each fish grouping compared to the high number of sample units (10,541 frames) may also have contributed to the high standard errors for coefficients and constrained our ability to confidently infer more about each category.

There is an increasing need to address spatial autocorrelation in distribution studies (Dormann 2007; Carl and Kuhn 2007) because it violates the assumption of independence. However, by plotting *Moran's I* correlograms using model residuals, we determined that substantial spatial autocorrelation existed for only one species (pygmy rockfish). To correct for this, we sub-sampled the data by removing every other point,

modeled this new data in the GLM set, and re-plotted the *Moran's I* correlogram. The new correlogram for pygmy rockfish (Appendix B) verified that *Moran's I* was no longer decreasing with increasing distance. Pygmy rockfish were the only fish to demonstrate spatial autocorrelation and they are known schooling fishes that occur in large groups (Yoklavich et al. 2000; Laidig et al. 2009). Pygmy schools were observed in this study spanning multiple consecutive frames, so removing adjacent frames in the culling step naturally reduced this violation of assumption. Culling in some circumstances may be unavoidable depending on the behavior, life history, and ecological niches of certain fishes. Since spatial autocorrelation was only observed for this one species, we were able to address it with the culling process. Had more species demonstrated autocorrelation, we would have incorporated a term in the model. This approach is strategic because it 1) minimizes removal of data points from an already sparse set and 2) can confirm the assumption of independence. By using the model residuals rather than the raw data, we were able to detect spatial autocorrelation (or lack thereof) *after* the model had accounted for the habitat variables that we originally sought to explain and therefore minimized the removal of data points.

Overall, the generalized linear models, in combination with AIC weights, model averaging techniques, and *Moran's I* correlograms provided a robust analysis of the seafloor habitat associations of fish groupings to the extent that it is detectible using tow-sled technology. These techniques, when used in future model-fitting with additional landscape variables not investigated here, will ultimately construct an image of the landscape with the components and properties to which fish species and groups are being detected.

CHAPTER 3

SUMMARY OF THE APPLICATIONS OF
MARINE LANDSCAPE MODELING TO
MANAGEMENT AGENCIES

The research presented here was, from its inception, directed toward informing resource management at the federal level, with the Monterey Bay National Marine Sanctuary (MBNMS, NOAA) as well as at the California state level with the MPA Monitoring Enterprise and the California Department of Fish and Game (CDFG). MBNMS and CDFG manage large areas of the marine environments and yet they lack sufficient information on many of the resources they manage (MLMA 1998; NOAA 2008, 2009). Data on fish distributions and habitat characterizations are important for understanding how to manage fisheries and protect habitats (Airame et al. 2003). By evaluating imagery data collected by the sled and a multi-variable modeling approach to understanding how fish use habitat, we have provided information that is of potential value to two management agencies.

MONTEREY BAY NATIONAL MARINE SANCTUARY (NOAA)

As one of the nation's largest National Marine Sanctuaries, the MBNMS is faced with the daunting task of characterizing the many ecosystems that fall within its limits (NOAA 2008). Its 8000 km^2 are home to a vast number of diverse ecosystems including submarine canyons, deep seamounts, the productive rocky reef and soft-bottom shelf, with tidepools and sandy beaches scattered along its roughly 450 km of coastline.

The results presented in this study can answer and inform some of the questions and issues that the MBNMS must grapple with as a management agency. Three major documents outline the issues that MBNMS must address: 1) The MBNMS Condition Report (NOAA 2009); 2) The MBNMS Management Plan (NOAA 2008); and 3) The MBNMS Ecosystem-Based Management Initiative (NOAA 2011).

The Condition Report (NOAA 2009) asks questions about the status of knowledge of resources in the MBNMS. This report asks specifically about the "abundance and distribution of major habitat types and how [are they] changing?" The report recognizes that little is known about the offshore environment; however, the results presented here directly address this question by describing the habitats at Piedras Blancas, a previously uncharacterized area of the Sanctuary. Prior to these imagery surveys, very little was known about the seafloor habitats in the site.

The Management Plan (NOAA 2008) guides the process for understanding and, ultimately, protecting the resources within the MBNMS (NOAA 2008). Action plans within this document identify areas or issues in the MBNMS that are in need of attention. These plans can stem from concerned public citizens or from top-down issues presented from an umbrella government agency. The results from these analyses presented above can be specifically applied to the Sanctuary Integrated Monitoring Network (SIMoN) Action Plan with its goal to create an ecosystem-wide monitoring program. These data will serve as the baseline for ecosystem data collected in the MBNMS. In order to monitor the resources in the sanctuary, a baseline is needed by which to measure natural- and anthropogenic-induced changes in the future.

Characterization of these ecosystems is an ongoing objective in the MBNMS Management Plan (NOAA 2008) and defining these systems with increasing specificity will continue to improve the scale at which they are characterized. Prior to the imagery surveys of this project and multibeam mapping by the CSUMB Seafloor Mapping Lab, very little was known about the shelf seafloor of the south sanctuary other than from recreational fishing catches. These surveys and analyses have provided the MBNMS with fish and habitat data for a previously uncharacterized area. Managers can make decisions with increased understanding about the organisms and habitats found there.

The MBNMS Ecosystem-Based Management Initiative (EBMI, NOAA 2011) focuses on improving current management efforts by incorporating ecosystem-based approaches that consider the interactions within systems. The objectives of EBMI are: to address ecosystem health and function, protect unique and rare areas, and facilitate research to better understand human impacts and sustainable resource use. The data

collected here provides baseline characterization from which changes in these the ecosystem objectives can be measured.

In addition to these reports, a major goal of the MBNMS in general is to provide outreach and education about the sanctuary to the public. Aside from the nearshore areas around Monterey Bay, much of the MBNMS is fairly inaccessible to the public and thus there is a struggle in demonstrating how "their" sanctuary is valuable. Making these data and images available to the public engages awareness and interest in what may only look like endless blue water from where they stand or drive. Furthermore, making data available to managers allows them to make informed statements and decisions about their respective areas of management.

