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A Landscape Ecology Approach to Informing the Ecology and Management of Coastal Marine Species and Ecosystems

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A Landscape Ecology Approach to Informing the Ecology and Management of Coastal Marine Species and Ecosystems

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Mary A. Young

December 2014

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Abstract

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by

Mary A. Young

Understanding what drives the distribution, abundance, structure and dynamics of populations and communities, and how this knowledge can inform effective conservation and management, are among the most fundamental goals of basic and applied ecology. Approaches developed in the field of landscape ecology have much to offer for achieving these goals. For my dissertation, I first conducted an extensive review of the literature for different approaches to applying landscape ecology in advancing our understanding of attributes of populations, communities and ecosystems, and its application to spatial approaches to conservation and management. In Chapter 1, I applied some of these insights to determine the importance of environmental variables on the spatial and temporal persistence of stands of giant kelp (*Macrocystis pyrifera*) along the central coast of California. I also used that knowledge to create a model to predict geographic patterns of giant kelp persistence and tested the accuracy of those predictions with empirical data. This chapter revealed strong relationships between giant kelp persistence and several environmental variables, which contributed to a model that accurately predicted spatial patterns of kelp persistence. Chapter 2 used similar environmental variables to quantify the relationships between the density of seven species of nearshore fishes, as well as the structure of the fish assemblage, with geomorphic and oceanographic habitat attributes. Again, this chapter identified several environmental variables that explained and predicted variation in the density and diversity of nearshore fishes along the coast of central California. In Chapter 3, I used landscape ecology approaches to evaluate the design of a network of marine protected areas (MPAs) along the central coast of California. I tested how well habitat representation and replication was achieved in the design of the MPA network and found that across the network, these design criteria were well met, but shortfalls occurred for individual MPAs. This dissertation demonstrates how landscape ecology can be applied to the marine environment to understand what drives the distribution, abundance and dynamics of populations, the structure and diversity of the communities they constitute, and how this knowledge can be used in applications to conservation and management.

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Introduction

Some of the fundamental goals of ecology include understanding what drives the distribution, abundance, structure and dynamics of populations and communities and how this knowledge can be applied to conservation and management. Approaches developed in the field of landscape ecology can be used to meet these goals. Beginning in 1807, a natural historian, Von Humboldt, began describing the latitudinal and altitudinal variation of plants and provided a launch point from which botanists and zoologists began to study the geographic variation of species (McIntosh 1985). These studies found that the environmental factors across the landscape were largely responsible for species distributions (DeCandolle 1874; Merriam 1890; Turner 1989). In 1939, Troll coined the term "landscape ecology" to describe these studies of how species (i.e. vegetation) are geographically distributed across the landscape (Troll 1939; Turner 1989) and, throughout the 20th century, the use of landscape ecology began to gain impetus and helped advance understanding in many ecological systems (Turner 1989).

The study of landscape ecology combines concepts from geography and ecology to determine the effect of pattern (the spatial arrangement of the landscape) on the processes that drive the distribution and abundance of species (Wiens and Moss, 2005; Turner et al., 2001; Turner, 2005; Wiens, 2009). Landscape ecologists recognize that there is spatial heterogeneity throughout the landscape and that this heterogeneity influences the interactions of species with their environments (Risser et al., 1984; Wu, 2013). "Heterogeneity" may be the one term that sums up the entire field of landscape ecology and delineates it from other subdisciplines within ecology (Risser et al., 1984; Wu, 2013). Turner et al. (2001) emphasize two aspects of landscape ecology that distinguish it from other subdisciplines of ecology: (1) it addresses the importance of the spatial arrangement and heterogeneity of the landscape on ecological processes and (2) it focuses on spatial scales that are much larger than traditional ecological studies (i.e. expands over greater areas than what is seen by a human observer). Since its beginnings, landscape ecology has become a very important and pervasive discipline in ecology. As humans continue to encroach on and fragment many of the world’s ecosystems, landscape ecology is needed to determine the spatial dynamics of populations. Landscape ecology bridges many disciplines including but not limited to ecology, conservation biology, evolutionary biology, geography, and human land use. It provides a way to understand and map the interactions of species with their environment, how changes in the environment can drive evolutionary diversification, what determines species distributions, and how human impacts on the landscape can affect all of these processes (Wiens et al. 2006).

Although it began as a predominantly terrestrial discipline, landscape ecology is equally applicable to marine systems and has relatively recently emerged as a useful approach for studying the distribution and habitat associations of many important marine species (i.e., Bell et al., 1999; Hovel and Lipicus, 2001; Purkis et al., 2007; Hinchey et al., 2008; Hovel and Regan, 2008; Chatfield et al., 2010; Pittman and Brown, 2011; Chatfield et al., 2012; Claisse et al., 2012; Carroll and

Peterson, 2013; D'Aloia et al., 2013). Marine ecosystems support substantial biodiversity that is under threat by many human activities including increasing populations along the coast, fishing, other forms of resource extraction, destructive fishing activities, run-off from poor land use practices, pollution, and others (Agardy, 2000; Sloan, 2002; Lubchenco et al., 2003; Brown et al., 2009; Sherman et al., 2011). Loss of habitat or human encroachment on habitat are some of the leading causes of biodiversity decline (Polasky et al., 2005; Carroll and Miquelle, 2006; Falcucci et al., 2007; Nagendra, 2008; Schindler et al., 2008). With the continued increase in anthropogenic effects on species' habitats and the realization that the single species approach to management is inadequate (Polasky et al., 2005), an ecosystem-based approach to management has become prominent in the oceans and areas continue to be set aside as marine protected areas (Babcock et al., 2005). Spatially-explicit, landscape ecology approaches; therefore, will be required to understand the processes in the oceans and the environmental patterns that shape them (Friedlander et al., 2007). The purpose of my dissertation was to apply the techniques of landscape ecology developed in terrestrial studies to the marine realm. Through this process, I reviewed how landscape ecology is being applied to the study of marine ecosystems, applied landscape ecology approaches to understanding the spatial and temporal persistence of marine metapopulations, linked environmental variables to the distributions of fish species associated with kelp forests, and then applied metrics of landscape ecology to evaluating a network of marine protected areas along the central coast of California.

Marine ecologists have already begun to apply principles of landscape ecology to the oceans but there still are far fewer applications than in terrestrial ecology. In the development of my dissertation research, I first reviewed the current application of landscape ecology metrics in studies of both terrestrial and marine ecosystems and assess how landscape ecology is being applied to the design and evaluation of protected areas. Then, using the recently designated network of MPAs along the central coast of California, I considered how different metrics of landscape ecology can be successfully applied to evaluating the effectiveness of a MPA network using several case study examples. Through this review, I found that the application of landscape ecology is much more extensive in the terrestrial literature and, although many of the tools associated with landscape ecology are being applied in marine studies, the rigor with which they are being applied is still far below that of terrestrial applications. In addition, the application of landscape ecology to assessing protected areas is much more common in terrestrial studies but there is great promise in the application of landscape ecology to evaluating protected areas in the marine realm. From this review, it became clear that recently available, broad-scale data collected in the marine environment, allows for landscape scale assessments of drivers of species distributions, the ecosystems they constitute, and spatial conservation approaches, including networks of MPAs.

In Chapter 1, I applied landscape ecology techniques to determine the environmental factors responsible for the spatial and temporal persistence of a structure forming kelp species, *Macrocystis pyrifera*, along the central coast of

California. Giant kelp, *Macrocystis pyrifera*, is the world's most widely distributed kelp species (Henriquez et al., 2011) and is the foundation species for one of the most productive ecosystems on Earth (North, 1971; Foster and Schiel, 1985; Dayton, 1985, DeMartini and Roberts, 1990; Steneck et al., 2002; Carr and Reed *in press*). Along the Pacific coast of North America from Central California to Baja California, *M. pyrifera* is the most common and competitively dominant canopy forming kelp species (Bushing, 2000; Graham et al., 2007; Carr and Reed, *in press*) but varies spatially and through time (Dayton et al., 1992, Edwards 2004). The purpose of Chapter 1 was to determine what environmental parameters are correlated with the spatial and temporal persistence of *M. pyrifera* along the central coast of California and how well those environmental parameters can be used to predict areas where *M. pyrifera* is likely to persist. The environmental variables used in this study included depth of the seafloor, the structure of the rocky reef (complexity and topographic position), the proportion of rocky reef, the size of kelp patch, the biomass within a kelp patch, the distance from the edge of a kelp patch, sea surface temperature, wave orbital velocities, and the population connectivity of individual kelp patches. Using a generalized linear mixed effects model (GLMM), the persistence of *M. pyrifera* was found to have a significant association with depth, complexity of the rocky reef, proportion of rock, patch biomass, distance from the edge of a patch, population connectivity, and wave orbital velocity. These environmental variables were then used to predict the persistence of kelp across the central coast and these predictions were compared to a reserved dataset of *M. pyrifera* persistence, which was not used in the creation of the GLMM. The Pearson correlation between these predictions and the reserved dataset was 0.71 and significant. Therefore, this study demonstrated that environmental variables can be used to accurately predict the persistence of kelp within the central coast of California. As a foundation species that can support upwards of 1,000 different species, understanding those factors that support persistent populations of *M. pyrifera* are important when attempting to protect the marine communities associated with kelp forests.

Along with the distributions of kelp, understanding the distributions of economically and ecologically important species that inhabit kelp forests is also needed. As management policies have moved towards a more habitat-based approach, there is a need to acquire reliable spatial information on species distributions (Fielding and Bell, 1997; Manel et al., 1999; Costello et al., 2010). A landscape approach, therefore, is necessary to differentiate the habitat types and the associations of species with those habitats to better understand how populations are distributed throughout their environment and, as a result, better inform management (Sala et al., 2002; Monaco et al., 2005; Appeldoorn et al., 2003; Friedlander et al., 2007). The purpose of Chapter 2 was to determine the species-habitat associations for a variety of nearshore, kelp forest associated fish species along the central coast of California by answering the following questions: 1) Do densities of fish species vary predictably with environmental variables including the structure of the rocky reef, latitude, kelp biomass, and exposure to ocean swell (wave orbital velocities). If so, what is the relative importance of the variables in explaining this variation and how does it vary among species? 2) Do species diversity and richness of the kelp forest fish assemblage vary predictably with environmental variables? 3) Can species distribution models (SDMs) generate reliable extrapolations of species densities, diversity and richness? 4) Do estimates of fish abundance generated by the SDMs differ substantially (both higher and lower) from those generated by simple uniform extrapolation of density estimates across the kelp forest habitat? My general approach to answering these questions was to test for predictive SDMs (in this case, generalized additive models) based on variables extracted from seafloor habitat maps, oceanographic variables and species densities estimated by the ecological surveys (Question 1), and use those models to extrapolate densities over the study area as well as species diversity and richness (Question 2). I tested the accuracy of these predicted extrapolations using an independent dataset not used in the creation of the models (Question 3). I then used the SDMs to estimate larger scale species densities and abundances to compare and with other estimates of species abundance (Question 4). Using generalized additive models (GAMs), I found that seven of the ten fish species I looked at had strong relationships with at least three of the environmental variables and that the relationships of those species with the environmental variables varied by species and community attribute (richness and diversity). In addition, the extrapolations proved to be fairly accurate and significant for all species but one. Finally, comparison of different methods for extrapolating species' abundances showed that those methods where variation in rocky reef structure is taken into consideration produce much lower estimates of abundance than methods assuming all rocky habitat is the same. The results from this chapter show how landscape ecology approaches can be used to better understand and quantify the distributions of ecologically and economically important fish species across an entire network of marine protected areas.

For the final chapter, Chapter 3, I applied landscape ecology techniques to the evaluation of a network of MPAs along the central coast of California. Human impacts on the oceans continue to increase (Halpern et al. 2008, Halpern et al. 2009, Lester et al. 2010, Brown 2011) and many nations throughout the world have acknowledged the need for more ecosystem-based conservation measures in the marine environment (Douvere 2008, Gilliland & Laffoley 2008, Costello et al. 2010, Halpern et al. 2012). Among these approaches, the use of marine protected areas (MPAs) is becoming widely adopted to protect ecosystems, their biodiversity and to supplement traditional fisheries management (Roberts & Hawkins 2000, Curley et al. 2002, Allison et al. 2003, Carr et al. 2003, Lubchenco et al. 2003, Gaines et al. 2010, Halpern et al. 2010, Gleason et al. 2013). MPAs are areas within the ocean that are spatially protected from differing levels of human impacts, including resource exploitation and habitat alterations. MPAs can protect entire ecosystems, including habitats and unexploited species in addition to species targeted by fisheries (Agardy 1994, Allison et al. 1998, Sobel & Dahlgren 2004, Claudet 2011). The state of California recently implemented a coast-wide network of MPAs, a state-wide seafloor mapping program, and ecological characterizations of species and ecosystems targeted for protection by the network. Because the MPAs in the Central Coast region of California were set up prior to completion of the State’s Seafloor Mapping Program, one purpose of this study was to use these maps to evaluate how well seafloor features, as proxies for habitats, are represented and replicated across the network and how well the ecological surveys representatively sampled fish habitats within MPAs. The seafloor data were classified into broad substrate categories (rock and sediment) and finer scale geomorphic classifications standard to marine classification schemes using surface analyses (slope, ruggedness, etc) done on the digital elevation model derived from multibeam bathymetry data. These classifications were then used to evaluate the representation and replication of seafloor structure within the MPAs and across the ecological surveys. Both the broad substrate categories and the finer scale geomorphic features were proportionately represented for many of the classes with deviations of 1-6% and 0-7%, respectively. Within MPAs, there were more dramatic differences in seafloor structure and abundance inside the MPA than what was originally thought with differences ranging up to 28%. However, all of the habitats of sufficient availability for replication were replicated across the network, with those habitat classes appearing in at least three MPAs. Seafloor structure in the biological monitoring design was adequately represented but there are mismatches between sampling in the MPAs and their corresponding reference sites and some seafloor structure classes were completely missed. The geomorphic parameters derived from multibeam bathymetry data used in this study have been shown to be of importance to the biodiversity of many marine species (i.e. substrate type, depth, habitat complexity, etc.) and, therefore, can be used as a helpful and initial method of evaluating the MPAs across this region.

Through this dissertation, I have demonstrated the application of concepts developed within the field of landscape ecology to understanding the distributions of populations and species throughout broad regions of the marine environment and the use of landscape ecology techniques to evaluating the placement of MPAs along the central coast of California. The application of landscape ecology techniques towards preserving biodiversity is becoming more common (Barbault, 1995). The field has progressed in this direction past simple descriptions to more spatial modeling and simulations using GIS and sound methodology (Hobbs, 1997), allowing for the ability to create maps and other figures to communicate results to other disciplines and planners (Antrop, 2001).

1. Chapter 1: Explaining and predicting spatial patterns of persistence of giant kelp, Macrocystis pyrifera, forests in central California

1.1 Abstract

Rocky reefs in many temperate areas worldwide serve as habitat for canopy forming macroalgae and these structure forming species of kelps (order Laminariales) often serve as important habitat for a great diversity of species. *Macrocystis pyrifera* is the most common canopy forming kelp species found along the coast of California but the distribution and abundance of *M. pyrifera* varies in space and time. The structure (i.e. species composition and relative abundance) of communities associated with forests of *M. pyrifera* has been related to forest persistence. The purpose of this study is to determine what environmental parameters are correlated with the spatial and temporal persistence of *M. pyrifera* along the central coast of California and how well those environmental parameters can be used to predict areas where *M. pyrifera* is more likely to persist. Nine environmental variables considered in this study included depth of the seafloor, the structure of the rocky reef (complexity and topographic position), the proportion of rocky reef, the size of kelp patch, the biomass of kelp within a patch, the distance from the edge of a kelp patch, sea surface temperature, wave orbital velocities, and the population connectivity of individual kelp patches. Using a generalized linear mixed effects model (GLMM), the persistence of *M.*

pyrifera was significantly associated with seven of the nine variables considered: depth, complexity of the rocky reef, proportion of rock, patch biomass, distance from the edge of a patch, population connectivity, and wave orbital velocity. These seven environmental variables were then used to predict the persistence of kelp across the central coast and these predictions were compared to a reserved dataset of *M. pyrifera* persistence, which was not used in the creation of the GLMM. The Pearson correlation between these predictions and the reserved dataset was 0.71 and significant ($P<0.000$). Therefore, the environmental variables were shown to accurately predict the persistence of *M. pyrifera* within the central coast of California. As a foundation species, whose forests can support on the order of 1,000 species, understanding those factors that support persistent populations of *M. pyrifera* are important when attempting to protect these ecosystems.

1.2 Introduction

Rocky reefs in many temperate areas worldwide serve as habitat for canopy forming macroalgae (e.g. kelp; Schiel 1988; Graham et al., 2007; Connell & Irving 2008; Springer et al., 2010; Carr and Reed, *in press*) and these structure forming kelp species often serve as important habitat for numerous other species (Foster and Schiel, 1985; Steneck et al. 2002; Graham et al., 2007; Springer et al., 2010; Carr and Reed, *in press*). Giant kelp, *Macrocystis pyrifera,* is the world's most widely distributed kelp species (Henriquez et al., 2011) and is the foundation species for one of the most productive ecosystems (North, 1971; Foster and Schiel, 1985; Dayton, 1985, DeMartini and Roberts, 1990; Steneck et al., 2002). Along the Pacific coast of North America from Central California to Baja California, *M. pyrifera* is the most common and competitively dominant canopy forming kelp species (Bushing, 2000; Graham et al., 2007; Carr and Reed, *in press*) but varies spatially and through time (Dayton et al., 1992; Edwards 2004; Edwards and Estes 2006). The purpose of this study is to determine the environmental correlates with the spatial and temporal persistence of *M. pyrifera* along the central coast of California.

As a foundation species that provides food and habitat for a wide range of species including marine invertebrates and fishes (reviewed recently by Carr and Reed, *in press*), understanding the distribution and persistence of *M. pyrifera* throughout its range is important to understanding the community dynamics within these kelp forests (Bushing, 2000; Arkema et al., 2009; Byrnes et al. 2011). Ecological persistence is simply defined as the continued existence of a species through time (Connell and Sousa, 1983). Although *M. pyrifera* tends to persist in certain areas, it is spatially patchy and temporally variable throughout its range and this variability is believed to be caused by a number of abiotic and biotic phenomena including effects of currents, temperature, substrate, depth, nutrient availability, swell intensity, size of kelp patch, species assemblages within the forest, planktonic distribution, and others (Dayton, 1985; Dayton et al., 1992).

Temporal and spatial scales of many marine studies are often not broad enough to answer the questions under study (Dayton et al., 1999). Many of the processes responsible for the temporal and spatial heterogeneity of patterns of marine organisms occur over longer time periods and broader spatial scales than can be captured in the typical design of studies done in small, homogenous areas (Foster, 1990; Carpenter, 1998; Dayton et al., 1999). Therefore, the use of classical field sampling techniques makes it difficult to look at broad scale patterns in coastal marine ecosystems (Cavanaugh et al., 2010). With an increase in the availability of high-resolution remote sensing technology, however, there is now the potential to make observations over broad spatial and temporal scales (Jensen et al., 1980; Belsher and Mouchot, 1992; North et al., 1993).