Data from these surveys conducted at Piedras Blancas, as well as at several other areas of interest within MBNMS, have been compiled in an outreach report titled "Characterizing the Deep: Surveys in the Monterey Bay National Marine Sanctuary 2007-2010". In this report, readers are able to view photos and simplified data collected during characterization surveys (IfAME/MBNMS 2011). Sections highlight the importance of fish distributions throughout different study areas and the habitats types in each – a distilled version of the details provided in the analysis here. Also, a great deal of selected imagery from all IfAME-MBNMS Partnership surveys is made available in an online interactive database known as the Shelf Characterization and Image Display (SCID; http://sep.csumb.edu/ifame/scid). This GoogleMap-based interface allows the public to see all of the locations where surveys have been conducted and to view photos and videos from these sites, many of which support very diverse ecosystems, throughout the MBNMS. Aside from the small visitor's center in San Simeon, the southern stretch of the MBNMS from Point Lobos southward is fairly unreachable by the public; this highlights the importance of these products in portraying the more remote areas of the sanctuary.

The camera sled is owned and has been made available by the National Marine Sanctuary Program. A tremendous benefit of the sled is its ease of operation and availability to the individual sanctuaries for characterization surveys. Prior to these analyses, the imagery data collected from the sled had not been used to answer complex ecological modeling questions. However the results of this project suggest that this tool is

a very valuable asset and can provide a great deal of insight into questions of landscape modeling and fish distributions. Hundreds of hours of video have been collected with the sled at other sites in MBNMS and can potentially be used to answer other questions or expand upon these analyses.

THE MARINE LIFE PROTECTION ACT INITIATIVE: MPA MONITORING ENTERPRISE AND CALIFORNIA DEPARTMENT OF FISH AND GAME

Upon the creation in 2007 of the Central Coast Region MPA Network created under the MLPA, baseline data were needed to understand the state of the ecosystem at the time of implementation (CDFG 2007). Limited state funding was provided for projects to conduct baseline monitoring surveys at a limited number of MPA sites. While these data were robust and will provide valuable assessments of MPA efficacy, there will be gaps in reporting of baselines and changes in un-monitored MPAs. These data can be used by the CDFG for adaptive management measures, by adjusting the size and extent of the current MPAs, based on the assessments of MPA performance and recoveries of fish groups targeted for protection.

Piedras Blancas was not included in other MPA imagery surveys conducted in deep water (30-300 m). Therefore the data from this project are unique and will be made available during the Five-Year Review of the Central Coast MPA Network, scheduled for fall of 2012. This review is led by researchers and policymakers to synthesize baseline and monitoring data from CCR MPAs. A section of the review will focus on collaborative efforts by other agencies and organizations who have conducted monitoring within any CCR MPAs. Data from this study, as well as all other areas surveyed under the broad MBNMS Characterization project, are being be compiled into a database that will provide information on fish and select invertebrate diversity and abundance, as well as habitat availability and distributions. The overlap of jurisdictions of the MBNMS and state MPAs has allowed for sled imagery data collected near Piedras Blancas to serve a dual-purpose of providing baseline data on these otherwise un-monitored areas while characterizing the MBNMS.

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APPENDIX A

COMPLETE MODEL SETS

MS1: Substrate Classification Scheme

M0 = y ~ 0

M1 = y ~ SUBS1

M2 = y ~ SUBScombo

M3 = y ~ GS1

M4 = y ~ GScombo

M5 = y ~ HAB1

M6 = y ~ HABcombo

M7 = y ~ REL1

M8 = y ~ RELcombo

MS2: Full model set

M0 = y ~ 0

M1 = y ~ [result from MS1]

M2 = y ~ DEP

M3 = y ~ MODEP

M4 = y ~ BIOGEN

M5 = y ~ [result from MS1] + DEP

M6 = y ~ [result from MS1] + MODEP

M7 = y ~ [result from MS1] + BIOGEN

M8 = y ~ DEP + MODEP

M9 = y ~ DEP + BIOGEN

M10 = y ~ MODEP + BIOGEN

M11 = y ~ [result from MS1] + DEP + MODEP

M12 = y ~ [result from MS1] + DEP + BIOGEN

M13 = y ~ [result from MS1] + MODEP + BIOGEN

M14 = y ~ DEP + MODEP + BIOGEN

M15 = y ~ [result from MS1] + DEP + MODEP + BIOGEN

APPENDIX B

AVERAGED COEFFICIENTS FOR MS2

- Substrate Model Coefficients (Table B1)

- Relief Model Coefficients (Table B1)

- Grain-Size Model Coefficients (Table B2, B3)

- Habitat-Complexity Model Coefficients (Table B4, B5)

-

- Plots of Substrate Coefficients Relative to Each Other (B6 A, B, C)

Table B1. Averaged substrate coefficients for substrate variables (SUBS-primary and SUBS-combo) and relief (REL) variables. Shading indicates categories for which SE>2 and for which inferences regarding associations could not confidently be made.

Models that used primary substrate (SUBS-primary) in MS2

	BIO-HARD	BIO-SOFT	BIO - NONE	Depth	MODEPS-YES	MODEPS-NO	HH	HS	SH	SS
Painted greenling (*Oxylebius pictus*)										
Coefficient	-3.3	0.0	0.0	-0.1	0.2	0.0	-2.3	0.0	-20.6	-19.8
SE	4010.0	1820.0	0.0	0.0	1600.0	0.0	1.1	1.3	6750.0	1800.0
CI Low	-7870.0	-3580.0	0.0	-0.1	-3130.0	0.0	-4.5	-2.5	-13300.0	-3560.0
CI Upper	7870.0	3580.0	0.0	0.0	3130.0	0.0	-0.1	2.5	13200.0	3520.0
Rosy rockfish (*Sebastes rosaceus*)										
Coefficient	-1.4	0.0	0.0	0.0	0.0	0.0	-24.0	-6.2	-5.6	-4.8
SE	686.0	0.0	0.4	0.0	1000.0	0.0	1130.0	1.3	0.9	1.0
CI Low	-1350.0	-0.1	-0.7	0.0	-1960.0	-0.1	-2240.0	-8.8	-7.3	-6.8
CI Upper	1340.0	0.1	0.7	0.0	1960.0	0.1	2190.0	-3.6	-3.9	-2.8
Squarespot rockfish (*Sebastes hopkinsi*)										
Coefficient	-3.2	-2.3	0.0	0.0	-0.8	-0.2	-24.6	-24.5	-6.6	-6.5
SE	4220.0	1340.0	0.6	0.0	1630.0	1.1	1820.0	7930.0	2.1	2.3
CI Low	-8270.0	-2630.0	-1.2	0.0	-3200.0	-2.4	-3590.0	-15600.0	-10.7	-10.9
CI Upper	8260.0	2620.0	1.1	0.1	3200.0	2.0	3540.0	15500.0	-2.5	-2.0
Blue/black rockfish (*S. mystinus/melanops*)										
Coefficient	-4.4	-3.5	0.0	-0.1	0.0	6.2	-10.8	-2.1	-1.5	-1.2
SE	1510.0	591.0	0.0	0.0	0.1	595.0	595.0	0.8	1.0	1.0
CI Low	-2960.0	-1160.0	-0.1	-0.1	-0.1	-1160.0	-1180.0	-3.6	-3.5	-3.2
CI Upper	2950.0	1160.0	0.1	0.0	0.1	1170.0	1150.0	-0.6	0.4	0.8
Copper/gopher rockfish (*S. caurinus/carnatus*)										
Coefficient	0.0	0.8	1.2	0.0	-0.1	0.0	-6.5	-4.2	-3.2	-2.1
SE	0.0	0.7	1.4	0.0	0.8	0.0	1.4	1.3	0.8	0.9
CI Low	0.0	-0.7	-1.6	-0.1	-1.7	0.0	-9.2	-6.8	-4.8	-3.9
CI Upper	0.0	2.2	3.9	0.0	1.4	0.0	-3.8	-1.7	-1.6	-0.3
Flatfishes (Order Pleuronectiformes)										
Coefficient	-2.7	0.0	0.1	0.0	0.0	0.0	-20.6	-20.6	-5.9	-3.3
SE	556.0	0.0	0.1	0.0	0.0	0.1	352.0	1100.0	1.0	0.2
CI Low	-1090.0	0.0	-0.2	0.0	0.0	-0.1	-710.0	-2170.0	-7.8	-3.7
CI Upper	1090.0	0.0	0.3	0.0	0.0	0.2	669.0	2130.0	-3.9	-2.9

Models that used substrate combination (SUBS-combo) in MS2

	BIO-HARD	BIO-SOFT	BIO - NONE	Depth	MODEPS-YES	MODEPS-NO	Hard	Soft
Pygmy rockfish (*Sebastes wilsoni*)								
Coefficient	-4.2	0.0	0.0	0.1	0.0	0.0	-30.0	-10.1
SE	4650.0	2010.0	0.0	0.0	1520.0	0.0	1720.0	2.5
CI Low	-9120.0	-3940.0	0.0	0.0	-2970.0	-0.1	-3390.0	-15.0
CI Upper	9110.0	3940.0	0.0	0.1	2970.0	0.1	3330.0	-5.3
Ronquils (*Rathbunella* spp)								
Coefficient	-2.4	0.0	0.1	0.0	-7.3	0.0	-9.2	-5.1
SE	484.0	0.0	0.3	0.0	489.0	0.0	1.5	0.9
CI Low	-951.0	0.0	-0.6	0.0	-966.0	0.0	-12.1	-6.8
CI Upper	946.0	0.0	0.8	0.0	952.0	0.0	-6.3	-3.4

Models that used Relief in MS2

	BIO-HARD	BIO-SOFT	BIO - NONE	Depth	MODEPS-YES	MODEPS-NO	High	Moderate	Low	Crested
Combfish/lingcod (*Zaniolepis* spp & *Ophiodon elongatus*)										
Coefficient	-3.6	-0.6	-0.6	0.0	-1.2	-0.9	-20.6	-20.6	-7.3	-6.8
SE	825.0	2.3	2.2	0.0	2.7	2.7	2410.0	796.0	3.31	3.12
CI Low	-1620.0	-5.1	-4.8	0.0	-6.5	-6.1	-4750.0	-1580.0	-13.8	-12.9
CI Upper	1610.0	3.8	3.7	0.1	4.2	4.4	4710.0	1540.0	-0.81	-0.685

Table B2. Averaged substrate coefficients for primary grain-size (GS1; A) and grain-size combination (GS-combo; B) variables. Shading indicates categories for which SE>2 and for which inferences regarding associations could not confidently be made.

A) Canary/vermillion/yelloweye rockfish (*S. pinnager/miniatus/ruberrimus*)

	Rock	Boulder	Cobble	Pebble/Gravel	Sand	Mud
Coefficient	-4.6	-4.5	-6.1	-23.2	-5.5	-22.9
SE	0.6	0.7	1.2	11200.0	0.7	705.0
CI Low	-5.8	-5.8	-8.4	-22000.0	-6.9	-1410.0
CI Upper	-3.5	-3.1	-3.8	21900.0	-4.0	1360.0

B) Blackeye goby (*Rhinogobiops nicholsi*)

Secondary Habitat Type

Primary Habitat Type

	M	N	P	C	B	R
M	0.00	-11.00	5.60	-10.90	5.60	6.01
N	1.86	3.52	-11.30	5.08	4.82	6.01
P	5.60	3.23	-11.20	-11.20	5.60	5.60
C	-11.00	4.76	-11.40	5.07	4.23	4.27
B	-11.10	4.80	5.60	4.24	3.35	4.61
R	-11.20	4.51	-11.20	5.28	4.18	4.13

Table B3. Averaged coefficients for biogenic structure, depth, and bedform for primary grain-size (GS1; A) and grain-size combination (GS-combo; B) variables. Shading indicates categories for which SE>2 and for which inferences regarding associations could not confidently be made.