Because forests of *M. pyrifera* can form dense surface canopies, satellite images can be used to derive biomass estimates, which are verified through groundtruthing, to map the temporal and spatial extent of *M. pyrifera* biomass estimates (Cavanaugh et al 2010; Cavanaugh et al., 2011). These biomass estimates allow for the quantification of *M. pyrifera* over long time periods and over broad spatial scales and can then be combined with environmental information to determine those variables driving the distribution and persistence of *M. pyrifera* over its entire range. Previous studies have linked the distribution and persistence of *M. pyrifera* to attributes of the seafloor habitat such as bottom relief and wave action (Bushing, 2000) but these studies have been done using low resolution data at broader spatial scales. Spatial heterogeneity of the seafloor including susceptibility to disturbance (Sousa, 1984) and variation in structural complexity (Pearsons and Li, 1992), however, could also play a significant role in the persistence of kelp.

In this study, I use fine scale seafloor habitat variables derived from multibeam bathymetry along with other environmental factors to determine what habitat attributes are correlated with the temporal and spatial persistence of *M. pyrifera* along the central coast of California. The hypothesis is that *M. pyrifera* persistence will vary predictably with depth, variations in the structure of the rocky reef including complexity and relative elevation, patch characteristics including the size and biomass of individual patches, the distance from the edge of the patch, variations in wave orbital velocities, changes in sea surface temperature (SST), and the connectedness of a kelp patch. Specifically, the following relationships are predicted:

> **H1:** *M. pyrifera* persistence will have a non-linear (hyperbolic) relationship with depth of the seafloor; persistence will be greatest at intermediate depths, decreasing with shallower (Graham, 1996; Swanson & Druehl, 2000) and deeper depths (Cribb, 1954; Foster and Schiel, 1985; Graham, 1997; Graham, 2007).
>
> **H2:** *M. pyrifera* persistence decreases with increases in topographic complexity of the rocky reef (Grove et al. 2002; Deysher et al. 1998).
>
> **H3:** Because kelp patches have a moderating effect on currents and waves, *M. pyrifera* found in larger patches, more abundant patches, and further toward the center of a patch will increase in persistence (Jackson and Winant, 1983; Jackson, 1984; Rosman et al., 2007).

H4: *M. pyrifera* persistence will increase with higher proportions of rocky substratum. because *Macrocystis* plants require rocky substrate for attachment (Cribb, 1954; Foster & Schiel, 1985; Westermeier & Möller, 1990; Schiel et al., 1995; Carr and Reed, *in press*) and can be disturbed with increases in sediment (Devinny and Volse, 1978; Geange et al., 2014, Shaffer and Parks, 1994; Spalding et al., 2003; Shepherd et al., 2009).

H5: *M. pyrifera* persistence will decrease with increases in wave orbital velocities (Dayton et al., 1984, Seymour et al., 1989; Edwards, 2004).

H6: *M. pyrifera* persistence will decrease with increases in SST (Zimmerman & Robertson, 1985; Tegner et al., 1996; Hernández-Carmona et al., 2001).

H7: *M. pyrifera* persistence will increase with the population connectivity of a kelp patch (Reed et al., 2004; Alberto et al., 2011)

H8: Strong relationships between *M. pyrifera* with some combination of environmental variables will allow for accurate predictions *M. pyrifera* persistence.

These hypotheses are addressed using a spatially-explicit, predictive modeling approach to determine the habitat variables important to the persistence of *M. pyrifera*. Then, these predictions are used to predict the persistence of *M. pyrifera* across the region and tested against a reserved dataset to see how well the habitat can determine the persistence of *M. pyrifera* .

1.3 Methods

1.3.1 Study Location

The study area for this project is along the central coast of California, which extends from Pigeon Point in the north (37°10'57" Lat 122°23'38" Long) to Point Conception in the south (34°26'55" Lat 120°28'14" Long). *M. pyrifera* has a patchy and variable distribution along this section of the California coast (Figure 1-1). In addition there is also variation in seafloor substrate complexity, depth, currents, temperature, and wave orbital velocities, making it an ideal area to determine the relative extent to which these different environmental parameters correlate with the persistence of *M. pyrifera*.

1.3.2 Using Satellite Data to Estimate Kelp Canopy Biomass and Persistence

M. pyrifera forms very distinct, dense floating canopies at the ocean surface, which are distinguishable with satellite imagery (Jensen et al., 1980; Belsher and Mouchot, 1992; North et al., 1993). Using the methods developed by Cavanaugh et al. (2010, 2011), high resolution satellite imagery was used to quantify *M. pyrifera* biomass along the central coast of California. To calculate persistence, those estimates of *M. pyrifera* biomass for each of the 30m resolution Landsat pixels within the region were converted to binary presence/absence maps derived from the annual mean biomass. With absence assigned a value of "0" and presence assigned a value of "1", these binary maps were collated to produce a map of the number of years that *M. pyrifera* was present in each of the Landsat pixels (Figure 1-2). A centroid point from each of the Landsat pixels within the region was created and used as the response variable in the predictive models.

1.3.3 Environmental Variables

Seafloor Structure Variables

Multibeam data coverage is available for the majority of the region under study and at 2m resolution within the depth range of the kelp distribution with the completion of the California Seafloor Mapping Program (CSMP) in the Central Coast Region (http://seafloor.otterlabs.org/csmp/csmp.html). There is a gap in data coverage between the shore and where multibeam data ends (anywhere between the 2m and 10m contour). This gap exists because multibeam data cannot be acquired using traditional, ship-based mapping methods due to navigation hazards such as breaking waves and rocks exposed at the surface. Therefore, the analyses in this study were limited to the region where multibeam data is available. Where available, multibeam data provide full coverage depth values for the seafloor, which were converted into 2m resolution digital elevation models (DEMs). The resulting DEMs were used to provide depth information and to derive other structure variables likely to be of importance to the distribution and persistence of *M. pyrifera* within the central coast region of California.

The first variable derived from the multibeam data was the complexity of the rocky reef. Complexity of the rocky reef is likely to be associated with the persistence of *M. pyrifera* through the increase in microhabitats (Sousa 1984; Pearsons and Li, 1992). More complex reefs also have more variation in physical conditions (i.e. light, sediment cover, water motion, etc) (Toohey, 2007), which can influence the presence of algae (Seymour et al., 1989; Thomson et al., 2012). In this study, complexity of the rocky reef is based on the slope of slope of the terrain (rate of change of slope) and was calculated within ArcGIS 10.x using the Spatial Analyst toolbox (ESRI, 2014). Slope of slope is computed by using the "Slope" tool within Spatial Analyst surface analysis tools to calculate the slope between each of the 2m cells of the DEM and their eight neighbors and then repeating this process on the resulting slope raster. This process yields a raster with slope of slope values specified for each of the 2m resolution cells throughout the DEM. Previous work has shown that slope of slope is a useful measure of complexity for better understanding how species are distributed throughout the marine environment (Pittman & Brown, 2011).

The next variables derived from the DEM included varying scales of topographic position index (TPI). TPI is a measure of relative elevation and can be used to delineate features such as valleys and peaks at multiple spatial scales. TPI provides another measure of the complexity of the rocky habitat. To compute TPI for the study region, the Benthic Terrain Modeler (BTM) toolbox was used within ArcGIS. TPI uses an annulus-shaped neighborhood and the scale of the analyses can be specified by the user choosing the radius of the annulus (for more information on how TPI is calculated, see Lundblad et al., 2006). For this study, TPI was calculated at both fine (50m) and broad (250m) scales. These layers were then standardized using the "Standardize BPI" tool within the BTM to provide standardized measures of TPI for better comparison across scales.

Along with those variables measuring the complexity of the rocky reef, the amount of hard substrate is likely to be important to the persistence of *M. pyrifera*. With only a few exceptions, kelp forests occur on hard substrates where they are better able to attach their holdfasts (Dayton, 1985; Smith et al., 2004; Carr and Reed, *in press*). Additionally, greater coverage of rock reduces the amount of soft sediment in the area that could potentially result in sediment coverage of hard substrate. Coverage of hard substrate by sediment has been shown to affect the recruitment of kelp (Devinny and Volse, 1978; Geange et al., 2014). In addition, increased sediment could result in increases in turbidity and reduced irradiance and, as a result, affect abundance and depth distribution of kelp (Shepherd et al., 2009). Therefore, the rock/sediment substrate maps developed in the seafloor mapping project using a measure of "rugosity" as a threshold for rock or sediment, were used to calculate the proportion of hard substrate within each of the Landsat pixels. The resulting layer provides a measure of available suitable habitat within each of the Landsat pixels.

All of the 2m resolution seafloor habitat variables were scaled to the 30m resolution Landsat pixels by using the "Focal Statistics" tool within ArcGIS Spatial Analyst. The mean and standard deviation of depth, complexity and TPI were computed with a 30m by 30m square moving window. The resulting 900m^2 scale focal statistics maps were then spatially associated with the kelp persistence values to be used in the predictive models.

Patch-Based Variables

In addition to the effect of seafloor on the persistence of *M. pyrifera* throughout the central coast of California, there are also likely to be effects of the kelp patches themselves. For example, structure of the kelp plants has been shown to buffer against wave action as you move away from the edge of the kelp patch (Jackson and Winant, 1983; Jackson, 1984; Rosman et al., 2007; Rosman et al., 2010). Rosman et al. (2007) found that currents are reduced at a rate correlated with the coverage of surface canopy. In addition to the inward distance from the edge of the kelp patch (i.e. toward the center), the overall size of a kelp patch and abundance within the patch is potentially correlated with the persistence of the *M. pyrifera*. To include the effect of the individual patches on the persistence of *M. pyrifera*, the kelp patches had to be defined for the region. To define the kelp patches, Landsat pixels that contained *M. pyrifera* at any time during the duration of this study were designated as "kelp presence", and contiguous "presence" pixels were combined to form individual patches (Figure 1-3a). Once the patches were defined, the "Euclidean Distance" tool within the "Spatial Analyst Tools" toolbox was used to find the distance from the edge of these patches and the "Calculate Geometry" tool was used to calculate the area of each of these patches. To account for patch abundance, using the biomass for each of the kelp patches, the average annual biomass was computed for each Landsat pixel across the entire region. These values were then summed within each individual patch to estimate total biomass of each patch for the time period of the study.

Connectivity of Kelp Populations

In previous work, Cavanaugh et al. (2014) developed a framework using graph theory and spatial autocorrelation for distinguishing “subpatches” (subpopulations) within contiguous "mega-patches" of *M. pyrifera* off the coast of southern California. The dynamics of subpatches within these megapatches match theoretical expectations better than any other scale of patches and, therefore, likely represent subpopulations within metapopulations (Cavanaugh et al., 2014). These methods were employed in the central California region in this study to delineate patches of *M. pyrifera* representing subpopulations within the overall metapopulation (Figure 1-3b). These subpatches were used to determine the relative connectivity of *M. pyrifera* across the study region.

Connectivity of kelp patches based on spore transport times using oceanographic models has proven an effective tool for understanding gene flow across populations of *M. pyrifera* (Alberto et al., 2011). To estimate connectivity between kelp patches, I used a three step process (Raimondi unpublished manuscript). The first step was the determination of biomass for patches of *M. pyrifera* in central California. This was done as described using Landsat information for 30 by 30 meter pixels that were aggregated into patches of coherent synchrony as described by Cavanaugh et al. (2014). Because biomass is strongly related to spore production, it was used as a measure of transportable individuals in the metapopulation context. The second step was to determine the number of days it would take a spore to transit among pixels. This was accomplished using Regional Ocean Modeling Systems (ROMS) simulations for the central coast study region. Because ROMS cells are much larger than kelp patches, the relationship between transit time and distance was evaluated and the fit was very strong ($r^2 > 0.9$) when the model was run separately for transits to the north vs to the south. In this way it was possible to calculate the estimated transit time between any patches of kelp. In ROMS modelling particles are immortal and never settle, which is obviously wrong. Thus, the third step was to incorporate a reasonable loss rate of spores during transit between patches. I used a rate of 90% per day, which is consistent with the results of Reed et al (1998), who showed that swimming in spores ended with 24 hours, indicating a loss of lipid reserves also necessary for successful settlement and metamorphosis. The relative connectivity of each patch could therefore be estimated as the sum of the products of the biomass, transit time (between the recipient and donor patch) and loss rate for all other patches in central California.

Sea Surface Temperature

Nitrogen limitation is one of the key factors that has been found to reduce the productivity of kelp (Jackson, 1977, Dayton et al., 1999) and ocean temperature is correlated with an absence of detectable nitrogen in waters at 16°C or greater in southern California and, therefore, can be used as a proxy for nitrogen availability

(Jackson, 1977; Zimmerman and Robertson, 1985; Tegner et al., 1997; Reed et al., 1997). Sea surface temperature (SST) data were downloaded from the NOAA website using the Marine Geospatial Ecology Toolbox (MGET) within ArcGIS. The SST data used in this study come from the NOAA AVHRR satellite data, which provides monthly averaged daytime SST data for the region of interest at a resolution of 4.5 km^2. These monthly averages were used to calculate annual averages to match the temporal resolution of the kelp data. In addition, because the scale of the rest of the analyses were done at 30m resolution, the SST data were binned into four categories of SST based on 1°C bins and treated as a categorical variable in the models.

Wave Orbital Velocity

Wave exposure is often one of the main environmental factors affecting the distribution of marine organisms (Denny, 1988; Utter and Denny, 1996; Sundblad et al., 2014) and has been shown to affect the distribution and persistence of kelp in many regions throughout the world (Foster and Schiel, 1985; Graham 1997; Graham et al., 1997, 2007; Reed et al 2011, Carr and Reed, in press). Wave forces (velocities and acceleration) can tear *M. pyrifera* stipes away from the remainder of the plant or remove entire plants (Koehl and Wainwright, 1977; Seymour et al., 1989). In fact, Seymour et al. (1989) showed that predictions of maximal velocity were strongly correlated with the dislodgment of kelp. As a result, the magnitude of local wave forces could greatly impact the local and regional persistence of kelp.

The measure of wave forces used in this study is wave orbital velocity and models developed at USGS were used. Patterns of wave energy and orbital velocities along the California coast were simulated with the numerical wave model SWAN (Simulating Waves Nearshore, Delft University of Technology, The Netherlands). SWAN is a third-generation spectral wave model capable of simulating wind-wave growth, propagation, refraction, dissipation, and depth-induced breaking (Booij et al., 1999; Ris et al, 1999). A set of 15 SWAN model grids were developed and used to simulate wind-wave growth and propagation across the inner portion of the California continental shelf. All grids were curvi-linear, with an average cross- and along-shore resolution of 30 to 50 m and 60 to 100 m, respectively, in the shallow inshore regions. Model grid cells were smaller in the cross-shore direction, in shallow water, and around complex bathymetry to enable accurate wave refraction and shoaling. Latitudinal extents were defined based on local geography and computation limitations. The offshore extent of the model grids were defined by 64 Wave Information System (WIS, *http://wis.usace.army.mil/*) model output stations located approximately 20 km offshore along the entire California coast. Wave parameters (significant wave heights, peak wave period, and mean wave direction) derived from the WIS database were applied at the boundaries of the 15 SWAN grids. The WIS data encompass the 32 years from 1980 through 2011 were used to calculate seasonal (arithmetic) mean and extreme (arithmetic mean of highest 5%) conditions. Seasons were defined as: winter = December through February; spring = March through May; summer = June through August; and fall = September through November.

Parametric wave descriptors (wave heights, periods, and wave direction) derived from the WIS database were applied along the open boundaries of the SWAN domains; these were represented in spectral space with a JONSWAP shape and a 3.3 peak enhancement factor. In all grids, 10-degree direction bins and 36 frequencies spaced log-normally from 0.0417 Hz to 1.0000 Hz were used. The bottom friction coefficient was set to 0.038m^2/s for swell conditions (Hasselmann et al., 1973 in SWAN technical documentation, 2013), whitecapping was computed with the Komen et al. (1984) formulation, and depth induced breaking with the Battjes and Janssen (1978) formulation. Winds from the most centrally located WIS station of each grid were applied uniformly across the domains to allow for inclusion of locally wind-generated waves in addition to (usually greater) energy contributions from distantly generated swell waves. All grids were solved in the spherical coordinate system and run in a stationary mode. In shallow water, the orbital motions of water particles induced by surface waves extend down to the seabed. The resulting wave-induced orbital velocities near the seabed are considered to be a representative measure of how waves influence the sea floor and as such are a focus of this study; SWAN calculates bottom orbital velocity (U_{orb}) as the maxima of the root mean square (rms) bottom velocity (U_{rms}).

The ability of the SWAN model to accurately simulate wave propagation was tested by running the model forced with hourly wave parameters of the WIS database over a week long time period from 18-25 January 2010. The simulation period encompasses a large storm event when wave heights exceeded 9 m (e.g., CDIP Pt.

Reyes buoy) and affected the entire California coast. The ability of the SWAN model to reproduce observed wave conditions was evaluated with a skill score (Willmott 1981); the skill score ranges from 0 to 1, with a skill score of 1 indicating perfect agreement. The analysis was done over the entire simulated time-series. The skill scores were quite good (mean±1 SD = 0.89±0.05; range = 0.81-0.97) at all sites evaluated. Although observations are not available within all grids, the high skill scores and lack of clear geographic trend in changes of the skill score suggest that model results in grids with no buoys are likely also reflective of true conditions.

1.3.4 Tests of Hypotheses

Tests of Assumptions of Analyses

Prior to testing hypotheses regarding the relationship between *M. pyrifera* persistence and habitat variables, I tested for violations of assumptions of the analyses (e.g., independence, normality, linearity, homogeneity of variance) following the guidelines of Zuur et al., (2009). Cleveland dotplots were used to view the distribution of the variables to determine if there were outliers and if any variables required transformation. Multi-panel scatterplots, Spearman-rank correlation coefficients, and variance inflation factors (VIF) were applied to test for collinearity between explanatory variables. Those paired variables that had a correlation coefficient greater than 0.50 or a VIF greater than three were not included in models together (Zuur et al., 2009). Elimination of VIF values greater than three is a conservative approach for eliminating collinearity in the models. The only variable that required a square-root transformation was the measure of mean topographic complexity (slope of slope). Relationships between *M. pyrifera* persistence and depth and wave orbital velocity were non-linear, so a quadratic function was used within the models for both of these variables.

Spatial autocorrelation violates the assumption of independence of observations and is common in spatially defined observations (Zuur et al., 2009). I used Moran's *I* to test for spatial autocorrelation among the *M. pyrifera* persistence values. I detected significant spatial autocorrelation in the response variable (*M. pyrifera* persistence) and used a modeling approach that accounted for it (see Results).