A) Canary/vermillion/yelloweye rockfish (*S. pinnager/miniatus/ruberrimus*)

	BIO-HARD	BIO-SOFT	BIO - NONE	Depth	MODEPS-YES	MODEPS-NO
Coefficient	0.0	-1.6	0.0	0.0	-2.6	0.0
SE	0.3	694.0	0.0	0.0	484.0	0.0
CI Low	-0.5	-1360.0	0.0	0.0	-951.0	0.0
CI Upper	0.5	1360.0	0.0	0.0	946.0	0.0

B) Blackeye goby (*Rhinogobiops nicholsi*)

	BIO-HARD	BIO-SOFT	BIO - NONE	Depth	MODEPS-YES	MODEPS-NO
Coefficient	-0.2	0.1	0.0	0.0	-0.6	0.0
SE	0.4	0.5	0.0	0.0	0.8	0.0
CI Low	-0.9	-0.8	0.0	0.0	-2.2	0.0
CI Upper	0.5	1.0	0.0	0.0	1.0	0.0

Table B4. Averaged substrate coefficients for habitat complexity combination (HABCOM-combo) for large rockfish. Shading indicates categories for which SE>2 and for which inferences regarding associations could not confidently be made.

	Secondary Habitat Type											
	MCS	NCS	MLO	NLO	CLO	BLO	RLO	CMD	BMD	RMD	BHI	RHI
MCS	-10		-10				-10.48					
NCS	-10	3.06	-10	3.87	-10	5.88	5.20	-10.48	-10.48	7.77		
MLO	-10	-10	0.00	-10	-10		-10.48			7.16		
NLO	3.53	4.23	4.51	3.71	5.05	5.01	4.86		-10.48	5.87		-10.48
CLO			7.15	5.11	4.54	5.32	4.35	-10.48	5.78	5.37		
BLO		-10	-10	6.09	5.78	5.34	5.38		5.20	6.91		
RLO		-10	7.14	6.02	5.57	6.01	4.44	-10.48	6.22	5.85		-10.48
CMD												
BMD		-10		5.03	5.62	5.48	5.91	-10.48	5.96	6.16	5.88	5.08
RMD			-10	6.32	6.12	5.37	5.61		6.29	5.87		6.01
BHI	7.13									-10.48		
RHI				-10	-10		-10.48		6.01	6.43		5.40

Primary Habitat Type (row labels)

Table B5. Averaged coefficients for biogenic structure, depth, and bedform for large rockfish (only fish for which HABCOM was the best classification scheme).

	BIO-HARD	BIO-SOFT	BIO - NONE	Depth	MODEPS-YES	MODEPS-NO
Coefficient	0.6	0.8	0.0	0.0	0.3	0.0
SE	0.2	0.7	0.0	0.0	0.7	0.0
CI Low	0.1	-0.5	0.0	0.0	-1.1	0.0
CI Upper	1.0	2.2	0.0	0.0	1.7	0.0

Figure B1. Plot of substrate coefficients relative to each other for the substrate class scheme (SUBS; A), grain-size scheme (GS; B), and habitat complexity scheme (HABCOM; C). Values to the right indicate that the fish shows a stronger association to the corresponding substrates than values on the left. Categories corresponding to coefficient values for which SE>2 are not shown. Only fish groups with more than two coefficients are shown. Bars in a darker shade indicate the reference coefficient, if it was included (i.e., was within SE limits).
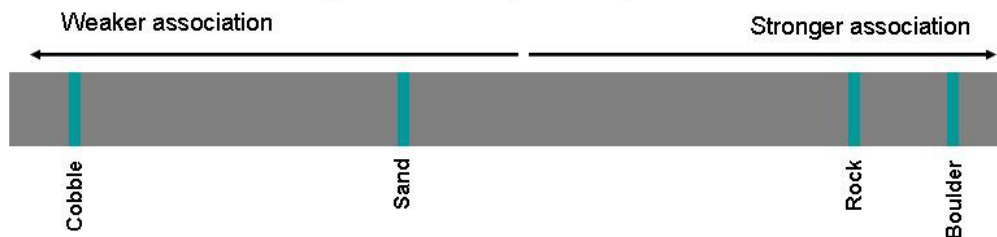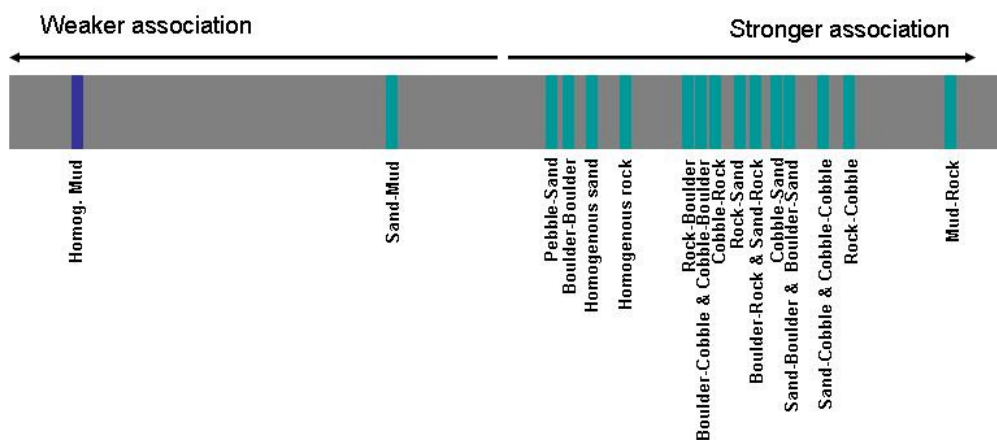
A)
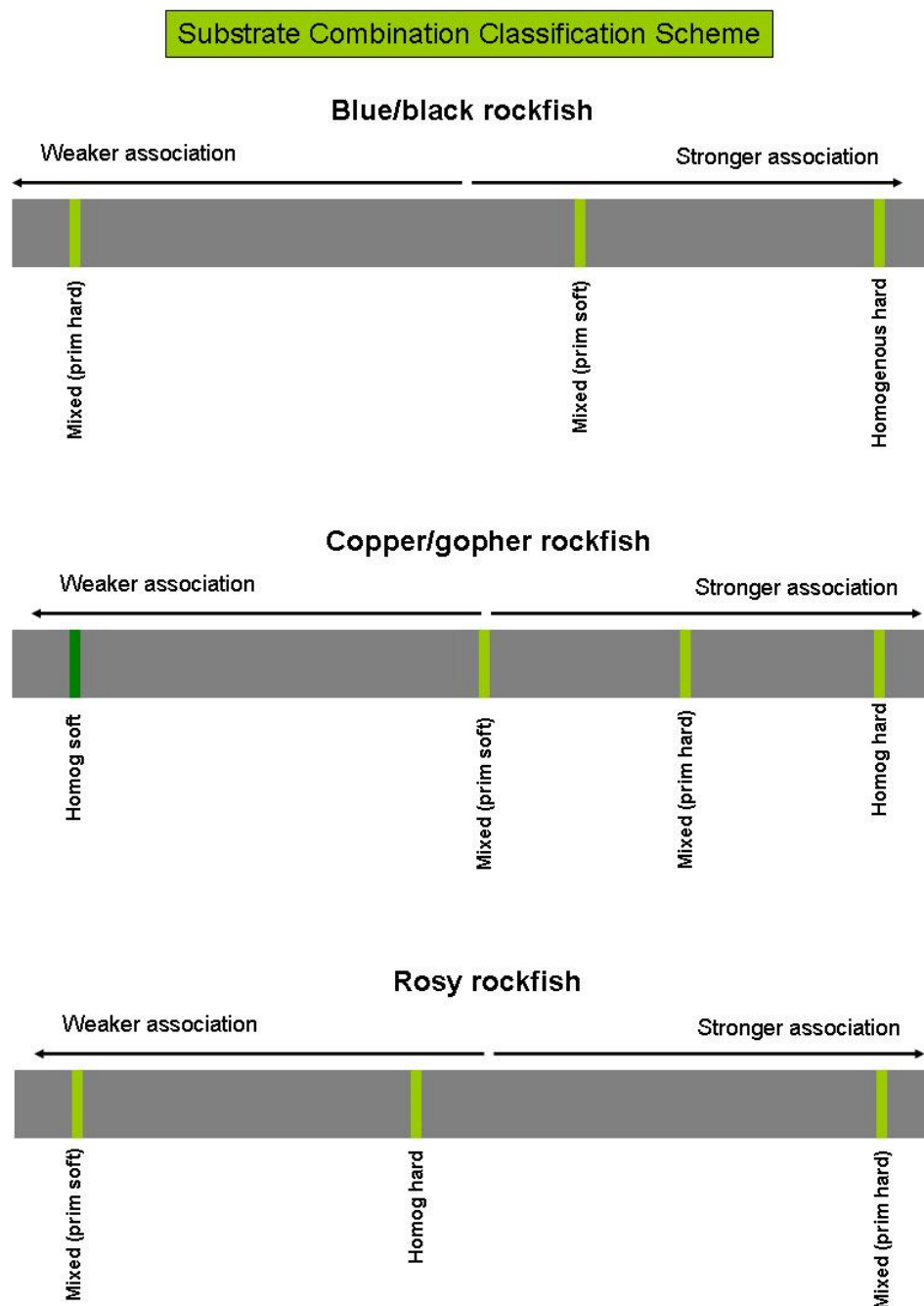
B)