Modeling Approach

To test the hypothesized relationships between persistence of *M. pyrifera* and habitat variables, I applied a generalized linear mixed effects model (GLMM). The persistence data met the assumptions of the Poisson distribution so I used a GLMM with a Poisson distribution and a log-link function. The GLMM was trained using half of the persistence observations to determine the relationship between persistence and the environmental variables (30,785 points were used to train the models while 30,784 points were reserved to test the accuracy of the predictions). I used a GLMM because this modeling approach allows for datasets that are hierarchically structured and accounts for dependencies within those hierarchical groups by the use of random-effects (Pinheiro and Bates, 2000; Zuur et al., 2009). Persistence of *M. pyrifera* was spatially autocorrelated within subpatches. I accounted for this spatial autocorrelation by using the subpatch as a random-effect in the GLMM. I used a spline correlogram of the Pearson residuals to verify that the spatial autocorrelation was accounted for in the GLMM. The spline correlogram used was smoothed using the spline function (Bjornstad and Falck, 2001; Zuur et al., 2009) (see results). The relative variance explained by variables in the GLMM cannot be modeled for fixed effects using restricted maximum likelihood approximation, therefore the relative importance of the variables is ranked by their absolute values of the z scores, reflecting the likelihood of their explanatory value.

The “lme4” package in R v3.1.0 was used to run the GLMM. Prior to running the GLMM, all of the variables were standardized using the "scale" function in R. The standardization of the coefficients removes the unit of measurement for the variables and allows for the comparison of coefficients across a variety of scales. Once standardized, I ran a series of GLMM models to determine the best model for explaining the persistence of kelp along the central coast of California by using AIC model selection and the significance of variables. Once the best model was chosen, I used the "predict" function to come up with predicted persistence values across the central coast and compared these to the actual values within the reserved persistence points to determine the accuracy of the model in predicting kelp persistence.

1.4 Results

1.4.1 Using Satellite Data to Estimate Kelp Canopy Biomass and Persistence

Landsat data for the central coast of California estimated 61.4 km^2 of *M. pyrifera* canopy cover within the shallow subtidal. The majority of *M. pyrifera* was on hard substrate within the 5m to 30m depth range. Annual persistence (number of years) of *M. pyrifera* varied throughout this region, ranging from 1 to 29 years, but was fairly persistent throughout the region with over 60% of the Landsat pixels containing kelp for 15 or more years (Figure 1-3; yellow, orange and red hues).

1.4.2 Tests of Hypotheses

There were a total of 61,569 points of *M. pyrifera* observations within the study region that overlapped with the environmental variables. Comparison of spatial autocorrelation of residuals from a generalized linear model (GLM), which did not account for spatial autocorrelation, with spatial autocorrelation of residuals of the GLMM indicated that spatial autocorrelation was better and adequately accounted for in the GLMM (Figure 1-4). The best GLMM (i.e. with lowest AIC containing all significant variables) generated from the restricted subset of the dataset to explain persistence of *M. pyrifera* included depth (squared), topographic complexity, top five percent orbital velocity (squared), the distance to the edge of the patch, relative connectivity, the area of the patch, and the proportion of rock (Table 1-1).

H1: *M. pyrifera* persistence will have a non-linear (hyperbolic) relationship with depth of the seafloor; persistence will be greatest at intermediate depths, decreasing with shallower and deeper depths

The depth distribution of *M. pyrifera* in the central coast region varied from 0.1 meters to 50 meters with an average depth of 15.1 meters and the majority of the kelp, as predicted, occurred in the intermediate 10-20 meter depth range (Figure 1-5a). As predicted, the relationship between persistence and depth was non-linear (hyperbolic) and highly significant (GLMM: $P < 0.000$). Depth was the second most important variable of those tested (Z score= -40.98; Table 1-1).

H2: *M. pyrifera* persistence decreases with increases in topographic complexity of the rocky reef.

Contrary to my prediction based on the literature, I detected a positive relationship between persistence and both complexity and higher topography. *M. pyrifera* was found on hard substrate of varying complexity with mean slope of slope values of 40.1 (moderate complexity) with a range of 0.38 (very low complexity) to 139.2 (very high complexity). The majority of the kelp, however, occurs in the 30-40 range, or moderate complexity (Figure 1-5b). The relationship between persistence and geomorphic complexity was highly significant (GLMM: $P < 0.000$) and the third most important variable of those tested (Z score= 37.30; Table 1-1). In addition to complexity, *M. pyrifera* was found on "peaks" of topography, with an average TPI value of 2.54. However, TPI values ranged from -8 to 28 in locations where kelp was present along the central coast (Figure 1-5c). TPI was removed from the GLMM for explaining variation in persistence of *M. pyrifera* because it was not significant.

> **H3:** Because kelp patches have a moderating effect on currents and waves, *M. pyrifera* found in larger patches, more abundant patches, and further toward the center of a patch will increase in persistence.

There were a total of 409 contiguous patches defined within the central coast study region and, along with the seafloor structure variables, the frequency of *M. pyrifera* occurrences varied with variation in each of the variables derived from these patches. The size (area) of the contiguous kelp patches varied from 0.004 km^2 to 2.47 km^2, with an average kelp patch size of 0.89 km^2 (Figure 1-6a). Biomass within those kelp patches varied from 33.18 kg to 6,864,400 kg, however, the distribution is highly skewed to the right, many more pixels at the lower end of the biomass levels and a median biomass across all patches of 808,717 kg (Figure 1-6b). The relationship between persistence and patch biomass was highly significant (GLMM: $P< 0.000$) and the fourth most important variable of those tested (Z score= 30.19; Table 1-1). The distance from the edges of these patches ranged from 0 meters to 566 meters with an average distance of 75.2 meters. The relationship between *M. pyrifera* persistence and distance inward from the edge of the patch was highly significant (GLMM: $P< 0.000$) and was the most important variable in the model (Z score= 105.66; Table 1-1).

H4: *M. pyrifera* persistence will increase with higher proportions of rocky Substratum because *Macrocystis* plants require rocky substrate for attachment.

The average proportion of rock found within each Landsat pixel was 0.58 with an increase in *M. pyrifera* occurrences as the proportion of rock increases (Figure 1-4d). The relationship between *M. pyrifera* persistence and proportion of rock cover was very significant (GLMM: $P< 0.006$) the sixth most important variable (i.e. likelihood) in explaining variation in persistence (Z score= 2.84; Table 1-1).

H5: *M. pyrifera* persistence will decrease with increases in wave orbital velocities.

M. pyrifera is found across a variety of wave environments from areas where the wave orbital velocity values are close to 0 m/s to areas where the velocity reaches 2.27 m/s. The average orbital velocity values where *M. pyrifera* occurs is 0.89 m/s (Figure 1-6d). I detected collinearity between the mean and the top five percent orbital velocity, so only one of the variables from that pair was included in the different GLMM runs. The relationship between *M. pyrifera* persistence and wave orbital velocity was highly significant (GLMM: $P< 0.000$) and was the fifth most important variable in the model (Z score= 3.98; Table 1-1).

H6: *M. pyrifera* persistence will decrease with increases in sea surface temperature (SST).

Where kelp was present, SST for the central coast region generally ranged from just over 11°C to just under 15°C with an average temperature of 13.6°C. SST was not included as an explanatory factor in the GLMM for explaining variation in persistence of *M. pyrifera* because it was not significant.

H7: *M. pyrifera* persistence will increase with the population connectivity of a kelp patch.

The definition of subpatches across the study region resulted in a total of 168 individual subpatches (or subpopulations) within the metapopulation. The relative connectivity values computed for these subpatches ranged from almost no connectivity (<0.000) to complete connectivity (1.00) with a 90% rate of spore loss (Figure 1-6c). The relationship between *M. pyrifera* persistence and connectivity of a patch was significant (GLMM: P< 0.043) and the least most important variable in the model (Z score= 1.92; Table 1-1).

H8: Strong relationships between *M. pyrifera* with some combination of environmental variables will allow for accurate predictions *M. pyrifera* persistence.

When the best GLMM (Table 1-1) was used to predict the spatial patterns of *M. pyrifera* persistence for of a dataset not used in the creation of the model, the predictions from the GLMM and the actual observed persistence in the reserved dataset were strongly and significantly correlated (Pearson correlation coefficient= 0.71, P<0.000).

1.5 Discussion

Understanding the spatial and temporal patterns of persistence of *M. pyrifera* and the factors responsible for its persistence is critical to understanding the distribution and abundance of the highly diverse and economically important species that associate with forests of *M. pyrifera* and the communities they constitute. I found that persistence of *M. pyrifera* is significantly correlated with many environmental variables including depth, the structural complexity of the seafloor, the proportion of rock in an area, the distance from the edge of a kelp patch, the biomass of a kelp patch, the oceanographic connectivity of the subpopulations, and the wave environment. These variables can be used to accurately predict those locations where kelp is likely to be more persistent and potentially predict into the future where kelp may persistently occur as the wave environment changes with the effects of climate change.

The non-linear, quadratic relationship between kelp persistence and depth is expected based on previous knowledge of the depth distribution of *M. pyrifera*. As you move into deeper depths, *M. pyrifera* becomes less abundant as water clarity decreases (Graham et al. 2007; Carr and Reed *in press*). On the other hand, the inshore, shallower limit of kelp is related to increases in wave action (Dayton et al. 1992) and an increase in irradiance (Graham 1996; Swanson & Druehl, 2000). The significant, non-linear relationship between kelp persistence and depth, therefore, is expected but nonetheless contributes to the overall quantitative predictions of persistence.

In contrast to other studies that have looked at the relationship of kelp persistence with the complexity of the hard substrate and found that kelp is more persistent on lower relief, less complex rocky habitat (Grove et al. 2002; Deysher et al. 1998), my results indicate that *M. pyrifera* persistence increases with increases in the structural complexity of the substrate. These contrasting results are likely due to differences in rocky substrate in southern California, where the majority of *M. pyrifera* studies have been done, versus central California. In southern California, the majority of the hard substrate is made up of low relief, sedimentary rock while central California is made up of granitic rocky reef of much higher and more varying topographic complexity and is much less susceptible to erosion than the sedimentary formations in southern California.

Increases in the proportion of rock were found to be significantly correlated with increases in the persistence of *M. pyrifera* as well. Not only does *Macrocystis* require rocky substrate for attachment (Cribb, 1954; Foster & Schiel, 1985; Westermeier & Möller, 1990; Schiel et al., 1995; Carr and Reed, *in press*) but the increase in the proportion of rock also signifies a decrease in sediment. Areas of lower sediment cover are less likely to experience periodic coverage of rock by sediment (Devinny and Volse, 1978; Geange et al., 2014) and sediment in the water column, which results in higher turbidity and lower irradiance (Shaffer and Parks, 1994; Spalding et al., 2003; Shepherd et al., 2009).

As expected, *M. pyrifera* persistence increased with the distance from the edge of kelp patch. The moderating effect of kelp on the currents and waves is probably responsible for this pattern. With increasing distance from the edge of a patch and into the center, the effects of currents and waves decrease (Jackson and Winant, 1983; Jackson, 1984; Rosman et al., 2007; Rosman et al., 2010). In addition, the biomass of the patch may have a role in moderating water motion as it was also found to be important. Those kelp patches that have higher biomass values also experience higher persistence. The effect of increasing biomass; however, could be tied to other processes not related to water motion such as higher abundance for reproduction and recruitment. Although the size of a patch was included as a variable in the GLMM, it did not come out as significant. Therefore, the abundance within a kelp patch appears to be more important to persistence than the overall size of the patch.

The significant, non-linear (quadratic) relationship between *M. pyrifera* persistence and wave orbital velocity was not expected but makes sense in hindsight. It was predicted that *M. pyrifera* persistence would increase as wave orbital velocity decreases because waves are the most frequent disturbance responsible for tearing out plants (Graham, 1997) and bull kelp (*Nereocystis luetkeana*) persists in areas of higher wave intensity (Foster and Schiel, 1986; Graham, 1997). The results from this study show, however, that *M. pyrifera* occurs across the range of wave orbital velocity values along the central coast of California but is most abundant in a moderate wave environment (average 0.86 m/s orbital velocity). One reason for this result could be the solid, granitic rocky reefs available for attachment along the central coast of California. By providing a solid surface for attachment, the rocky reefs could decrease the susceptibility of *M. pyrifera* to being torn out by strong wave forces (Carr and Reed, *in press*). Additionally, the rugosity of the rocky reefs was used in the models to produce the maps of wave orbital velocity and higher rugosity values are associated with higher wave orbital velocities. Consequently, the relationship of *M. pyrifera* persistence with higher complexity rocky habitat results in the plants attaching to habitat found in areas of higher orbital velocities.

Population connectivity between the subpatches was also found to be a significant variable in the model. Previous studies have shown that the population connectivity of marine species within the coastal environment is linked to the 'oceanographic distance' between populations, as measured by oceanographic currents (Mitarai et al., 2009; Alberto et al., 2011). In this study, using a loss rate of 90% (Reed et al. 1998), it was found that those subpatches at closer oceanographic distances were more persistent than those subpatches that were more isolated. Population connectivity is, understandably, an important factor in the persistence of kelp because those patches that are more 'connected' to the rest of the patches are more likely to experience more consistent spore recruitment and greater persistence through time.

One of the main limitations on the distribution of *M. pyrifera* throughout the world is nutrient availability, mostly nitrogen (Ladah et al., 1999; Hernández-Carmona et al., 2000; Edwards, 2004; Graham et al., 2007). Because nitrogen availability has been linked to the temperature of the ocean in previous studies, I used sea surface temperature (SST) as a proxy for nitrogen. Along the central coast of California, however, SST varies only slightly and this variable did not have an effect on the persistence of kelp. In southern California, south of Point Conception, it is more likely that nitrogen would play a role in the persistence of kelp populations because there is more variability and greater temperature extremes within that region (Carr and Reed, *in press*).

Another factor that is often linked to the presence of kelp but was not explored in this study is the abundance of grazers. In many parts of the world, kelp populations are dramatically affected by the overgrazing by marine organisms (Graham et al., 2007). Along the coast of California, sea urchins are one of the main grazers of kelp (Carr and Reed, *in press*). In this study, however, the presence of grazers was not taken into consideration due to the presence of a population of sea otters that overlaps with the range of this study. The sea otters forage on the urchins and keep their populations in check, greatly diminishing their numbers (Carr and Reed *in press*). In the areas outside of the range of sea otters, including southern California and north of Pigeon Point, sea urchin populations increase greatly in size and can have a large impact on the population of *M. pyrifera* (Carr and Reed, *in press*).

1.6 Conclusions

Overall, this study shows that the persistence of *M. pyrifera* along the central coast of California has predictable relationships with a suite of environmental variables and that these environmental variables can be used to predict those areas where this important structure-forming kelp species is likely to persist. In addition, the incorporation of oceanographic variables including the wave environment, the currents affecting the connectivity between kelp patches, and the sea surface temperature allows for forecasting of how changes in the ocean environment due to climate change are likely to affect the persistence of *M. pyrifera*. As a foundation species that can support upwards of 1,000 different species (Foster and Schiel, 1985), understanding those factors that support persistent populations of *M. pyrifera* are important when attempting to protect the marine communities associated with kelp forests.

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1.8 Figures

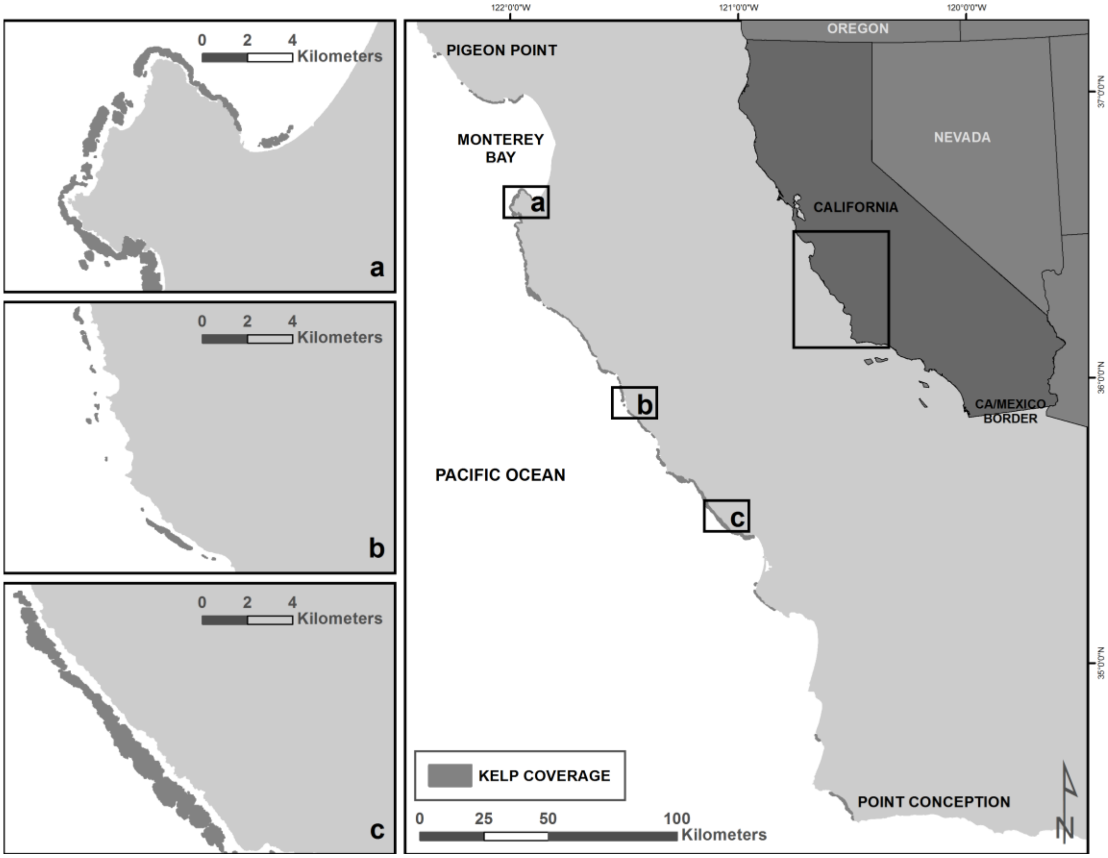

Figure 1-1: The study region is shown in the map on the right, which extends from Pigeon Point in the north to Point Conception in the south along the central coast of California. *M. pyrifera* coverage derived from the Landsat imagery is shown in dark gray. Figure 1a, 1b, and 1c correspond to the boxes shown in the map on the right and display the patchy distribution of kelp along small sections of the coastline.