Primary Grainsize Classification Scheme

Canary/vermillion/yelloweye rockfish

Weaker association ← → Stronger association

Cobble

Sand

Rock

Boulder

Grainsize Combination Classification Scheme

Blackeye goby

Weaker association ← → Stronger association

Homog. Mud

Sand-Mud

Pebble-Sand
Boulder-Boulder
Homogenous sand
Homogenous rock

Rock-Boulder
Boulder-Cobble & Cobble-Boulder
Cobble-Rock
Rock-Sand
Boulder-Rock & Sand-Rock
Cobble-Sand
Sand-Boulder & Boulder-Sand

Sand-Cobble & Cobble-Cobble
Rock-Cobble

Mud-Rock

C)

Primary Habitat Complexity Substrate Scheme

Small rockfish (<5cm)

Weaker association — Stronger association

Crested Sand | Moderate Boulder | Low Sand | Moderate Rock | Low Boulder | Low Rock | Low Cobble | Crested Mud

Olive/yellowtail rockfish

Weaker association — Stronger association

Low Sand | Low Rock | Low Boulder | Moderate Boulder | Moderate Rock | High Rock

Sebastomus rockfish

Weaker association — Stronger association

Low Mud | Crested Sand | Low Sand | High rock | Low Rock | Low Cobble | Moderate Boulder | Moderate Rock | Low Boulder | Crested Mud | High Boulder
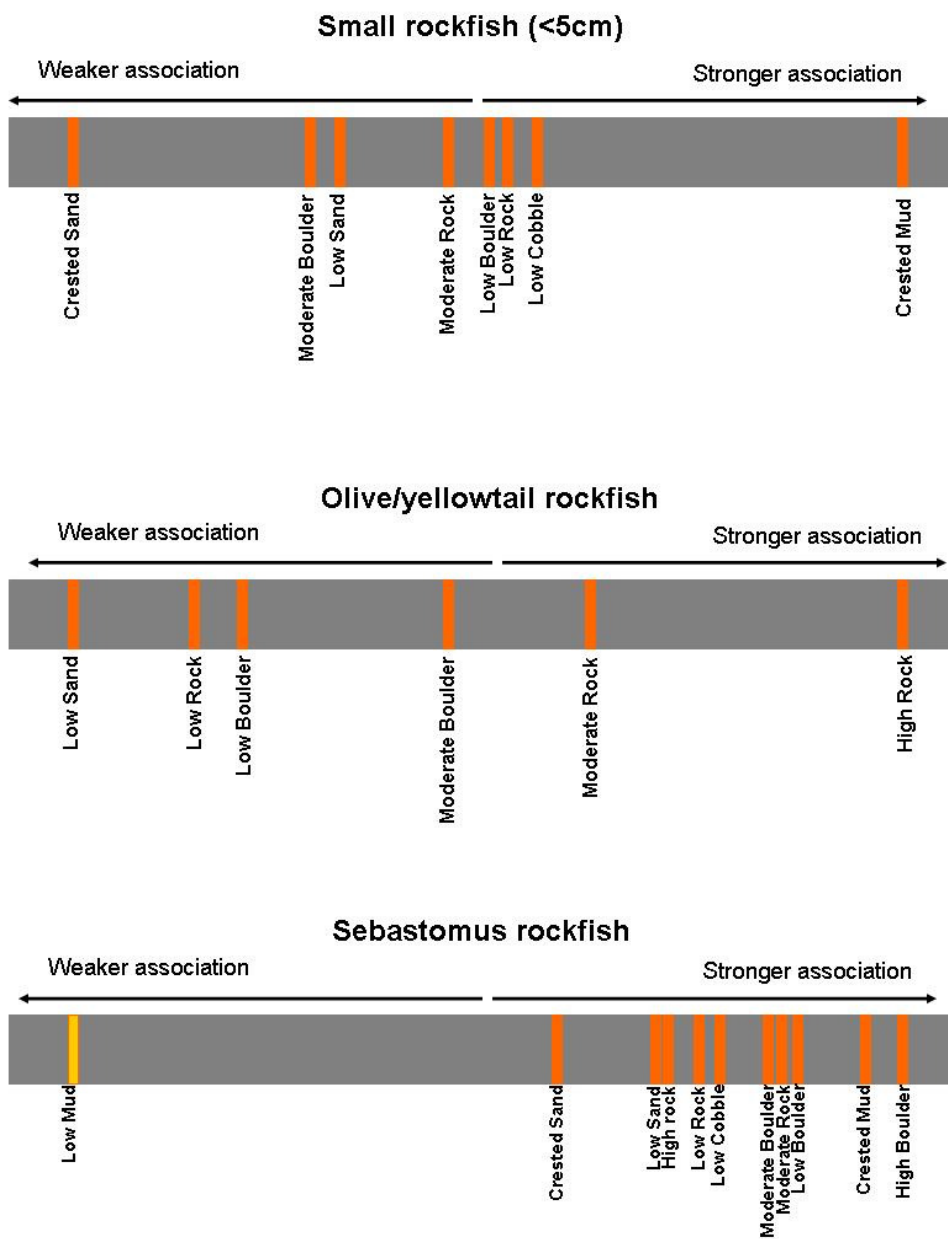
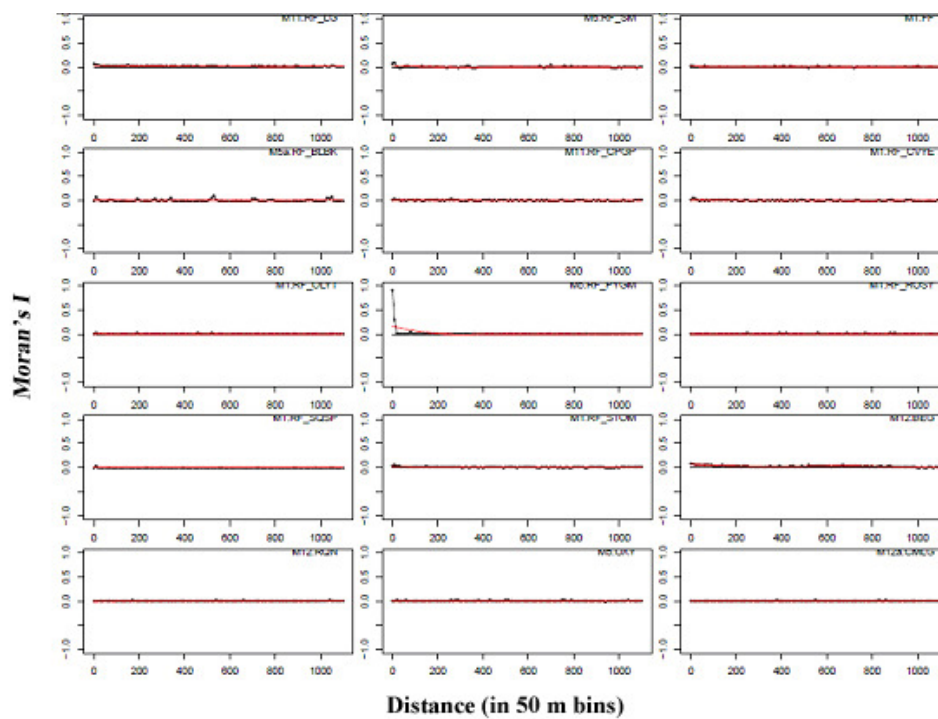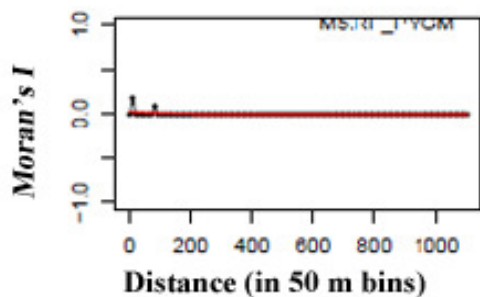**Figure B2. Correlograms of Moran's I plotted at 50m bins for each fish grouping.**

Figure B3. Correlogram for pygmy rockfish after data culling (to remove adjacent frames)