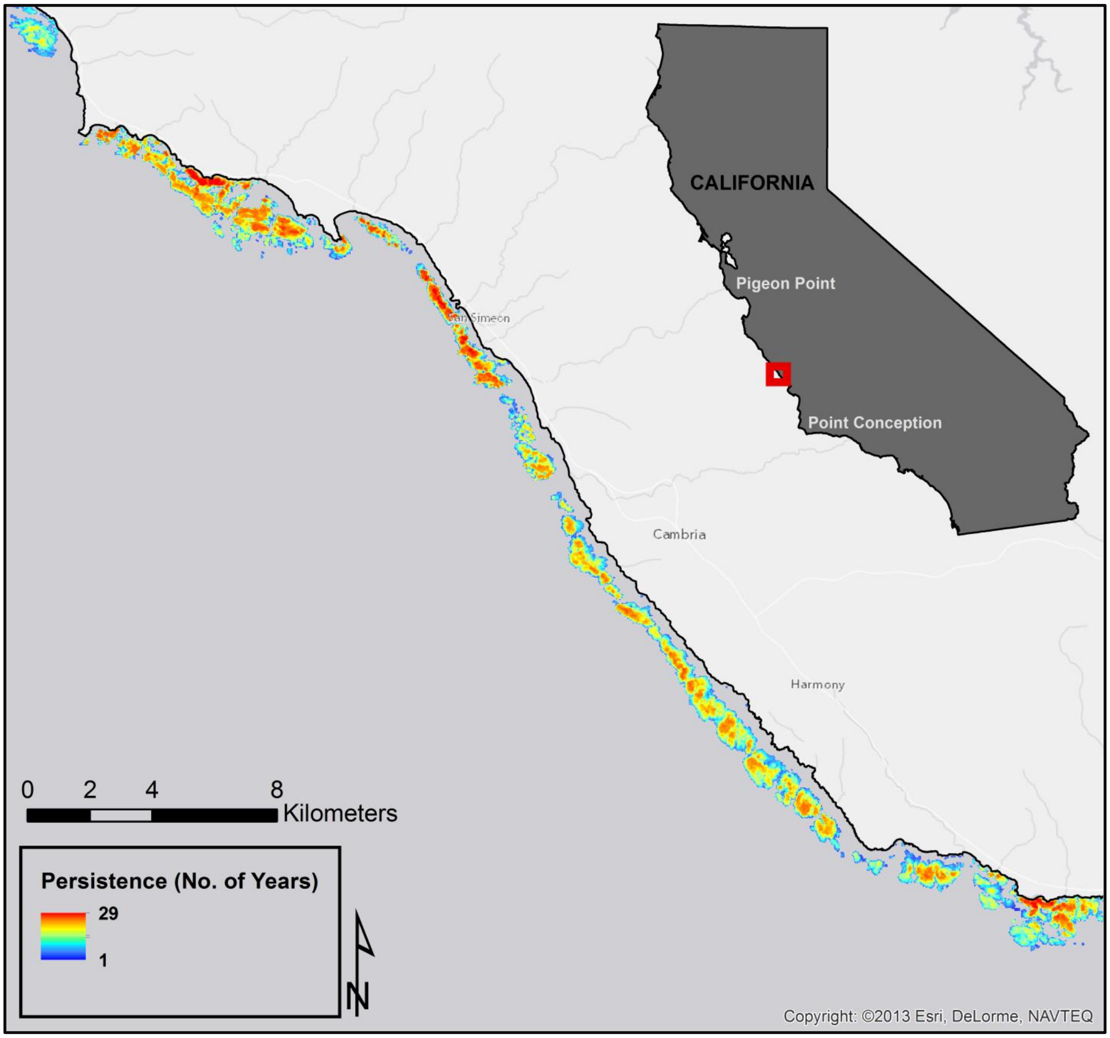

Figure 1-2: The persistence of *M. pyrifera* along a small portion of the central coast of California. The warmer colors represent higher persistence (greater number of years when *M. pyrifera* is present in a certain location) compared to the cooler colors, which represent areas where *M. pyrifera* is less persistent. Persistence is measured at 30m resolution (the resolution of the Landsat data).

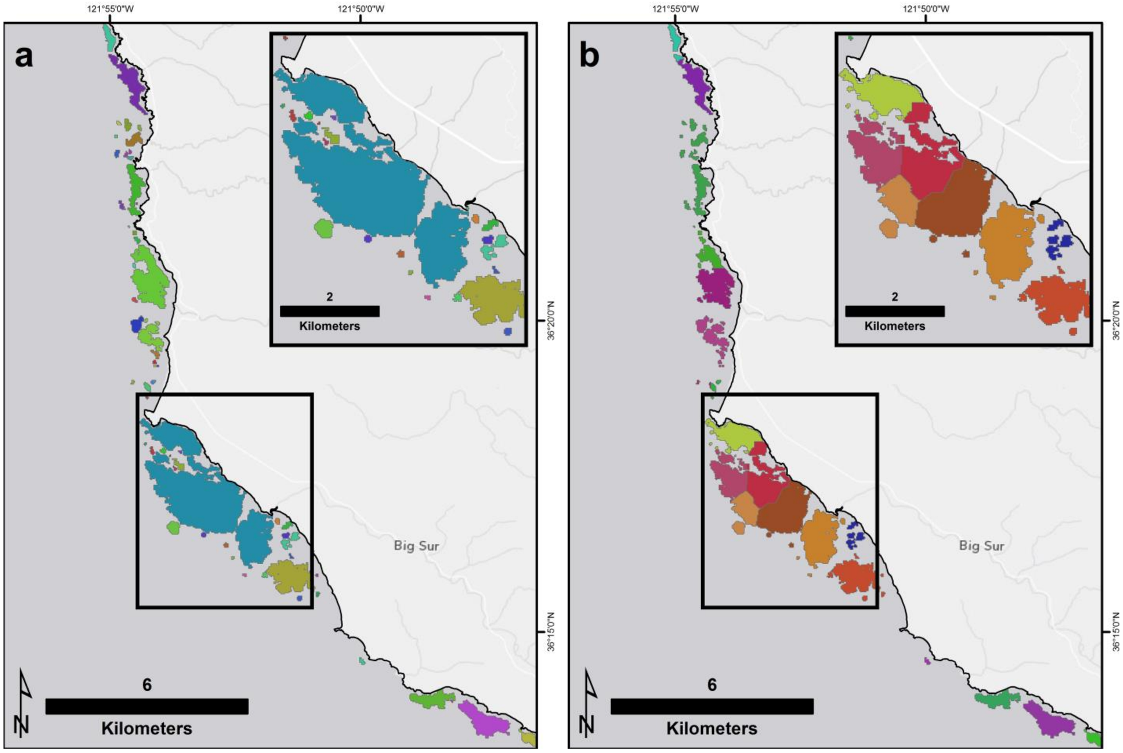

Figure 1-3: Examples of the contiguous patches used to calculate the patch variables (a) and the subpatches used to calculate the connectivity between the subpopulations (b). The different colors in both maps represent different patches and the inset maps show a close-up view of one area of patches to highlight the variation in the different methods for defining patches within the central coast of California. (Service Layer Credits: Copyright @2013 Esri, DeLorme, NAVTEQ)

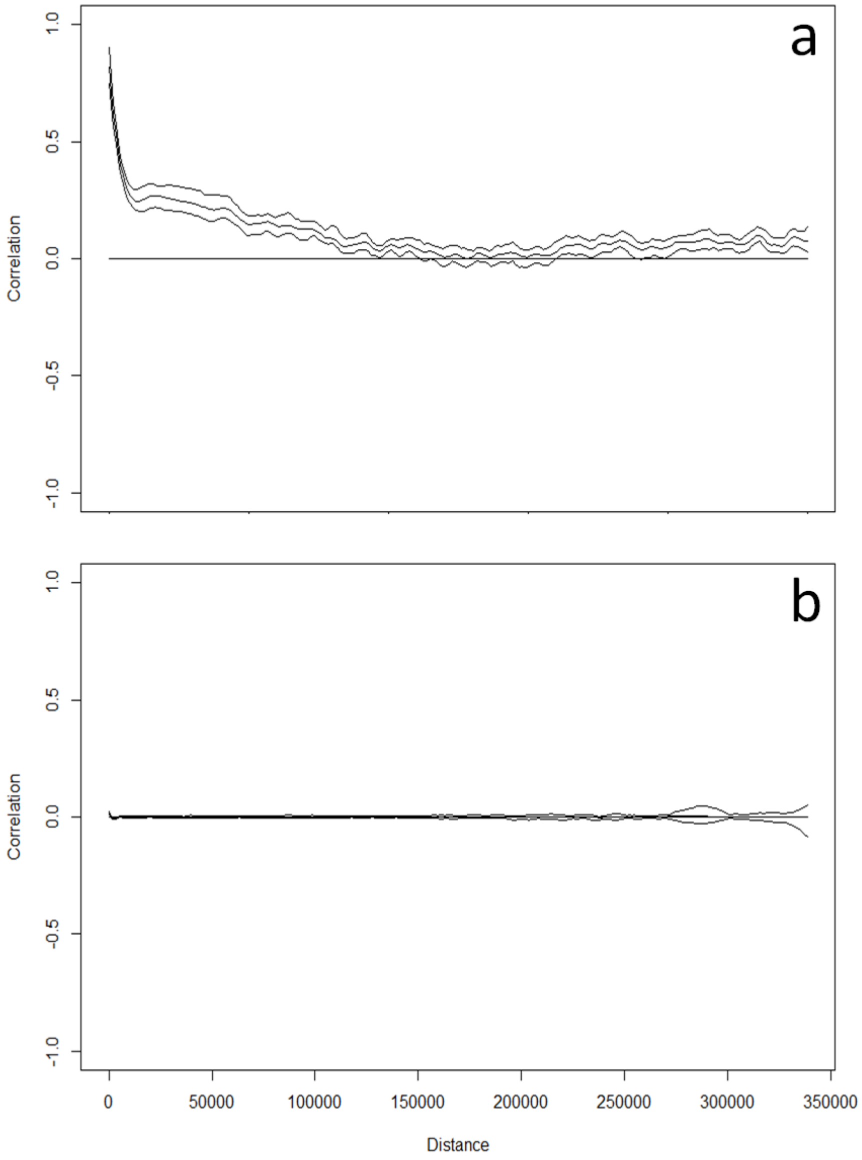

Figure 1-4: Spline correlegrams showing the comparison of (a) the spatial autocorrelation of the residuals of a generalized linear model (GLM), which does not take into account spatial autocorrelation, and (b) the spatial autocorrelation of the residuals from the generalized linear mixed model (GLMM). The correlation of the residuals at close distances in the GLM were significantly correlated, whereas there is almost no spatial autocorrelation at any distance class in the GLMM.

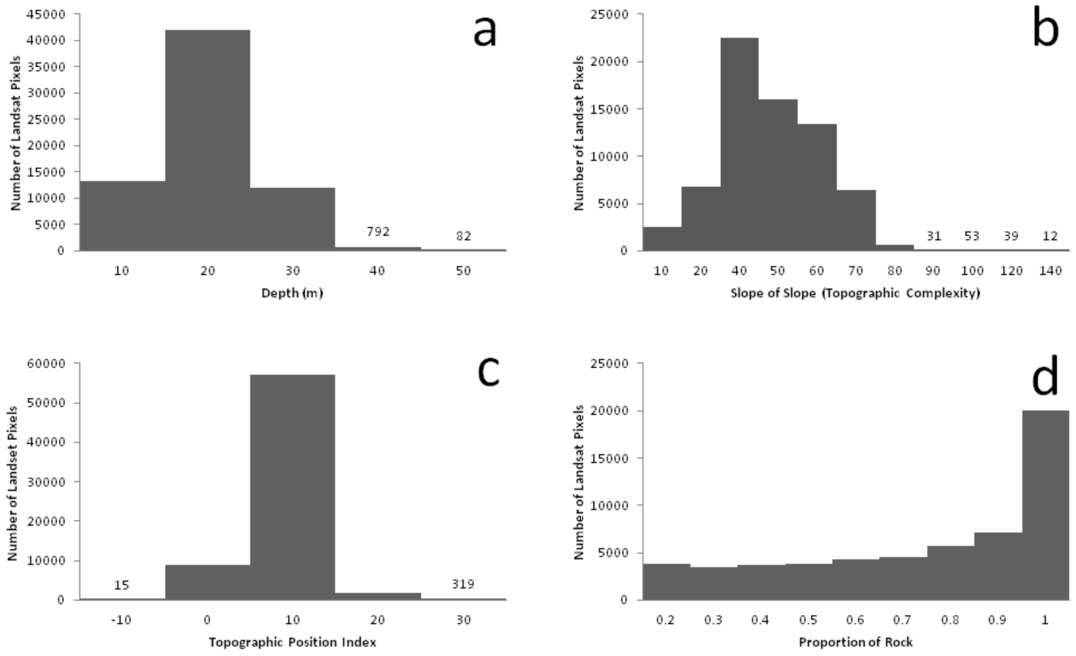

Figure 1-5: Frequency distributions of the occurrence of *Macrocystis pyrifera* in relation to variation in depth (a), slope of slope or topographic complexity (b), topographic position index (c), and the proportion of rock (d). Vertical axes are the number of Landsat pixels where kelp is present within each of the categories of geomorphic structure.

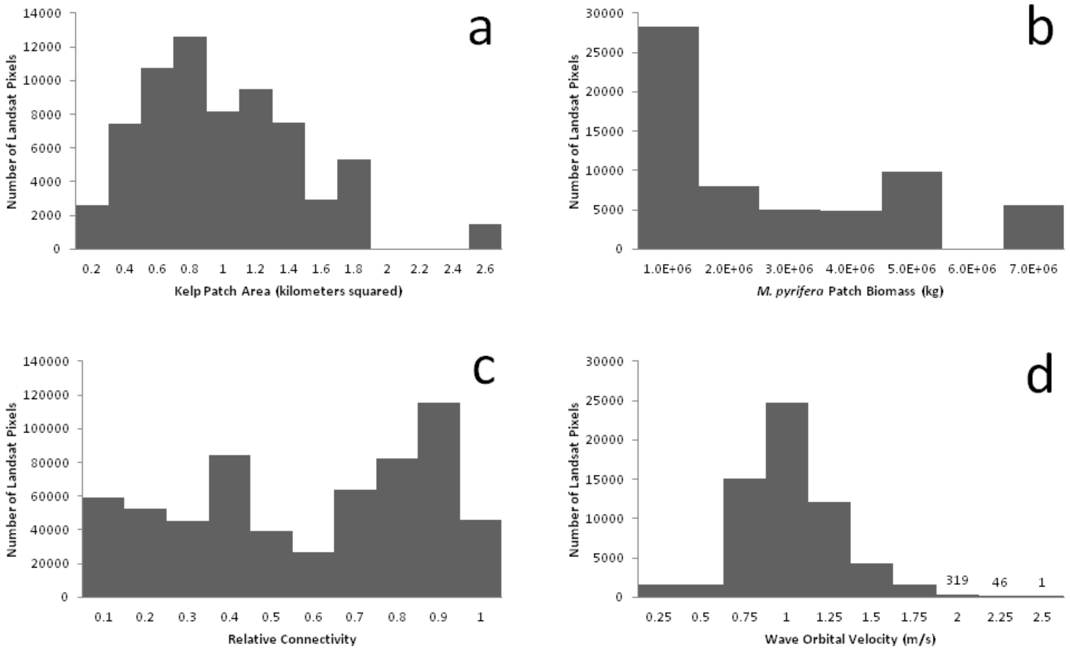

Figure 1-6: Frequency distributions of the occurrence of *Macrocystis pyrifera* in relation to variation in kelp patch area (a), total biomass within a kelp patch (b), the relative connectivity of the patch (c), and the wave orbital velocity (d). Vertical axes are the number of Landsat pixels where kelp is present within each of the categories of the patch-based and environmental variable categories.

1.9 Tables

Table 1-1: The results from the best GLMM for predicting the persistence of kelp on the central coast of California based on AIC and deviance explained. The variables used as fixed effects are shown with their corresponding z scores and p-values. Variance and standard deviation of the random effect used (SubPatch) is shown.

FIXED EFFECTS			
	Coefficient	**abs(Z score)**	**P-Value**
(Intercept)	3.067	85.72	< 0.000
Distance to Edge of Patch	0.162	100.68	< 0.000
Depth	-0.019	37.91	< 0.000
Mean Complexity	0.125	35.44	< 0.000
Patch Biomass	0.152	29.06	< 0.000
(Depth)^2	-0.022	17.71	< 0.000
Wave orbital Velocity	-0.033	14.89	< 0.000
(Wave orbital Velocity)^2	-0.011	11.75	< 0.000
Proportion Rock	0.011	3.46	0.001
Subpatch Connectivity (survivorship = 0.10)	0.152	2.76	0.006
RANDOM EFFECTS:			
	Variance	**Std. Dev.**	
SubPatch (168 individual subpatches)	0.151	0.389	

2. Chapter 2: Application of species distribution models to explain and predict the distribution and abundance of nearshore temperate reef fishes

2.1 Abstract

As the fields of resource management and conservation continue to move toward more spatial and ecosystem-based approaches, there is a growing need for spatially explicit, quantitative information on species distributions and a better understanding of the biotic and abiotic determinants of those distributions. To address the need for making quantitative predictions of how species densities are distributed over broader spatial scales, species distribution models (SDMs), also known as predictive habitat distribution models, have been developed and applied. The purpose of this study was to create predictive SDMs (generalized additive models) for temperate fish species densities and fish assemblage diversity and richness by associating them with variables extracted from seafloor habitat maps, biogenic structure, and oceanographic variables and extrapolating densities and fish diversity and richness over the study area. The accuracy of these predicted extrapolations was tested using an independent dataset not used in the creation of the models and the SDMs were used to estimate larger scale species densities and abundances to compare with other estimates of species abundance (uniform density extrapolation over rocky reef and density extrapolations taking into account variations in geomorphic structure). The SDMs successfully modeled the species-habitat relationships of seven kelp forest associated fish species and showed that the species densities varied with their relationships to the environmental variables. Topographic complexity was the only variable that was found to be significant across all models. The predictive accuracy of the SDMs ranged from 0.26 to 0.60 (Pearson's r correlation between observed and predicted density values). The SDMs created for the fish diversity and richness were much simpler with only one and two variables used, respectively. The accuracies of the predictions from these community-level models were higher with Pearson's r values of 0.61 for diversity and 0.71 for richness. The comparisons of the different methods for extrapolating species densities over a single MPA varied greatly in their abundance estimates with the uniform extrapolation (density values extrapolated evenly over the rocky reef) always estimating much greater abundances. The other two methods, which took into account variation in the geomorphic structure of the reef, provided much lower abundance estimates. The application of landscape-scale approaches shows great promise for both explaining and predicting the distribution and abundance of species and communities in the marine environment and for informing spatial and ecosystem-based approaches to conservation and fisheries management.

2.2 Introduction

As the fields of resource management and conservation continue to move toward more spatial and ecosystem-based approaches, there is a growing need for spatially explicit, quantitative information on species distributions and a better understanding of the biotic and abiotic determinants of those distributions (Franklin 1995; Austin 1998; Elith and Burgman 2002) Landscape approaches that discriminate habitat types and quantify species-habitat associations at broad geographic scales have become critical to increasing our understanding of how and why populations are distributed throughout their environment and, as a result, better inform spatial ecosystem-based management (Guisan and Zimmermann 2000; Hirzel and Guisan 2002). While the need for and application of landscape ecology for informing spatial and ecosystem-based management has long been recognized by managers and conservation scientists in terrestrial environments (Saunders et al. 1991; Franklin 1993), it has more recently been recognized in the marine environment (Sala et al. 2002; Monaco et al. 2005; Appeldoorn et al. 2003; Friedlander et al. 2007). This more recent interest by marine managers and scientists reflects both a growing interest in spatial, ecosystem-based management in the marine environment and the recent development of technologies (e.g., high resolution seafloor mapping, remotely sensed environmental information, GIS tools) to support landscape approaches. Of particular interest in marine ecosystem-based management is the growing application of marine protected areas (MPAs) and coastal and marine spatial planning (Douvere 2008; Halpern et al. 2008; Crowder et al. 2008; Foley et al. 2010).

To address the need for making quantitative predictions of how species densities are distributed over broader spatial scales, species distribution models (SDMs), also known as predictive habitat distribution models, have been developed and applied (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Chatfield et al. 2010). The past few decades have seen a large increase in the development and use of SDMs (Guisan and Thuiller 2005; Mellin et al. 2010) and these models are becoming recognized as an important aspect of conservation planning, especially in terrestrial ecosystems (Austin 1998; Guisan and Zimmermann 2000; Austin 2002). SDMs combine quantitative species surveys with environmental data to identify quantitative species-habitat relationships and predict how species are distributed across landscapes (Guisan and Thuiller 2005). SDMs were originally developed in the terrestrial realm (Guisan and Zimmermann 2000; Brown et al. 2011) and are now being applied to the marine environment (Mellin et al. 2010).

In temperate marine environments, numerous studies have detected strong spatial associations between, for example, temperate demersal fishes and either biotic (e.g., Choat and Ayling 1987; Levin and Hay 1996; Dean et al. 2000; Anderson and Millar 2004) or abiotic (e.g., Carr 1991; Curley et al. 2002; Harman et al. 2003; Pittman et al. 2007) environmental variables. Unfortunately, many of these descriptions of species-habitat associations are strictly qualitative and do not allow for making quantitative predictions of species densities beyond the areas sampled (Chatfield et al. 2010). However, the development and application of SDMs in the marine environment has increased with recent advances in acoustic technology to collect high resolution habitat maps (Hughes Clarke et al. 1996; Anderson et al. 2008; Cogan et al. 2009), the ability to collect spatially explicit information on species distributions and abundance (Valavanis et al. 2008), and the development of geographic information systems (GIS) tools that allow the integration of species distribution with habitat structure (Rotenberry et al. 2006; Young et al. 2010). While researchers now have the resources necessary to create and apply SDMs in many areas of the marine environment, demonstration of this approach and its application for informing spatial, ecosystem-based management approaches are rare.

The purpose of this study is to develop an analytical approach to creating SDMs that integrates high resolution bathymetric maps with *in situ* species surveys to (i) characterize benthic habitats, (ii) determine species-habitat associations, (iii) generate species density distributions across coastal seafloor landscapes, which I use to (iv) estimate species abundances. To develop the approach, I use several species of nearshore fishes along the central coast of California. I focus on central California because of the confluence of sources of information (habitat maps, ecological surveys) required to develop SDMs and the need for this information to inform the evaluation and adaptive management of the recently established network of marine protected areas there.

The state of California, USA, recently (2007-2012) established a state-wide network of marine protected areas along the 1200 km coastline (13,688 km^2 of state waters, 2207 km^2 or 16% in MPAs; http://www.dfg.ca.gov/mlpa/). Combined with ecological and oceanographic monitoring programs, the network provides resource managers and scientists with unique opportunities to inform and advance a variety of marine spatial and ecosystem-based management approaches and policies (Kirlin et al. 2013; Gleason et al. 2013). These policies include advances in ecosystem-based management, marine spatial planning, fisheries, and climate change (Gaines et al. 2010; Halpern et al. 2010; Carr et al. 2011). Characterizing the distribution and abundance of species, communities and ecosystems both inside and outside of MPAs across the network is also necessary for evaluating how effective MPAs are at protecting ecosystems and the biodiversity of economically and recreationally important species they support (Hamilton et al. 2010; Carr et al. 2011; Grorud-Colvert et al. 2011, 2014; Botsford et al. *in press*). The development and application of SDMs could be particularly valuable for both the evaluation and adaptive management of California's network of MPAs and realizing its application for informing spatial and ecosystem-based management.

Recognizing the need for more and better information on the structure of the seafloor to inform spatial, ecosystem-based management, including the design of California's network of MPAs, the state simultaneously designed and implemented a state-wide seafloor mapping project (California Seafloor Mapping Program; CSMP). One objective of this program was to inform the placement and evaluation of marine protected areas (MPAs) by characterizing habitats and their distributions and using that information to ensure the network of MPAs representatively included the variety of seafloor features and the biodiversity and communities they support (Kvitek and Iampietro 2010). Because many species display preferences for specific depths and habitat types (Wright and Heyman 2008; Dunn and Halpin 2009; Brown et al. 2011), the highly-detailed maps of seafloor geomorphology produced by the CSMP are also likely to provide an extremely valuable resource for developing SDMs. By combining these maps with species data generated by ecological surveys, species-habitat relationships to inform SDMs can be created and advance the understanding of ecosystems further than what is achievable through the use of ecological data alone (Brown et al. 2011).

In conjunction with the implementation of the California network of MPAs, ecological surveys were initiated to characterize the structure and distribution of populations and biological communities. These surveys of kelp forest ecosystems conducted by SCUBA divers were continued at several MPAs to characterize initial ecological responses to the establishment of the MPAs and develop ecological time series that would allow the MPAs to inform various marine management issues (e.g., fisheries management, climate change). Among the ecological metrics of interest are estimates of species abundance that inform how abundances respond to MPA establishment, including potential larval production that contributes to replenishment of coastal populations. Surveys were designed to estimate these and other ecological metrics by stratifying sampling across the forest ecosystems., One limitation of this sampling design, however, is the inability to extrapolate the *in situ* observations over broader spatial areas (within and outside MPAs) to make predictions as to the distributions of species and communities where they did not make direct observations.

In this study, I draw from these sources of information and use geographic information systems (GIS), to create SDMs for the purpose of estimating species distributions and abundances at spatial scales relevant to informing the adaptive management and application of a network of MPAs. I use the SDMs to answer the following suite of questions:

1) Do densities of fish species vary predictably with environmental variables including the structure of the rocky reef, latitude, kelp biomass, and exposure to ocean swell (wave orbital velocities)? If so, what is the relative importance of the variables in explaining this variation and how does it vary among species?

2) Do species diversity and richness of the kelp forest fish assemblage vary predictably with environmental variables?

3) Can SDMs generate reliable extrapolations of species densities, diversity and richness?

4) Do estimates of fish abundance generated by the SDMs differ substantially (both higher and lower) from those generated by simple uniform extrapolation of density estimates across the kelp forest habitat?

Collectively, answers to these questions may demonstrate the utility of SDMs in enhancing our ability to estimate species distributions and abundances and their application for informing spatial and ecosystem-based management approaches.

2.3 Methods

My general approach to answering these questions was to test for predictive SDMs (generalized additive models) based on variables extracted from seafloor habitat maps, oceanographic variables and species densities estimated by the ecological surveys (Question 1). The fish assemblage diversity and richness from the ecological surveys were also associated with the environmental variables using the same methods as for the densities (Question 2). The SDMs were then use those models were used to extrapolate densities, diversity, and richness over the study area. I tested the accuracy of these predicted extrapolations using an independent dataset not used in the creation of the models (Question 3). I then used the SDMs to estimate species abundances and compare with other methods for estimating species abundance (Question 4).

2.3.1 Study System

I focus on fish assemblages that inhabit shallow (5-20 m depth) forests of giant kelp, *Macrocystis pyrifera*, along the central coast of California, USA (Figure 2-1A), extending from Pigeon Point in the north (37°10'57" Lat 122°23'38" Long) to Point Conception in the south (34°26'55" Lat 120°28'14" Long). This study area corresponds to the Central Coast Study Region of the state Marine Life Protection Act (MLPA) Initiative that created a network of 29 MPAs with differing levels of fishing restrictions across the study area (Figure 2-1B). The depth range for this study is restricted to 20 meters depth due to the limited depth range of the ecological surveys.

I focused analyses on ten focal species of fishes that were frequently observed in the surveys of the central California kelp forests: tubesnout (*Aulorhynchus flavidus*), black surfperch (*Embiotoca jacksoni*), striped surfperch (*Embiotoca* *lateralis*), kelp greenling (*Hexagrammos decagrammus*), olive rockfish (*Sebastes serranoides*), kelp rockfish (*Sebastes atrovirens*), gopher rockfish (*Sebastes carnatus*), black rockfish (*Sebastes melanops*), and blue rockfish (*Sebastes mystinus*). In contrast, species diversity and richness was estimated for the entire assemblage of the 70+ conspicuous species of fishes recorded on ecological surveys.

2.3.2 Estimates of fish densities, diversity and richness

Fish densities were estimated for the ten focal species by visual surveys using SCUBA, conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO: *http://www.piscoweb.org/research/science-by-discipline/ecosystem-monitoring/kelp-forest-monitoring/subtidal-sampling-protoco*) at 85 sampling sites distributed across the study area (Figure 2-1B). Surveys were conducted from 2007 to 2011 at each site. Three consecutive 30m long by 2m tall by 2m wide (120m^3) transects were sampled in each of four depth zones (5m, 10m, 15m, and 20m) at each sampling site. Transects are stratified from the offshore to onshore margins of the forests and at mid-depth and along the bottom to encompass the 3-dimensional habitat of the kelp forests (Figures 2-1C, D). I combined the three transects, including the two portions of the water column, as a single 720m^3 transect as a more conservative estimate of the location of the surveys relative to the seafloor maps (Figure 2-1C, D). The locations of these transects were recorded using a GPS unit to mark the location at the beginning of each transect. Only those transects with available position data and overlap with mapped seafloor data were used in this study. From these transects, the mean density of each of the ten species within each depth zone. Species diversity (H’, Shannon Diversity Index) and richness (number of species) was also calculated for each 720m^3 transect.

2.3.3 Quantifying Habitat Characteristics

Seafloor maps generated by the CSMP were used to derive a variety of habitat variables that were potentially useful for predicting the density distributions and diversity and richness of the ten fish species. Geomorphic variables from the seafloor included depth, slope, slope of the slope (complexity), topographic position at multiple scales, and substrate type (rock versus sediment). In addition to these variables, latitude, wave orbital velocities (a metric of exposure to ocean swell), and kelp biomass estimates were used (Figure 2-2).

Depth is likely to be an important predictor of fish distributions due to the known associations of species within specific depth ranges (Eschmeyer et al. 1983, Allen and Pondella book chapter 4). Depth information was derived directly from the digital elevation models (DEMs) produced by the CSMP. DEMs are raster datasets that consist of depth values at regularly spaced intervals and all DEMs used in this study were at 2m resolution.

The Spatial Analyst extension in ArcGIS 10 (ESRI 2012) was used to calculate both slope and slope of the slope from the DEMs. Previous studies have shown that species distributions vary with changes in slope and areas of high slope are often correlated with greater densities of fish than areas with little to no slope

(McClatchie et al. 1997). The slope of the slope, which is a measure of topographic complexity, has been shown to be an important predictor of fish species distributions in coral reefs (Pittman and Brown 2011).

Topographic position index (TPI) is a measure of relative elevation and is calculated by comparing the elevation of each cell in a DEM to the cells in the surrounding landscape. TPI is useful for delineating features that could be of importance to many species of fish such as peaks, ridges, flat plains, valleys, and crevices. TPI was calculated using the algorithm of Weiss (2001), which uses an annulus ('donut') shaped neighborhood and were created using the bathymetric position index (BPI) tool within the Benthic Terrain Modeler (BTM) toolbar. TPI was calculated at 20m and 50m scales with a 5 cell (10m) annulus thickness. Previous studies have used TPI to explain variation in the distribution of multiple species (Weiss 2001; Iampietro et al. 2005; Lundbland et al. 2006; Young et al. 2010).

To create rasters that distinguish between rock and sediment, vector ruggedness measure (VRM) grids were created from the DEMs using the Terrain Tools toolbox in ArcGIS 9.x (Sappington et al. 2007). VRM is a measure of terrain ruggedness using vector analysis where the 3-dimensional orientation of the grid cells is taken into account, allowing for variation in slope and aspect (Hobson 1974). The values associated with VRM vary from 0 (flat, smooth areas) to 1 (areas of higher complexity). Because rock is often more complex than the surrounding sediment, VRM can be used to help distinguish between rock and sediment areas (i.e. "rough" and "smooth" areas, respectively). VRM was, therefore, used as a proxy for "rock" and "sediment." From the VRM analysis, a binary raster was created with 0 signifying soft sediment and 1 signifying rocky substrate. The breakpoints for these two classes were based on a threshold of VRM that captured the majority of the "rock" without erroneously classifying artifacts or sediment features. If necessary, a substrate mask was used to mask out any problematic areas. The resulting, classified raster was used as factor input into the model.

In addition to variations in reef structure, fish assemblages have been shown to change with variation in latitude (McClatchie et al. 1997; Stephens et al. 2006 in Allen book (chapter 9); Carr and Reed *in press*) and kelp (Dean et al. 2000; Stephens et al 2006 in Allen book (chapter 9); Carr and Reed *in press*). In order to account for the latitudinal variation, a latitude raster was created using the ArcGIS raster calculater '$$YMAP' function. Kelp biomass rasters were created from kelp biomass values derived from high-resolution satellite imagery and aerial photography (Cavanaugh et al. 2010, 2011).

2.3.4 Wave Orbital Velocity

The measure of wave forces used in this study is wave orbital velocity and extracted from wave maps developed by USGS using the following methods. Patterns of wave energy and orbital velocities along the California coast were simulated with the numerical wave model SWAN (Simulating Waves Nearshore, Delft University of Technology, The Netherlands). SWAN is a third-generation spectral wave model capable of simulating wind-wave growth, propagation, refraction, dissipation, and depth-induced breaking (Booij et al. 1999; Ris et al. 1999). A set of 15 SWAN model grids were developed and used to simulate wind-wave growth and propagation across the inner portion of the California continental shelf. All grids were curvi-linear, with an average cross- and along-shore resolution of 30 to 50 m and 60 to 100 m, respectively, in the shallow inshore regions. Model grid cells were smaller in the cross-shore direction, in shallow water, and around complex bathymetry to enable accurate wave refraction and shoaling. Latitudinal extents were defined based on local geography and computation limitations. The offshore extent of the model grids were defined by 64 Wave Information System (WIS, *http://wis.usace.army.mil/*) model output stations located approximately 20 km offshore along the entire California coast. Wave parameters (significant wave heights, peak wave period, and mean wave direction) derived from the WIS database were applied at the boundaries of the 15 SWAN grids. The WIS data encompass the 32 years from 1980 through 2011 were used to calculate seasonal (arithmetic) mean and extreme (arithmetic mean of highest 5%) conditions. Seasons were defined as: winter = December through February; spring = March through May; summer = June through August; and fall = September through November.

Parametric wave descriptors (wave heights, periods, and wave direction) derived from the WIS database were applied along the open boundaries of the SWAN domains; these were represented in spectral space with a JONSWAP shape and a 3.3 peak enhancement factor. In all grids, 10-degree direction bins and 36 frequencies spaced log-normally from 0.0417 Hz to 1.0000 Hz were used. The bottom friction coefficient was set to 0.038m^2/s for swell conditions (Hasselmann et al. 1973 in SWAN technical documentation, 2013), whitecapping was computed with the Komen et al. (1984) formulation, and depth induced breaking with the Battjes and Janssen (1978) formulation. Winds from the most centrally located WIS station of each grid were applied uniformly across the domains to allow for inclusion of locally wind-generated waves in addition to (usually greater) energy contributions from distantly generated swell waves. All grids were solved in the spherical coordinate system and run in a stationary mode. In shallow water, the orbital motions of water particles induced by surface waves extend down to the seabed. The resulting wave-induced orbital velocities near the seabed are considered to be a representative measure of how waves influence the sea floor and as such are a focus of this study; SWAN calculates bottom orbital velocity (U_{orb}) as the maxima of the root mean square (rms) bottom velocity (U_{rms}).

The ability of the SWAN model to accurately simulate wave propagation was tested by running the model forced with hourly wave parameters of the WIS database over a week long time period from 18-25 January 2010. The simulation period encompasses a large storm event when wave heights exceeded 9 m (e.g., CDIP Pt. Reyes buoy) and affected the entire California coast. The ability of the SWAN model to reproduce observed wave conditions was evaluated with a skill score (Willmott 1981); the skill score ranges from 0 to 1, with a skill score of 1 indicating perfect agreement. The analysis was done over the entire simulated time-series. The skill scores were quite good (mean±1 SD = 0.89±0.05; range = 0.81-0.97) at all sites evaluated. Although observations are not available within all grids, the high skill scores and lack of clear geographic trend in changes of the skill score suggest that model results in grids with no buoys are likely also reflective of true conditions.

Sampling of Environmental Variables

After quantifying the seafloor and environmental variables within the study region, all variables except for substrate type were sampled for the mean and standard deviation at a 50m spatial scale using the focal statistics geoprocessing function in ArcGIS's Spatial Analyst extension. Fifty meters was the finest scale at which predictions could be made with the ecological survey data due to the spatial uncertainty of the sampling locations. For substrate, the proportion of rocky substrate was computed within each of the buffers. To spatially associate species density and diversity with corresponding habitat data, these 50m units were then sampled using ArcGIS's Extract Multi-values to Points tool within Spatial Analyst at each of the ecological survey sites.

2.3.5 Do densities of fish species vary predictably with environmental variables? If so, what is the relative importance of the variables in explaining this variation and how does it vary among species?

To test the hypotheses that species densities vary predictably with environmental variables and that the relative importance of these variables differ among species, I used generalized additive models (GAMs). Because the response variables in the majority of ecological studies do not have a linear relationship with environmental data, the use of linear regression techniques is often not appropriate (Austin 1999). Other regression techniques including generalized linear models (GLMs) and generalized additive models (GAMs), however, allow for nonlinear relationships (Yee and Mitchell 1991; Austin 1999). Therefore, GLMs and GAMs have become widely used in modeling the distribution of species (Guisan and Zimmermann 2000; Scott et al. 2002). I initially conducted analyses with both GLM and GAM models and found that GAMs explained greater variation in, and produced more accurate predictions for, fish density. Therefore, within the "mgcv" package in R, GAMs were used to test for significant predictive relationships between density of each species of fish and environmental variables and to identify the relative importance of each environmental variable in contributing to the model. A smoother was applied to those variables in the GAM that did not have a linear relationship with density. The total number of transects used in these models were combined across 2007 and 2008 sampling years (n=265). Best fit models were developed for each species through a process of elimination; variables were removed from the models based on their lack of significance and their collinearity with other variables until the model with the lowest AIC and highest deviance explained was produced. I then compared models among the focal fish species to determine differences in the relative importance of environmental variables in explaining and predicting variation in density.

Prior to these analyses, a data exploration was carried out following the protocols of Zuur et al. (2009). Cleveland dotplots were created for each of the habitat variables and each of the density estimates resulting in a square root transformation for the slope of slope standard deviation and the TPI standard deviations at the 50m scale. None of the other habitat variables required data transformation. Multi-panel scatterplots, Pearson correlation coefficients, and variance inflation factors (VIF) were used to test for collinearity between explanatory variables. Those paired variables that had a Pearson correlation coefficient greater than 0.50 were not included in models together. In addition, variables producing a VIF greater than 3 were excluded from the models, although most VIF values were below two in all the models used (Zuur et al. 2009).