APPENDIX C

R-CODE FOR GLM AND AIC COMPARISONS

GLM and AIC R-Code

(example of fish grouping RF_LG is provided, all other fish groupings
were the same code, but call their data instead, i.e. "OLYT")

```
#Import and name raw data from CSV (Excel file)
raw.table<- read.csv(file.choose())

#Code to create AIC comparison table
AICtable <- function( aic, n) {
 K <- aic$df
 AICc <- aic$AIC + 2 * K * (K+1) / ( n - K - 1 )
 delAIC<- AICc - min( AICc )
 AICw <- exp(-0.5*delAIC) / sum( exp(-0.5*delAIC))
 data.frame( aic, AICc, delAIC , AICw)
}

#re-leveled categories so the reference is the lowest, softest
#possibility (ie soft, mud, lo-relief, no MODEP or biostructure)
raw.table$Subs1<-relevel(raw.table$Subs1, ref = "S")
raw.table$SubsCombo<-relevel(raw.table$SubsCombo, ref = "SS")
raw.table$GS1<-relevel(raw.table$GS1, ref = "M")
raw.table$GScombo<-relevel(raw.table$GScombo, ref = "MM")
raw.table$REL1<-relevel(raw.table$REL1, ref = "LO")
raw.table$Hab1<-relevel(raw.table$Hab1, ref = "MLO")
raw.table$HabCombo<-relevel(raw.table$HabCombo, ref = "MLOMLO")
raw.table$BIOSTRUCT<-relevel(raw.table$BIOSTRUCT, ref = "NONE")
raw.table$MODEPS<-relevel(raw.table$MODEPS, ref = "NO")

#For MS1: Large rockfish category(response) = RF_LG (all RF>10cm)
Hm0.RF_LG<-glm(raw.table$RF_LG~1, family=binomial)
Hm1.RF_LG<-glm(raw.table$RF_LG~raw.table$Subs1, family=binomial)
Hm2.RF_LG<-glm(raw.table$RF_LG~raw.table$SubsCombo, family=binomial)
Hm3.RF_LG<-glm(raw.table$RF_LG~raw.table$GS1, family=binomial)
Hm4.RF_LG<-glm(raw.table$RF_LG~raw.table$GScombo, family=binomial)
Hm5.RF_LG<-glm(raw.table$RF_LG~raw.table$Hab1, family=binomial)
Hm6.RF_LG<-glm(raw.table$RF_LG~raw.table$HabCombo, family=binomial)
Hm7.RF_LG<-glm(raw.table$RF_LG~raw.table$REL1, family=binomial)
```

```
Hm8.RF_LG<-glm(raw.table$RF_LG~raw.table$RELcombo, family=binomial)


AICtable( AIC( Hm0.RF_LG, Hm1.RF_LG, Hm2.RF_LG, Hm3.RF_LG, Hm4.RF_LG,
Hm5.RF_LG, Hm6.RF_LG, Hm7.RF_LG,
Hm8.RF_LG),length(Hm0.RF_LG$residuals)))


#For MS2: Large rockfish category(response) = RF_LG (all RF>10cm)
M0.RF_LG<-glm(raw.table$RF_LG~ 1 , family=binomial)
Mn.RF_LG<-glm(raw.table$RF_LG~ 0 , family=binomial)
M1.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo, family=binomial)
M2.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$Depth, family=binomial)
M3.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$BIOSTRUCT,
family=binomial)
M4.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$MODEPS, family=binomial)
M5.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$Depth, family= binomial)
M6.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$BIOSTRUCT, family= binomial)
M7.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$MODEPS, family= binomial)
M8.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$Depth +
raw.table$BIOSTRUCT, family= binomial)
M9.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$Depth + raw.table$MODEPS,
family= binomial)
M10.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$BIOSTRUCT +
raw.table$MODEPS, family= binomial)
M11.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$Depth + raw.table$BIOSTRUCT, family= binomial)
M12.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$Depth + raw.table$MODEPS, family= binomial)
M13.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$BIOSTRUCT + raw.table$MODEPS, family= binomial)
M14.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$Depth +
raw.table$BIOSTRUCT + raw.table$MODEPS, family= binomial)
MSAT.RF_LG<-glm(raw.table$RF_LG~ 0 + raw.table$HabCombo +
raw.table$Depth + raw.table$BIOSTRUCT + raw.table$MODEPS, family=
binomial)
```

```r
AICtable( AIC( M0.RF_LG, Mn.RF_LG, M1.RF_LG, M2.RF_LG, M3.RF_LG,
M4.RF_LG, M5.RF_LG, M6.RF_LG, M7.RF_LG, M8.RF_LG, M9.RF_LG, M10.RF_LG,
M11.RF_LG, M12.RF_LG, M13.RF_LG, M14.RF_LG, MSAT.RF_LG),
length(M0.RF_LG$residuals) )

#Residuals for the RF_LG winning model (M11)
RF_LG.res<-matrix(residuals(M11.RF_LG))
summary (M11.RF_LG)
par(mfrow=c(2,2))
plot (M11.RF_LG)
```