I tested for violations of the assumption of independence of observations, including spatial autocorrelation (Hurlbert 1984; Zuur et al. 2009). Spatial autocorrelation is a common occurrence in spatially defined observations where observations that are made close together are more similar than those that are further apart (Zuur et al. 2009). For this study, Moran's *I* was used to test for spatial autocorrelation among the observations and no significant spatial autocorrelation was found.

2.3.6 Do species diversity and richness of the kelp forest fish assemblage vary predictably with environmental variables?

I also used generalized additive models (GAMs) to test the hypotheses that species diversity and richness vary predictably with environmental variables. The Shannon Diversity Index (H') and species richness (number of species) calculated for each 720m^3 transect was used as the response variable and the same environmental variables used to test density relationships were used as the independent variables. The total number of transects used in these models were combined across 2007 and 2008 sampling years (n=265). I tested for violations of assumptions of these GAMs as described for the density models.

2.3.7 Can SDMs generate reliable extrapolations of species densities, diversity and richness?

Significant density-habitat relationships were detected for seven of the ten species tested. Following model selection for each these seven species, the GAM tools within the marine geospatial ecology toolbox (MGET) were used to create predictive maps extrapolating the density predictions over the study area (Roberts et al., 2010). I used 70% (n= 178) of the survey transects for these models, reserving the remaining 30% (= 87 transects) for the test of accuracy of the density extrapolations. I used Pearson's correlation coefficient to test the accuracy of density extrapolations of each species by testing for a significant correlation between the density values predicted by the GAM and the actual density values in the reserved dataset.

Additionally, to test if the Pearson correlation was statistically significant, a Markov chain Monte Carlo (MCMC) simulation was run with 1000 iterations to determine if the likelihood of these correlations were greater than random chance. The same procedure was used to generate and test the reliability of extrapolated distributions of diversity and richness of the entire sampled fish assemblage.

2.3.8 Effect of Different methods for Estimating Population Abundances within the Central Coast MPA Network

For this comparison, three methods were used to extrapolate species densities across the kelp forests in the 0-20m depth zone of one of the MPAs in this region: Point Sur State Marine Reserve (SMR). The first method used the assumption that all rock is similar (i.e. no difference in any of the environmental variables used in the GAMs). To extrapolate fish density assuming all rock is equal, I simply averaged the density of each species across all transects and multiplied that density by the total area of rocky reef identified in the 0-20m depth zone (the depth range of the biological transects) within the MPA. The resulting calculation gives an estimation of the total number (i.e. abundance) of each species in the 0-20m depth zone of the MPA**.**

The second method used data extracted from the CSMP seafloor maps and habitat categories for slope (four levels) and rugosity (five levels) defined by Greene et al. (2007) and for two spatial scales (20m and 50m) of six levels of TPI defined by Iampietro et al. (2005) to characterize transects by the relative area of these geomorphological categories. Samples based on the ecological surveys conducted across the entire study area included a 10m buffer to both sides of each transect (total area= 2000m^2) to incorporate the spatial uncertainty in the exact location of that transect, with the assumption that the transect was conducted within that 20m-wide band. In addition to transects from the ecological surveys, I sampled 3250 transects that I placed randomly throughout the entire study area in rocky habitat at comparable depths of the kelp forest surveys to assess the general availability of rocky habitat types across the region. Transects were the same dimensions used by the ecological surveys, including a 10m buffer around each transect. The relative (percent) area of slope, rugosity and TPI levels was calculated for each transect across the study area.

I then used these transects characterized by their relative area of the slope, rugosity and TPI levels in a cluster analysis within the statistical software package Primer to identify discrete habitat classes comprised of transects of similar combinations of slope, rugosity and TPI levels across the entire study area. Once clustered, the dendrogram was searched for the appropriate merging distance to break transects into a number of geomorphic classes suitable for the sample size of actual surveyed transects. These geomorphic classes were defined by unique combinations of the relative abundance of the slope, rugosity and TPI levels (Table 2-1). The proportion of transects of each of the geomorphic classes and the total reef area within the Point Sur MPA was used to calculate the area of each geomorphic class. Then, the average density of each species within those geomorphic classes was calculated and multiplied by the total area of the corresponding class to generate an abundance estimate for each species within the geomorphic class. The abundances were then added up across all geomorphic classes to get a total abundance estimate for each species within the MPA.

For the third method, the predictive density maps created from the spatially-explicit species-habitat associations developed in this study were used to calculate the total abundance of each species across the region. To do this, the density values for each of the 2m pixels from the predictive density maps were used to calculate total abundance within the Point Sur MPA.

2.4 Results

2.4.1 Do densities of fish species vary predictably with environmental variables? If so, what is the relative importance of the variables in explaining this variation and how does it vary among species?

The GAMS detected strong correlations between fish density and environmental variables for seven of the ten species analyzed. Three species, *A. flavidus, H. decagrammus*, and *S. mystinus*, did not have strong associations with the habitat variables and the predictive power of these models was very weak so they were not used further in the analysis. Densities of the other seven species showed strong positive or negative correlations (i.e. predictive models) with at least three environmental variables (Table 2-2). Topographic complexity (slope of slope) was the only variable that was consistently significant in all the GAMs. Across all species, the densities had an asymptotic relationship with topographic complexity and, therefore, a smoother was applied to this variable in all models (Appendix A). Density of three species, *S. atrovirens, S. chrysomelas,* and *S. melanops,* were significantly correlated with kelp biomass. *S. atrovirens* and *S. melanops* had a positive, linear relationship with mean kelp biomass. The remaining species, *S. chrysomelas* had a non-linear but positive trending relationship with kelp biomass (Appendix A). Density of *E. lateralis* and *E. jacksoni* increases with shallower depths. *S. chrysomelas* and *S. carnatus* had a unimodal relationship with depth where the densities tended to be highest in the middle depths of the depth range. Densities of three species exhibited negative correlations with exposure to ocean swell (mean orbital velocity) and density of only one species, *S. chrysomelas*, was positively correlated with orbital velocity. Density of three species, *E. lateralis, S. serranoides* and *S. melanops* was positively correlated with latitude and only one species, *S. carnatus,* increased in density to the south.

2.4.2 Do species diversity and richness of the kelp forest fish assemblage vary predictably with environmental variables?

Species diversity (H') and richness of the fish assemblage were both positively correlated with increases in mean complexity (i.e. slope of slopes) (Table 2-3). Species richness was negatively correlated with exposure to ocean swell (mean orbital velocity). No other environmental variables contributed significantly to predictive models of species diversity or richness.

2.4.3 Can SDMs generate reliable extrapolations of species densities, diversity and richness?

For all but one of the seven species tested, correlation between densities predicted by the GAMs and densities observed in ecological surveys not included in development of the models was strongly significant (Pearson's r, $P < 0.000$). Predicted densities of *S. serranoides* were not significantly correlated with observed densities (Pearson's $r = 0.26$, $P = 0.35$). Of the significant models, correlation coefficients varied among species from a high of 0.60 ($P < 0.000$) for *S. atrovirens* to a low of 0.40 ($P < 0.000$) for *S. chrysomelas*. Correlations for the two surfperch species, *E. jacksoni* and *E. lateralis* were similar; Pearson's $r = 0.42$, $P<0.000$, and $r = 0.46$, $P<0.000$, respectively. GAMs for the remaining two species, *S. carnatus* and *S. melanops*, were 0.55 ($P<0.000$) and 0.44 ($P<0.000$), respectively. Thus, the average accuracy of the models based on the Pearson’s correlation coefficient across all the models was 0.45. Using the same validation approach, the GAMs were good at predicting spatial patterns of diversity (Pearson’s $r= 0.61$; $P< 0.000$) and richness ($r= 0.71$; $P< 0.000$) of the entire fish assemblage sampled across the study area.

2.4.4 Effect of Different methods for Estimating Population Abundances within the Central Coast MPA Network

The comparison between the three methods for calculating species abundances (uniform geomorphology, non-spatial geomorphometric-based, and SDM) indicate that density extrapolations assuming spatially invariant geomorphology produces much greater estimates of species abundance than the variable geomorphology and spatially explicit environment-based estimates (Table 2-4). The magnitude of the differences in estimated abundance varied markedly among the seven species, ranging from two to 17-times greater abundance estimates. With the exception of *Embiotoca jacksoni*, the abundance estimates from the SDM calculations produced the lowest predicted abundance of the three methods. In addition, the difference between the non-spatial geomorphic and the spatially explicit SDM-based extrapolations were more similar to each other than either predictions were to the uniform geomorphic extrapolation (Table 2-4).

2.5 Discussion

Most of the temperate, nearshore fishes examined in this study exhibited strong associations with environmental variables that constitute their habitat, which allowed for accurate extrapolation of their densities within kelp forests across the study region. Quantitative relationships between fish density and environmental variables also made it possible to better understand potential sources of variation in the distribution of six of the ten species originally targeted in the study. Across all six species with significant density-habitat relationships, species density was correlated with more than one variable, indicating multiple aspects of the environment must be considered when explaining spatial variation and mapping species distributions. All six of these species density models were characterized by relatively low Pearson's r and very significant ($P< 0.0001$). These two results reflect the large number of samples that were used to create the models. Although combinations of environmental variables best explained spatial variation in density of the six species, their densities were also strongly correlated with single environmental variables, indicating strong species associations with individual variables that can explain spatial variation in density of a species. Moreover, the individual environmental variables differed markedly in the strength of these relationships as well as the number of species for which they explained variation.

The three-dimensional complexity (topographic complexity) of the rocky habitat (slope of slope) was the only variable that was significant across all seven species models. Three-dimensional complexity was measured as slope of slope of the terrain. The relationship between complexity and all the response variables, including species-specific density and the fish assemblage characteristics, was asymptotic. The fish densities, diversity, and richness all increased with increasing complexity up to slope of slope values between 10 and 20. After that, there was not a lot of variation in the response variables with complexity. This signifies that complexity values associated with suitable habitat begin between slope of slope values of 10 to 15 and any slope of slope value greater than that provides suitable habitat. The significance of structural complexity of the reef in explaining variation in fish densities is consistent with other species distribution models generated for coral reef fishes (Beger et al. 2003; Kendall and Miller 2010; Pittman and Brown 2011). Thus, heterogeneity of the rocky substratum is a key correlate with the distribution of many demersal species and a likely critical component of any predictive species distribution model.

The proportion of rock was not a significant variable in any of the GAMs for the species successfully modeled. Topographic complexity; however, was a strong correlate with density. During the design of the network of MPAs along the central coast of California, "rock" and "sediment" were the only substrate variables considered across four depth ranges (0-30m, 30-100m, 100-200m, and >200m; Gleason et al. 2013; Saarman et al. 2013). The magnitude to which topographic complexity explains variation in fish density of the species examined here indicates that consideration of rock substratum alone without recognition of topographic complexity can fail to identify important patterns of species abundance. Given the number of species whose density distribution correlated with topographic complexity, and that diversity and richness were also strongly correlated with topographic complexity, these results indicate that spatial and ecosystem-based management should strive to identify and consider patterns of topographic complexity.

Correlations between species density and depth reflected the relative spatial scale of the ecological surveys and the depth ranges of the species. First, depth contributed to models only in those species whose depth range did not span the entire depth range of the surveys and for which depth has previously been shown to be an important correlate with density across the depth range sampled by the ecological surveys. The distribution of two species pairs, *E. lateralis* and *E. jacksoni,* and *S. chrysomelas* and *S. carnatus,* are depth stratified, reflecting interspecific competition within these pairs. *E. lateralis* and *S. chrysomelas* inhabit shallower depths relative to their respective congeners within the depth range sampled (Hixon 1980; Larson 1980a,b; Schmitt and Holbrook 1990). Nonetheless, for both species of surfperches (genus *Embiotoca*) and *S. chrysomelas*, density was more strongly correlated with variables other than depth (e.g., topographic complexity, swell exposure). Only for *S. carnatus*, was depth the strongest correlate with density, probably because their distribution includes only the deeper depths surveyed. These results suggest that within the depth range of kelp forests (5-20m depth) other variables are as important correlates with density. This effect of the relative spatial scales of surveys to the species depth range is greater for those species for which depth was not a significant correlate. Depth ranges of all of these species (e.g., *S. atrovirenss, S. melanops, S. serranoides*) span and extend beyond the depth range of the surveys. To better understand the relative contribution of depth to species-habitat relationships for these species, observations across their entire depth range would need to be incorporated in the models.

Latitude was an important variable in helping to explain the distribution of *E. lateralis, S. carnatus, S. melanops* and *S. serranoides* and the distribution and abundance of rocky reef fishes is known to vary latitudinally along the coast of California (McClatchie et al. 1997; Stephens et al. 2006 in Allen book (chapter 9); Carr and Reed *in press*). Of these four species, *S. carnatus* was the only one whose density decreased to the north along the central coast of California. These correlations with latitude likely reflect relationships with other environmental variables that co-vary with latitude along the coast including temperature, upwelling, exposure to ocean swell and the persistence of kelp forests (Graham et al. 2008, Reed et al. 2011, Carr and Reed *in press*).

The majority of fine-scale species distribution modeling studies generated in the past has only looked at the association of species with the benthic habitat. The water column, however, also plays an important role in the distribution and abundance of species. In this study, only two aspects of the water column were taken into account: the biomass of the structure-forming marine macroalgae, *Macrocystis pyrifera*, and variation in swell exposure (wave orbital velocities) along the central coast of California. Biomass of *M. pyrifera* proved to be an important variable, positively correlated with the density of three species, and was the most important variable in explaining the distribution of *S. chrysomelas*. These results add to a number of other studies that have identified correlations between fish density and the presence or density of *M. pyrifera* (reviewed by Stephens et al. 2006, Carr and Reed *in press*). Wave orbital velocities had a negative relationship with the density of *E. jacksoni*, *S. serranoides*, and *S. atrovirens* and a positive relationship with *S. chrysomelas*. These limited results show that features of the water column are important correlates with the distribution and abundance of shallow dwelling fish species. Incorporation of features of the water column in species distribution models for shallow benthic species will likely increase their explanatory power and capacity to predict species distributions across nearshore seascapes (Hinchey et al. 2008).

Although the majority of the species showed strong habitat affinities, some of the species were not successfully modeled in this study. *Aulorhynchus flavidus*, *Hexagrammas decagrammas*, and *Sebastes mystinus* all failed to show any strong relationship with any of the habitat variables used. The reason for the lack of significance of the variables could be due to the number of observations of each of these species. *H. decagrammas* and *A. flavidus* both had fewer observations than the rest of the species used in this study. The fewer observations could have contributed to the failure of the model to find any significant relationship with habitat variables. On the other hand, *S. mystinus* had a large number of observations but were found over a wide variety of habitats and appeared to be more of a habitat generalist. *S. mystinus* and *A. flavidus* aggregate in the water column well above the reef surface. This behavior may have contributed to the lack of any significant relationship with finer scale habitat variables associated with the reef.

Models that predicted spatial variation in attributes of the fish assemblage (species diversity and richness), were much simpler than those for the individual species. Both richness and diversity were positively and strongly associated with the structural complexity of the rocky reef. Fish species richness was also negatively affected by wave orbital velocity. These community-level models were most likely simpler than the species-specific models because of the variety of fish species examined, which collectively exhibited more general habitat associations than the individual species. However, as with the individual fish species, complexity was still an important variable in explaining the distributions of the fish communities.

The comparison between the different methods for calculating abundance for the six species successfully modeled with the SDMs, showed that incorporating habitat heterogeneity greatly decreased estimates of abundance. The uniform extrapolation, where all rock is considered uniform, produces much higher estimates of abundance than both of the higher resolution habitat-based estimates. In addition, abundance estimates generated by the non-spatial and SDM derived estimates were closer to one another than those derived from the uniform extrapolations. These results warn that, by not accounting for habitat variation, calculations of abundance could greatly over-estimate population sizes. This has critical implications when, for example, larval production or stock/population biomass is being estimated for populations within an MPA or across a region.

2.6 Conclusions

The application of species distribution models along the central coast of California shows that many species of temperate, rocky reef associated fishes have predictable relationships with a number of habitat variables. These species-habitat associations can be used to model and predict the distribution and abundance of these species over the entire region, including areas where biological observations were not acquired. In addition, the results from these types of SDMs can be further used to better estimate the sizes of populations and evaluate their change through time across a network of MPAs. Overall, application of landscape-scale approaches shows great promise for both explaining and predicting the distribution and abundance of species and communities in the marine environment and for informing spatial and ecosystem-based approaches to conservation and fisheries management.

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2.8 Figures

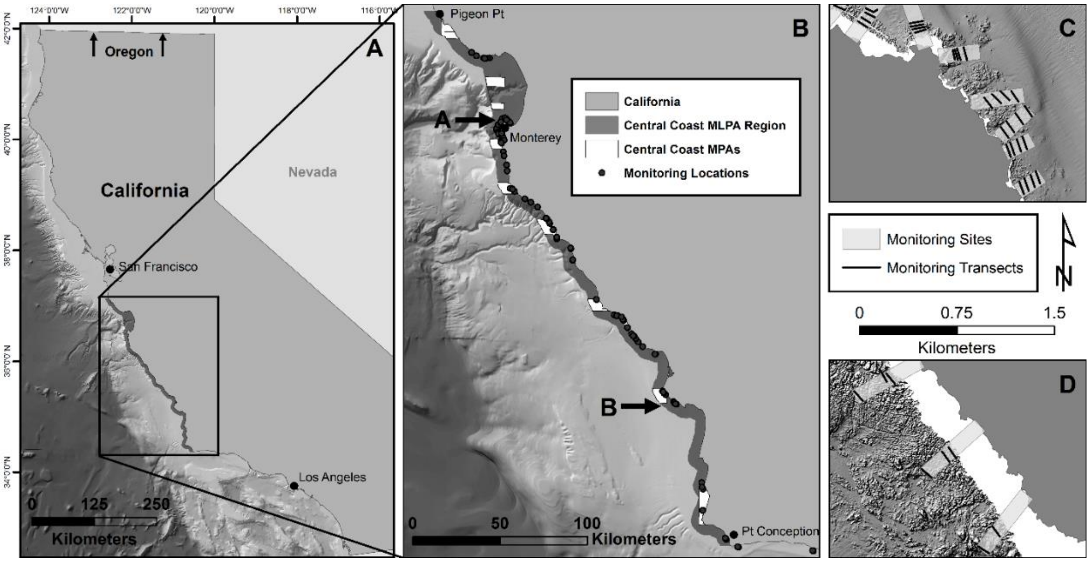

Figure 2-1: Study location: (A) Location of the study area along the central coast of California; (B) Central Coast MLPA Region indicated in dark gray with the MPAs across the region shown in white, and the points signifying the locations of ecological monitoring sites; (C and D) Zoomed in views of the ecological monitoring sites (light gray boxes) with the 100m survey transects (black lines) overlaid on the 2m resolution seafloor data.

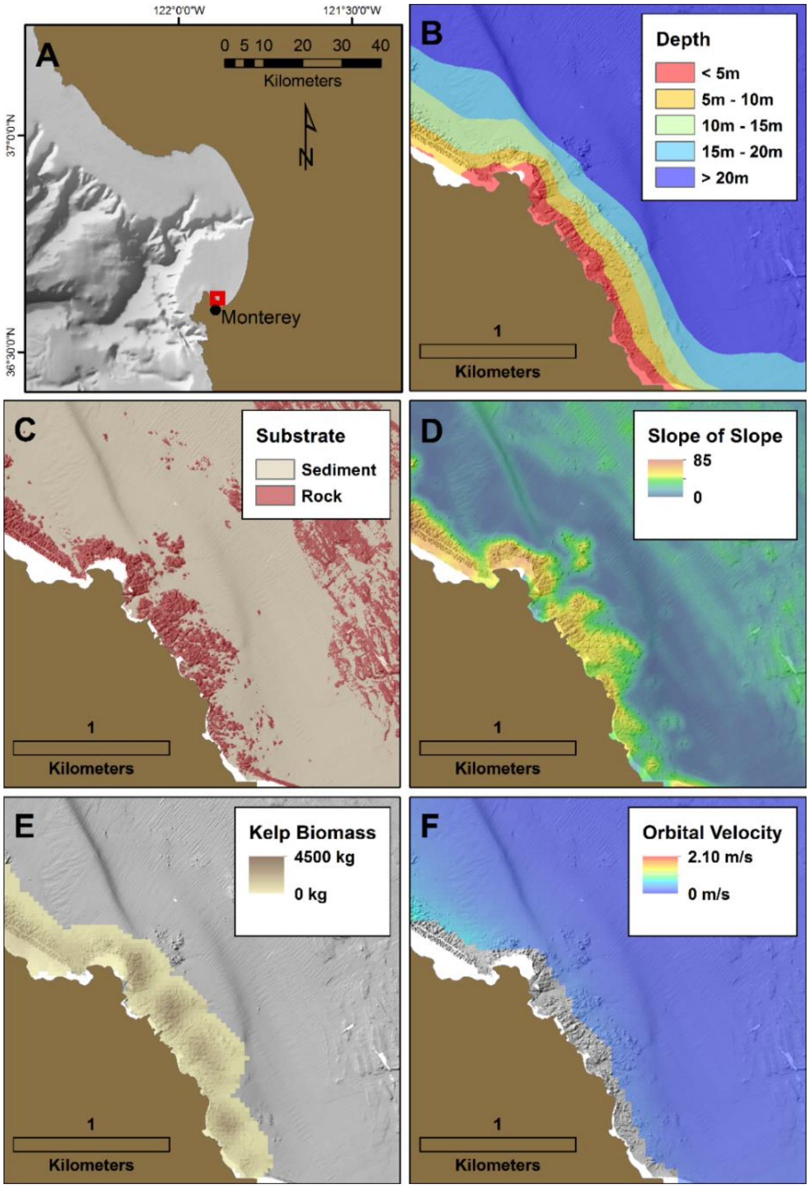

Figure 2-2: Close-up view of a small portion of the study area on the Monterey peninsula along the central coast of California (A), along with examples of the habitat variables (B-F) used in the species distribution models. Depth values (B) derived from the 2m bathymetric DEM with warmer colors representing shallower depths and cooler colors representing deeper depths. Substrate map (C) classified from the VRM analysis with red areas representing "rock" and tan areas representing "sediment". The complexity (slope of slope) of the habitat (D) derived from the 2m bathymetric DEM with warmer colors representing more complex structure. Map of kelp biomass values (E) derived from LANDSAT data with the darker browns representing greater biomass. Map of wave orbital velocity values (F) with the warmer colors representing higher velocities.

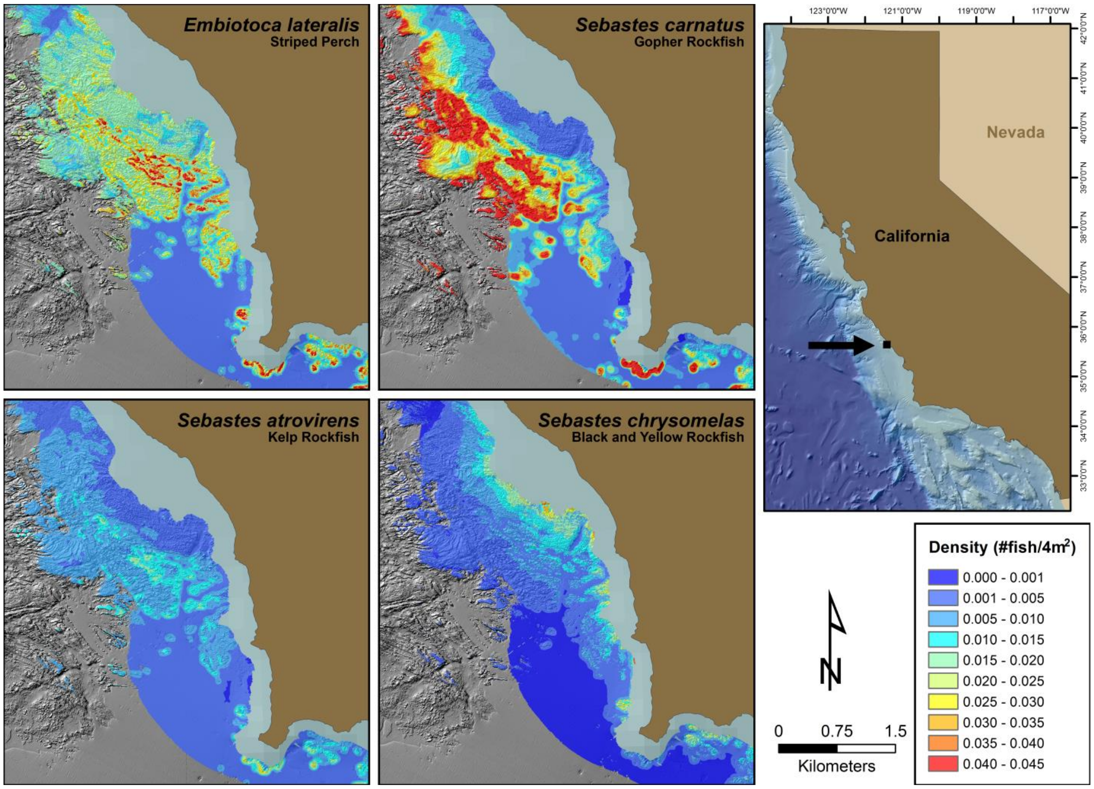

Figure 2-3: Examples of the species density distribution maps created for four of the seven species successfully modeled in this study. The warmer colors represent higher densities. The variation in density distribution for these four species can clearly be seen in this one small area within the Central Coast MLPA region.

2.9 Tables

Table 2-1: Summary of the geomorphic classes defined in the Central Coast MLPA region from the cluster analysis with the habitat class, the characterists that define that habitat class, and the percentage of habitat that class makes up in the region.

Geomorphic Class	Characteristics Defining Geomorphic Classes	Percentage of Class in the CA CC
A	Low complexity rock with broad scale peaks	8%
B	Low to moderate complexity rock on slightly sloping terrain	5%
C	Moderate complexity rock with broad scale peaks	26%
D	Moderate to high complexity rock with broad scale peaks	11%
E	High complexity rock with moderate to high broad scale peaks	9%
F	Moderate to high complexity rock on sloping terrain with broad scale peaks	42%

Table 2-2: Results from the GAM analysis for the seven species of kelp forest associated fishes and the fish community variables for which significant relationships with environmental variables were detected. Significance of each environmental variable and the deviance explained by the GAM model are presented for each species. Those variables that required a smoothing function are followed by an “(s)” in the environmental variables column.

Species	**Common Name**	**Environmental Variables**	**Variable Significance (p-value)**	**Deviance Explained**
Embiotoca jacksoni	Black Perch	Topographic Complexity (s)	3.73e-08	0.42
		Orbital Velocity (s)	6.66e-05	
		Mean Depth	0.0229	
Embiotoca lateralis	Striped Perch	Topographic Complexity (s)	8.18e-13	0.62
		Orbital Velocity	1.14e-06	
		Latitude	0.038	
Sebastes serranoides	Olive Rockfish	Orbital Velocity (s)	1.28e-09	0.55
		Latitude (s)	1.38e-09	
		Topographic Complexity (s)	4.34e-06	
Sebastes atrovirens	Kelp Rockfish	Orbital Velocity	3.58e-07	0.51
		Kelp Biomass	1.64e-05	
		Topographic Complexity (s)	0.0001	
Sebastes carnatus	Gopher Rockfish	Depth (s)	<2e-16	0.69
		Latitude	2.27e-15	
		Topographic Complexity (s)	0.009	
Sebastes chrysomelas	Black and Yellow Rockfish	Depth (s)	4.21e-07	0.51
		Topographic Complexity (s)	5.8e-07	
		Kelp Biomass (s)	0.001	
		Orbital Velocity (s)	0.011	
Sebastes melanops	Black Rockfish	Kelp Biomass (s)	5.47e-09	0.48
		Orbital Velocity (s)	7.51e-09	
		Topographic Complexity (s)	0.001	

Table 2-3: Results from the GAM analysis for the community variables of the fish assemblages. Significance of each environmental variable and the deviance explained by the GAM model are presented for each species. Those variables that required a smoothing function are followed by an "(s)" in the environmental variables column.

Community Attribute	Environmental Variables	Variable Significance (p-value)	Deviance Explained
Species Diversity (Shannon-Weiner)	Mean Topographic Complexity (s)	5.64e-12	0.83
Species Richness (no. of species)	Mean Topographic Complexity (s)	<2e-16	0.83
	Mean Orbital Velocity (s)	5.27e-07	

Table 2-4: Comparison of methods for extrapolating species density within the Point Sur MPA for seven species of fish: uniform extrapolation treating all rock as equal, non-spatial habitat-based extrapolation, and the abundances predicted from the spatially-explicit species distribution models.

Species	**Common Name**	**Uniform Extrapolated Abundance**	**Geomorphic-Based Extrapolated Abundance**	**SDM-Based Extrapolated Abundance**
Embiotoca jacksoni	Black Perch	9,149	2,897	4,890
Embiotoca lateralis	Striped Perch	59,065	23,014	22,655
Sebastes serranoides	Olive Rockfish	157,071	46,466	19,895
Sebastes atrovirens	Kelp Rockfish	38,133	13,313	9,198
Sebastes carnatus	Gopher Rockfish	69,650	19,072	14,621
Sebastes chrysomelas	Black & Yellow Rockfish	20,977	11,315	10,817
Sebastes melanops	Black Rockfish	161,165	12,844	8,666

3. Chapter 3: Assessment of habitat representation across a network of marine protected areas with implications for the spatial design of monitoring

3.1 Abstract

Networks of marine protected areas (MPAs) are being adopted globally to protect ecosystems and supplement fisheries management. The state of California recently implemented a coast-wide network of MPAs, a state-wide seafloor mapping program, and ecological characterizations of species and ecosystems targeted for protection by the network. Because the MPAs in the central coast region of California were set up prior to completion of the seafloor mapping project, one purpose of this study was to use these maps to evaluate how well seafloor features, as proxies for habitats, are represented and replicated across the network and how well the ecological surveys representatively sampled fish habitats within MPAs. Seafloor data were classified into broad substrate categories (rock and sediment) and finer scale geomorphic classifications standard to marine classification schemes using surface analyses (slope, ruggedness, etc.) done on the digital elevation model derived from multibeam bathymetry data. These classifications were then used to evaluate the representation and replication of seafloor structure within the MPAs and across the ecological surveys. Both the broad substrate categories and the finer scale geomorphic features were proportionately represented for many of the classes with deviations of 1-6% and 0-7%, respectively. Within MPAs, however, representation of

seafloor features differed markedly from original estimates, with differences ranging up to 28%. All of the habitats except for 30-100m sediment habitat had sufficient replication per the linear distance and area guidelines outlined in the goals for the MPAs. Seafloor structure in the biological monitoring design was adequately represented, but there are mismatches between sampling in the MPAs and their corresponding reference sites and some seafloor structure classes were missed entirely. The geomorphic variables derived from multibeam bathymetry data for these analyses (i.e. substrate type, depth, habitat complexity, etc.) are known determinants of the distribution and abundance of marine species and for coastal marine biodiversity. Thus, analyses like those performed in this study can be a valuable initial method of evaluating and predicting the conservation value of MPAs across a regional network .

3.2 Introduction

Human impacts on the oceans continue to increase (Halpern et al. 2008, Halpern et al. 2009, Lester et al. 2010, Brown 2011) and several governments throughout the world have acknowledged the need for more ecosystem-based conservation measures in the marine environment (Douvere 2008, Gilliland & Laffoley 2008, Costello et al. 2010, Halpern et al. 2012). Among these approaches, the use of marine protected areas (MPAs) is becoming widely adopted to protect ecosystems, their biodiversity and to supplement traditional fisheries management

(Roberts & Hawkins 2000, Curley et al. 2002, Allison et al. 2003, Carr et al. 2003, Lubchenco et al. 2003, Gaines et al. 2010, Halpern et al. 2010, Gleason et al. 2013). MPAs are areas within the ocean that are spatially protected from differing levels of human impacts, including resource exploitation and habitat alterations. MPAs can conserve habitats and unexploited species in addition to species targeted by fisheries (Agardy 1994, Allison et al. 1998, Sobel & Dahlgren 2004, Claudet 2011).

One major consideration when designing a network of MPAs for the purpose of conserving biodiversity and ecosystems is the representation of habitat and the ability to capture the diversity and heterogeneity of habitat features that support biodiversity (Roberts et al. 2003, Jordan et al. 2005, Stevens & Connolly 2005, Gaines et al. 2010, Halpern et al. 2010, Gleason et al. 2013, Saarman et al. 2013). MPAs will only be successful tools for biodiversity conservation if they protect the diversity of habitats that support the variety of ecosystems that generate and sustain the biodiversity targeted for protection. In addition, especially when designing networks of MPAs, replication of habitats among MPAs is required for reducing the likelihood of losing an ecosystem targeted for protection to a natural (e.g., hurricane) or anthropogenic (e.g., oil spill) perturbation, contributing to larval connectivity of species populations and communities across the network, and for the analysis and evaluation of MPA effects to inform their adaptive management (Allison et al 1998, 2003, Saarman et al. 2013; Grorud-Colvert et al. 2014; Botsford et al in press). Also, for MPAs to contribute to a network based on larval connectivity, individual MPAs have to contain enough habitat to support large enough populations to provide sufficient larval production, and MPAs have to be spaced at appropriate distances to one another. Therefore, representation and replication of sufficiently sized habitats across MPA networks has major implications for the ecological connectivity of populations and the resulting effectiveness of the network (Carr et al. 2010; Saarman et al. 2013; Grorud-Colvert et al 2014 Botsford et al *in press*).

Seabed mapping, both *in situ* and remotely sensed, has emerged as a much needed endeavor to determine the level of representation of the different habitat types inside and outside MPAs (Stevens & Connolly 2005, Cogan et al. 2009, Copeland et al. 2013). Habitat assessments using *in situ* observations such as SCUBA or remotely operated vehicles (ROVs) are widely utilized but are limited in their depth ranges and the ability to efficiently sample large areas (Jagielo et al. 2003). With the advent and improvements in remote sensing equipment and techniques, remote sensing in the marine environment has become a very efficient and cost effective means for comprehensive habitat mapping by covering large areas of the ocean floor at high resolution (Hughes Clarke et al. 1996, Nasby-Lucas et al. 1996, Cogan et al. 2009). Once mapped, the seafloor can be combined with biological observation data and characterized into distinct habitat classes to be used for the placement of new and assessment of already existing MPAs at the scale of entire networks.

Products produced from remotely-sensed data have become fundamental to many applications of coastal marine science (Copeland et al. 2013). Maps generated from seafloor mapping have been used to help identify habitat of importance to many commercially important species (Kostyleve eta l. 2001, Young et al. 2010, Copeland et al. 2013) and to identify habitats associated with biodiversity "hotspots" (Copeland et al. 2013). Cogan et al. (2009) states that marine habitat mapping should be the "launch point" for ecosystem-based management (EBM) by allowing for the characterization of habitat features across the ecosystem of interest.

The state waters of California offer a unique opportunity to develop methods to assess the representation of habitat inside and outside of MPAs across a regional network and the replication of those habitats. Not only has California adopted the Marine Life Protection Act (MLPA), which produced a 1200 km state-wide network of MPAs (Gleason et al. 2010), but they also implemented the California State Mapping Program (CSMP); a statewide mapping program resulting in a high-resolution geologic and habitat basemap for much of the 14,500 square kilometers of California state waters (Kvitek & Iampietro 2010). For this study, I used the multibeam echosounder (MBES) and inter-ferometric sonar data because they provided the best available seafloor data for the region of interest.

There is also a need to evaluate the design of monitoring programs that are being used to assess the efficacy of networks of MPAs. Many fish populations have been shown to vary in abundance based on the three-dimensional structure of their environment (Garcia-Charton & Perez-Ruzafa 1998, Claudet et al. 2006, Hamilton et al. 2010; Pittman et al. 2011). It is important; therefore, for MPA monitoring programs to characterize and account for variability in that structure (Westera et al.

2003, Claudet et al. 2006, Carr et al. 2011) when comparing the biological data collected inside and outside MPAs so that variation in populations can be linked to the effect of the MPAs rather than confounded by differences in habitat characteristics (Claudet et al. 2006). The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) has characterized fish populations and kelp forest ecosystems within the nearshore (0-20m depth range) of the Central Coast MLPA region. The basic monitoring design for this region includes kelp forest sites within and outside each MPA. These monitoring sites, however, were set up with little knowledge of the underlying seafloor structure because the seafloor data did not exist at the time the monitoring sites were chosen.

The purpose of this study is to use multibeam bathymetry data acquired by the CSMP and the baseline monitoring data acquired by PISCO to evaluate the distributions of habitat in the Central Coast MPA network and the representation of those habitats in the kelp forest monitoring design. The seafloor structure data along the coast in this region were classified into potential habitat variables of known importance to many species (i.e. depth, rugosity, slope, etc.) and used to answer the following questions for the region:

1. How well does the current network of MPAs representatively (i.e. proportionately) capture the habitat types designated for protection by the MLPA design process?

2. How well are those same MLPA habitats replicated throughout the region (i.e. is there sufficient habitat within MPAs to contribute to population connectivity)?

3. How well are regional seafloor structure classes based on finer scale topographic metrics, which were not considered when the MPAs were designed, represented across the MPA network?

4. Does the kelp forest monitoring program adequately capture the variability in seafloor structure inside the MPAs?

5. How well does seafloor structure within reference sites outside MPAs match those sampled within the MPAs?

The null hypotheses are that relative amounts of habitat within the MPAs are representative of (proportional to) the region, the habitats are adequately replicated with sufficient habitat area based on the guidelines in the MLPA, and that the kelp forest monitoring program has adequately captured all available habitats in their monitoring design. Therefore, I test for deviation from these hypotheses.

3.3 Methods

The study site for this project is along the Central Coast of California in the Central Coast MLPA region (*http://www.dfg.ca.gov/marine/mpa/ccmpas_list.asp*). This region extends from Pigeon Point in the north (37°10'57" Lat 122°23'38" Long) to Point Conception in the south (34°26'55" Lat 120°28'14" Long) and consists of a network of 29 MPAs with differing levels of protection (Figure 3-1).