CORRELOGRAM CODE

```r
rm(list=ls());
graphics.off();if(.Platform$OS.type!="windows"){windows=function()
quartz()}
dev.corr=3;windows(w=10,h=10,xpos=900,ypos=30); par(mfrow=c(5,3));
par(mai=c(0.3,0.3,0.02,0.02))

#Import and name raw data from CSV (Excel file)
SAC1<-read.csv(file.choose())
N = length(SAC1[,1]); print( paste( "Total rows in all data:", N))

#Cull points too close too each other:
if(1) {
 print( "Culling frames that are too close to previous ones..." )
 cull_threshold = 2 # Meters
 # Pre-grab these as vectors, for speed later:
 x = SAC1$north; y = SAC1$east; cam = SAC1$Camline; cull = rep( FALSE,
N )
 for( i in 1:N ) {
  frame = SAC1[i,]
  if( i == 1 ) { prev = i; next }
  if( cam[i] != cam[prev] ) { prev = i; next }
  dist = sqrt( ( x[i] - x[prev] ) ^ 2 + ( y[i] - y[prev] ) ^ 2 )
  if( dist <= cull_threshold ) { cull[i] = TRUE; next }
  prev = i
```

```
 }
 SAC1 = SAC1[ cull == FALSE, ]
 N = length(SAC1[,1]); print( paste( "Total rows in all data AFTER
CULLING CLOSE ONES:", N))
}
```

```
#Re-level factors so the reference is the same for all models (soft,
#mud, lo-relief, no MODEP, no BIOSTRUCT):
SAC1$Subs1    <-relevel(SAC1$Subs1,     ref = "S")
SAC1$SubsCombo<-relevel(SAC1$SubsCombo, ref = "SS")
SAC1$GS1      <-relevel(SAC1$GS1,       ref = "M")
SAC1$GScombo  <-relevel(SAC1$GScombo,   ref = "MM")
SAC1$Hab1     <-relevel(SAC1$Hab1,      ref = "MLO")
SAC1$HabCombo <-relevel(SAC1$HabCombo,  ref = "MLOMLO")
SAC1$BIOSTRUCT<-relevel(SAC1$BIOSTRUCT, ref = "NONE")
SAC1$MODEPS   <-relevel(SAC1$MODEPS,    ref = "NO")

# Fit a the best-fit models for each fish group:
ms = list( name=NULL, form=NULL )
addm = function( name, form ) {
nextm = length(ms$name)+1; ms$name[nextm] = name; ms$form[[nextm]] =
form; return(ms)
}
ms = addm( "M11.RF_LG",   formula("SAC1$RF_LG   ~ 0 + SAC1$HabCombo + 0
+ SAC1$Depth + 0 + SAC1$BIOSTRUCT"))
ms = addm( "M5.RF_SM",    formula("SAC1$RF_SM   ~ 0 + SAC1$Hab1 +
SAC1$Depth"))
ms = addm( "M1.FF",       formula("SAC1$FF      ~ 0 + SAC1$SubsCombo"))
ms = addm( "M5a.RF_BLBK", formula("SAC1$RF_BLBK ~ 0 + SAC1$SubsCombo +
SAC1$Depth"))
ms = addm( "M11.RF_CPGP", formula("SAC1$RF_CPGP ~ 0 + SAC1$SubsCombo +
SAC1$Depth + SAC1$BIOSTRUCT"))
ms = addm( "M1.RF_CVYE",  formula("SAC1$RF_CVYE ~ 0 + SAC1$GS1"))
ms = addm( "M1.RF_OLYT",  formula("SAC1$RF_OLYT ~ 0 + SAC1$Hab1"))
ms = addm( "M5.RF_PYGM",  formula("SAC1$RF_PYGM ~ 0 + SAC1$Subs1 +
SAC1$Depth"))
ms = addm( "M1.RF_ROSY",  formula("SAC1$RF_ROSY ~ 0 + SAC1$SubsCombo"))
```

```
ms = addm( "M1.RF_SQSP",  formula("SAC1$RF_SQSP ~ 0 + SAC1$SubsCombo"))
ms = addm( "M1.RF_STOM",  formula("SAC1$RF_STOM ~ 0 + SAC1$Hab1"))
ms = addm( "M12.BEG",     formula("SAC1$BEG    ~ 0 + SAC1$GScombo +
SAC1$Depth + SAC1$MODEPS"))
ms = addm( "M12.RQN",     formula("SAC1$RQN    ~ 0 + SAC1$Subs1 +
SAC1$Depth + SAC1$MODEPS"))
ms = addm( "M5.OXY",      formula("SAC1$OXY    ~ 0 + SAC1$SubsCombo +
SAC1$Depth"))
ms = addm( "M12a.CMLG",   formula("SAC1$CMLG   ~ 0 + SAC1$Subs1 +
SAC1$Depth + SAC1$MODEPS"))


correlogram_type = "Residuals" # "Response" # vs Residuals


dev.set(dev.corr)
for( m in 1:length(ms$name)) {
  M.name      = ms$name[m]
  print(paste("FITTING MODEL:",M.name)); print("-----------------------
---");flush.console()
  M = glm( ms$form[[m]], fam=binomial )
  if( correlogram_type == "Response" ) {moran_x=M$y} else
{moran_x=residuals( M, type="response" )}

# Make Moran correlograms
  camlines = sort(unique(SAC1$Camline))
  bins = 110; correlogram = matrix( ncol=4, nrow=bins+1, data=0 )
  colnames(correlogram) = c( "Bin", "Dist <=", "Mean", "N" )
  bin_size =10; bin_range = bins * bin_size # bin_size is in meters.
  for( bin in 1:(1+bins) ) correlogram[ bin,1:2 ] = c( bin, (bin-1) *
bin_size )

#Only consider comparisons within camlines, but sum these over all
#camlines:
  moran_x_bar = mean( moran_x ); moran_denominator = 0;
moran_denominator_n = 0
  for( camline in camlines ) {
    included = ( SAC1$Camline==camline ); SUB = SAC1[ included, ]
    n = length(SUB[,1]); print(paste("Camline:",camline,"Rows:",n))
```

```r
#Using matrices is much faster than using data frames. Extract what we
need into a matrix.
    mat = matrix( nrow=n, ncol=3 ); colnames(mat) = c( "Resp", "E", "N"
)
    cR=1; cE=2; cN=3 # R=Response, E=Easting. N=Northing
    mat[,cR ] = moran_x[ included ]; mat[,cE ]= SUB$east; mat[,cN ] =
SUB$north


#Compare every row to every other row, compute contribution to Moran's
I
    # and add to appropriate bin of correlogram:
    for( i in 1:n ) {
      if(i<10 | (i<100 & i%%10==0) | i%%100==0 ) { print(i);
flush.console() }
      Ri = mat[i,cR]; Ei = mat[i,cE]; Ni = mat[i,cN]
      moran_denominator = moran_denominator + (Ri - moran_x_bar ) ^ 2
      moran_denominator_n = moran_denominator_n + 1
      if( i == n ) break
      for( j in (i+1):n ) {
        Rj = mat[j,cR]
        dx = Ei - mat[j,cE]; if( dx > bin_range ) next # Faster than
using sqrt.
        dy = Ni - mat[j,cN]; if( dy > bin_range ) next
        dist = sqrt( dx*dx + dy*dy ); if( dist > bin_range ) next
        bin = ceiling( dist / bin_size ); if( bin > bins ) stop("bin >
bin_size")
        moran_numerator = ( Ri - moran_x_bar ) * ( Rj - moran_x_bar ) #
*2
        correlogram[1+bin,3:4] = correlogram[1+bin,3:4] + c(
moran_numerator, 1 )
      }
    }
  }


#Complete the Moran's summations and averaging:
moran_denominator = moran_denominator / moran_denominator_n
```

```r
for( bin in 1:(1+bins) ) {
    if( correlogram[bin,4] == 0 ) { correlogram[bin,3] = NA; next }
    if( moran_denominator  == 0 ) { correlogram[bin,3] = NA; next }
    correlogram[bin,3] = correlogram[bin,3] / correlogram[bin,4] /
moran_denominator
}

#Plot
print("First 10 bins of correlogram:"); print(correlogram[1:10,]);
x=correlogram[,2]; y=correlogram[,3]
ylim=c(-1,1); plot(x,y,typ="l",xlab=NULL,ylab=NULL,ylim=ylim)
points(x,y,pch=19,cex=0.5 ); lines(c(0,1000),c(0,0)); text(
bin_range,ylim[2],pos=2,M.name)

#Add a smooth line through the noise:
if(!is.na(mean(y))){lines(x,predict(loess(y~x),new=data.frame(x=x)),col
="red")}
}
```