3.3.1 MLPA Habitat Classification

In the MLPA master plan, eight habitat classes were developed for the subtidal that described the substrate and depth zones that are associated with specific distributions of species and communities (Allen et al. 2006; MLPA Master Plan 2008, Saarman et al. 2013). These habitat classes were based on two substrate types (sediment vs. rock) in four depth zones. The following depth zones and substrates are often associated with changes in species composition and were used as the break points for the habitat classes: 0-30 meters, 30-100 meters, 100-200 meters, and greater than 200 meters. One of the products for the CSMP included the classification of the bathymetry data into these eight habitat classes and the resulting habitat products are posted online at http://seafloor.csumb.edu (i.e. Figure 3-2).

The MLPA habitat products were created using the digital elevation models (DEMs) from the multibeam bathymetry data. A DEM is a raster dataset with elevation values at regularly spaced intervals. The DEMs varied in resolution based on the range of bottom depths they captured (0-85m at 2m resolution, 85-250m at 5m resolution, and >250m at 10m resolution). To distinguish between rock and sediment, vector ruggedness measure (VRM) grids were created from the DEMs using the Terrain Tools toolbox in ArcGIS 9.x (Sappington et al. 2007). VRM is a measure of terrain ruggedness using vector analysis where the 3-dimensional orientation of the grid cells is taken into account, allowing for variation in slope and aspect (Hobson 1974). The values associated with VRM vary from 0 (flat, smooth areas) to 1 (areas of higher complexity). Because rock is often more complex than the surrounding sediment, VRM can be used to help distinguish between rock and sediment areas (i.e. "rough" and "smooth" areas, respectively). VRM was, therefore, used as a proxy for "rock" and "sediment."

From the VRM analysis, a binary raster was created with "0" signifying soft sediment and "1" signifying rocky substrate. The breakpoints for these two classes were based on a threshold of VRM that captured the majority of the "rock" without erroneously classifying artifacts or sediment features. When necessary, a substrate mask was used to mask out any problematic areas. To determine how well the class breaks matched up with a visual interpretation of the substrate type, 100 random points were placed throughout each block[1] and the substrate underlying those points was visually classified as either "sediment" or "rock." The visual classification was then compared to the results from the VRM classification to determine the accuracy of the habitat classification. Accuracies greater than 90% were considered sufficient. If the accuracy fell below 90%, the site was reclassified by adjusting the threshold value of the VRM.

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[1] The "blocks" are the original survey blocks from the CSMP mapping. Each region was broken up into a series of blocks for data acquisition purposes and does not have any significance for the habitat classification other than organizing the data in manageable pieces.

To make the final MLPA habitat classified raster, the DEM was reclassified into the specified depth zones and combined with the binary raster from the substrate classification. The resultant product from this combination is a raster with eight unique values: one for each of the designated MLPA habitat classes (i.e., Figure 3-2). These methods were completed on all of the existing bathymetry data for the Central Coast MLPA region

3.3.2Assessment of Regional Representation of MLPA-designated Habitats Within the Central Coast MPA Network

Once all the bathymetry data were classified into the MLPA habitat categories, I used these data layers to quantify the habitat across the entire region and within the MPAs. First, a regional ESRI shapefile was created for the Central Coast region based on the extents specified in the MLPA. Then, using the tabulate area tool within the spatial analyst toolbox in ArcGIS, I was able to quantify the total area of each habitat class within the region. To quantify the habitat within the MPAs, I used the MPA shapefile provided by the California Department of Fish and Wildlife and, using the same methods as for the region, I tabulated the area of each habitat class within the MPAs. The total area of each MLPA habitat class within the MPAs compared to the available MLPA habitat across the region. These values were compared to the predicted values derived from the best available data used at the time that the MPAs were designated (MLPA 2008a) to determine if the representation of habitat was different based on the habitat observed in the seafloor maps. For the purposes of this study, differences were determined based on a 20% threshold, which is a common threshold when comparing percentages (Mapstone 1996).

3.3.3 Assessment of Regional Replication of MLPA-designated Habitats Within the Central Coast MPA Network

Any differences found in the amount of habitat expected to be in an MPA compared to the amount that is actually in an MPA only matters if there is substantially less area than was required of that MPA to be considered a replicate for that type of habitat (i.e. contribute to larval production and connectivity of populations associated with that habitat). If individual MPAs are found to contain an inadequate amount of habitat, they may not contribute to the network (MLPA 2008a). Guidelines for the minimum abundance of a habitat within an MPA to qualify for replication of that habitat were generated by the MLPA Science Advisory Team for the North Central Coast Study Region (MLPA 2008b). These guidelines were calculated from species-area curves based on ecological surveys conducted in the Central Coast Study Region. The minimum area required to include 90% of the species in each habitat was the basis for the guideline. For shallow (0-30m depth) habitats (e.g., rocky reef, kelp forests and sand bottom), the guideline was a linear distance of habitat along the coast (1.8 km). Species-area curves were available for kelp forests, not shallow rocky reef, so the same guideline was applied to both habitats. Deeper (30-100m depth) habitats were area-based; deep rocky reef and sandy bottom were 0.52 km^2 and 26 km^2, respectively. To assess the adequacy of habitat within each MPA, I used the CSMP seafloor maps to measure the linear distance of shallow (0-30m depth) rocky reef and sand bottom habitat, and the area (km2) of deeper (30-100m depth) rocky reef and sandy bottom. The linear distance measurements for the kelp forest habitat were derived from the max coverage of kelp using LANDSAT data (Cavanaugh et al. 2010, 2011). Linear distance of shallow habitats was measured along the 15m depth isobath. In addition, the MLPA specifies that there needs to be a minimum of three, ideally five, replicate MPAs for each of the habitat classes (MLPA 2008a).

3.3.4 Assessment of Regional Representation of Finer-scale Rocky Habitat Classes within the Central Coast MPA Network

As specified in the MLPA, substrate (i.e. rock or sediment) was deemed an important habitat factor affecting the distribution of species. However, habitat structure, including habitat complexity and heterogeneity, is often shown to cause variation in fish population size and differences in assemblage structure (Luckhurst & Luckhurst 1978, Fowler 1990, McCormick 1994, Iampietro et al. 2005). Shown clearly in the CSMP data, there are obvious distinctions in rocky reef structure along the coast of California (Figure 3-3). Taking into consideration these finer scale differences in seafloor structure, therefore, would further help to analyze the representation of habitat within MPAs.

To look at the finer scale variations in rocky reef structure, the rocky reefs along the central coast region were broken up into slope, rugosity, and topographic position index (TPI) classes. These reef characteristics have been shown to explain some of the variation in species-habitat associations across rocky reefs (Iampietro et al. 2005, Young et al. 2010). Once the rocky reef was classified into the distinct geomorphic classes, the area of each of those classes was tabulated for both the regions and the MPAs within the region to determine the representation of those seafloor structure classes across the MPA networks.

Slope was calculated using the Spatial Analyst extension in ArcGIS 9.x (ESRI 2013). Slope is calculated by determining the max slope value between an individual DEM and its eight neighbors. These slope values were then classified into the slope categories from the deep water marine benthic classification scheme: "Flat", "Sloping", "Steeply Sloping", and "Vertical" (Greene et al. 1999).

Rugosity was calculated using the rugosity calculator within the Benthic Terrain Modeler toolbox [48] in ArcGIS 10.x (ESRI 2013). However, rather than using one threshold value to distinguish between rock and sediment, multiple thresholds were chosen to distinguish between differing degrees of "ruggedness" (i.e. very low, low, moderate, high, very high) (Greene et al. 1999).

Topographic position index (TPI) is a measure of relative elevation, which indicates the position of a given point in the overall surrounding landscape. TPI can be used to identify and delineate landforms such as peaks, ridges, cliffs, slopes, flat plains, and valleys, and is calculated by comparing the elevation of each cell in the DEM to that of its neighborhood. Because the neighborhood size can be adjusted, TPI can be calculated at various scales. For this analysis, I calculated TPI at two neighborhood sizes using the bathymetric position index (BPI) tool within the Benthic Terrain Modeler toolbar (BTM). I calculated TPI at 20m (fine scale) and 50m (broad scale) to look at features on these two scales, which have been shown to be good predictors of fish distribution (Young et al. 2010). These TPI grids were then standardized and classified into 6 "slope position" landscape feature values based on the relative elevation and slope of the cells following the classifications of Iampietro et al. (2005): "Valley/Crevice", "Lower Slope", "Flat/Plain", "Middle Slope", "Upper Slope", and "Peak/Ridge".

The proportionality of each of these fine-scale structure classes within the region was then compared to the proportions within the MPAs to see how well these classes represented their availability throughout the region. Again, a 20% difference threshold was used to determine if there were significant differences between the percentage of each of the habitat classes found throughout the region compared to the percentages observed in the MPAs (Mapstone 1996).

3.3.5 Assessment of Habitat Representation in the Kelp Forest Monitoring Transects

Because species assemblages vary across habitat types, it is important to design MPA monitoring programs to incorporate representative habitat inside and outside of MPAs so that any differences are not confounded by the sampling of different habitat types. To determine the habitat representation in the monitoring design, GPS waypoints along with the initial diver recorded compass heading for the kelp forest survey transects were used to replicate the location where the transects were conducted in ArcGIS. To do this, a 100m polyline was created from the waypoint utilizing the initial heading of the diver and adjusted to the bathymetric contours, as specified in the PISCO sampling protocols <http://www.piscoweb.org/research/science-by-discipline/ecosystem-monitoring/kelp-forest-monitoring/subtidal-sampling-protoco>. A 10m buffer was then placed around each transect to incorporate the spatial uncertainty in the exact location of that transect, with the assumption that the transect was conducted within that 10m buffer. In addition to the PISCO transects, I sampled 3,250 transects that I placed randomly throughout the region in rocky habitat at comparable depths of the kelp forest surveys to assess the general availability of rocky habitat types across the region. Transects were the same dimensions used by the kelp forest surveys, including a 10m buffer around each transect.

Once the buffered survey and random transects were created, the habitat within each of those was quantified using the same habitat categories that were used for the rocky reef classification and the diversity calculations. After quantifying the habitat within each of those transects, a cluster analysis was run within the statistical software package Primer to determine the breakage points to designate separate geomorphic classes. Once clustered, the dendrogram was searched for the appropriate merging distance to break transects into a number of geomorphic classes suitable for the sample size of actual kelp monitoring transects. These geomorphic classes were defined by certain characteristics of the rocky reef and were used to determine the extent of habitat representation within the kelp forest survey transects and to compare the MPA transects to those within the MPA reference sites. Because of the low number of monitoring transects that were collected, the presence of any number or percentage of transects falling within a habitat category was considered to be representative of that habitat category. Only 13 of the 29 MPAs were used in this analysis because they overlapped with the kelp forest monitoring sites.

3.4 Results

3.4.1 Assessment of Regional Representation of MLPA-designated Habitats in the Central Coast MPA Network

Across the Central Coast region, observed abundance of the four MLPA designated habitat categories in the 0-100m depth range, based on substrate classification derived from the CSMP data, produced values similar to those predicted from the best available data during the MPLA design process (Table 3-1). None of these differences between habitat areas observed from the seafloor maps and those predicted during the design process exceeded the 20% threshold. However, where comparisons could be made at deeper depths (>100m),differences in habitat abundance observed by the CSMP data and that predicted during the design phase did exceed the 20% threshold of dissimilarity and there was mismatch in one habitat, 100-200m rock, that was predicted but not observed in the CSMP data (Table 3-1). Overall, the absolute differences in observed and predicted habitat areas ranged from 0-4%. Sediment is the most dominant substrate type in all depth zones making up a total of 91% of the mapped state waters of the Central Coast region, with the largest percentage falling in the 30-100m depth zone. Rocky habitat, compared to sediment, makes up a much smaller percentage of the mapped state waters (9%) with the largest percent cover falling in the shallowest depth range (0-30m). Across the central coast region, shallow (0-30m depth) sediment and rock were over and under predicted by the MLPA planning process by 3% and 1%, respectively (Table 3-1). This level of difference ($\leq$ 3%) was similar for both sediment and rock habitats across the deeper depth zones as well. Within the MPAs, there was no difference in the observed and predicted areas of shallow (0-30m depth) sand and rock, and only 1% difference in sand or rock in the 30-100m depth zone (Table 3-1). With the exception of sediment at depths greater than 200m, all other deeper (> 100m) habitat categories differed by no more than 2% cover (Table 3-1).

Although the best data available when setting up the MPAs provided good region-wide estimates of habitat percent cover in shallow depth zones, the CSMP data revealed that, at the scale of individual MPAs, there were some very large differences in the predicted percentage of habitat and the observed habitat from the CSMP data across all depth zones. The percentage deviation between the predicted (MLPA) and observed (CSMP) substrate coverage of rock and sediment ranged from 0.2% to 332.8% across the Central Coast MPAs with an average deviation of 39.1% (Table 3-2). The Piedras Blancas MPA is a good example of where the original predictions grossly underestimated the observed area of rocky reef within the MPA and over-estimated soft sediment. In this case, the seafloor maps revealed over three times as much rock as to what was originally predicted (Table 3-2; Figure 3-4). In fact, at the scale of individual MPAs, there were large differences for many of the MPAs in the amount of habitat thought to be there compared to the habitat observed in the seafloor maps. Only four of the 23 MPAs used in this analysis fell below the percent deviation threshold of 20% when comparing the predicted and observed coverage of rocky reef. The predictions for sediment were slightly better, but only 14 of the 23 MPAs had predicted and observed coverage within the 20% deviation threshold (Table 3-2).

3.4.2 Assessment of Regional Replication of MLPA-designated Habitats within the Central Coast MPA Network

The CSMP seafloor map-based classifications of the MLPA habitat were also used to determine the number of replicates of each habitat class contained within the Central Coast network of MPAs. Three of the four habitat classes are adequately replicated within the MPAs as specified in the MLPA guidelines (Table 3-3). Based on the linear distance guidelines for rock, sediment, and kelp in the 0-30m depth range, 13, 8, and 9 MPAs serve as replicates, respectively. In addition, the rock habitat within the 30-100m depth range has sufficient replication with a total of 10 replicates. The only habitat that does not reach the minimum number of three replicates is sediment habitat in the 30-100m depth range with only two MPAs containing enough area of sediment in that depth range to serve as a replicate.

3.4.3 Assessment of Regional Representation of Finer-scale Seafloor Structure Classes Within the Central Coast MPA Network

The relative abundance of geomorphic categories based on fine-scale seafloor structure metrics within the MPA network were close approximations of the regional availability of these features for the majority of the habitat categories (Figure 3-5). The deviation in coverage of each of the categories varied from 0.5% to 119% and the majority of the habitat classes were well represented across the MPAs. The rarer habitat classes, however, were not well represented across the MPAs and their deviations from the regional availability fell outside the 20% threshold chosen (Figure 3-5).

3.4.4 Assessment of Habitat Representation in the Kelp Forest Monitoring Transects

The cluster analysis of the habitat within the surveyed and my randomly generated transects produced 6 distinct habitat classes that were defined by distinctive combinations of geomorphological characteristics. These geomorphic classes were defined by the complexity of the rocky reef and made up a certain percentage of the region: low complexity (8%), low to moderate complexity (5%), moderate complexity (26%), moderate to high complexity (11%), high complexity (9%), and high complexity on slope (42%). These geomorphic classes were significantly clustered at close distances. To reduce the number of unique geomorphic classes to a number of categories more amenable to the sample size of kelp monitoring transects, a distance cutoff of 1000 was used. This cutoff value allowed for the incorporation of slightly outlying clusters to be merged into larger clusters without forcing dissimilar clusters to become combined.

Using these geomorphic classes, I analyzed the percentage of each class found throughout the Central Coast MPAs and compared those percentages to the percentage of baseline monitoring transects that fell in those classes to determine how well the surveyed transects sampled representatively within the MPAs. From this analysis, I found that, in most MPAs, the monitoring sites allowed for sampling of all the geomorphic categories (Figure 3-6). In some MPAs, the classes were sampled proportionately very well (Edward F. Ricketts SMCA, Lovers Point SMR, Point Buchon SMR). In other MPAs, however, the classes were sampled disproportionately. For example, in the Carmel Bay SMCA, the "moderate complexity" class was over sampled while the "high complexity on slope" class was under sampled by large percentages (46% and 43%, respectively). In some MPAs, geomorphic classes were not sampled at all. In the Point Lobos SMR, the second most dominant class was not sampled and the third most dominant class in the Big Creek SMR was not sampled.

Using the same geomorphic classes from the cluster analysis used to look at the representation of MPA habitat in the PISCO monitoring design, I also looked at the match-up between the classes in the MPA sites and their corresponding reference sites. Only five of the thirteen MPAs had complete match-up with the types of seafloor structure sampled inside the MPAs compared to the types sampled in the reference areas (Figure 3-7). The remaining eight MPAs had structure classes that were not sampled across both the MPAs and their corresponding reference sites. For example, three types of geomorphic structure were sampled within the Asilomar MPA but only one of those classes was captured in the reference site. In addition, the representation of seafloor structure transect in the reference areas was fairly disproportionate except in a few cases.

3.5 Discussion

This study provides an assessment of the habitat representation and replication across a network of MPAs along the central coast of California. During the designation of these MPAs, there were limited data on the availability (i.e. amount and distribution) of habitat across the region. Since the completion of the California State Mapping Program (CSMP), an unprecedented dataset is now available that allows for the detailed delineation of the habitat categories used in the design of the network, as well as fine-scale geomorphic features. This assessment of habitat representation is a first step in evaluating how well the currently designated network of MPAs representatively include the marine ecosystems in California state waters and the biodiversity they support .

The results from this study showed that, during the implementation of the Central Coast MLPA network, the best available data allowed for adequate representation of habitat within the MPAs on a broad scale for the shallower MLPA depth classes (0-30m and 30-100m). On the other hand, there were larger discrepancies between the predictions of habitat coverage in the depths below 100m for both rocky reef and sediment. Therefore, proxies of habitat type such as the availability of kelp and local fishermen knowledge provided a good basis for the distribution of those habitat categories (i.e. rocky versus soft bottom by large depth zones) important to the species and ecosystems targeted for protection by the MLPA in the shallow nearshore. In addition, when finer scale geomorphic classifications were defined and compared between MPAs and regional availability, there was also good representation within the central coast network of MPAs for the more abundant classes. The fine-scale structure classes that were rarer throughout the region; however, were not sufficiently represented based on the 20% threshold chosen. The former result might not be too surprising, given (i) the ability of traditional technologies (e.g., sonar) to determine bathymetry and distinguish hard and soft substrata, (ii) over large sections of the central coast (from Monterey Bay to Point Buchon) kelp is a reasonable proxy for the presence of shallow (<20 m) rocky bottom, and (iii) the extensive human use of the shallow subtidal of the central coast to generate spatially extensive characterizations of the seafloor across the region. However, it is surprising that the finer-scale categories of reef structure were well represented, given no knowledge of these features from these traditional sources. One key implication of this result is that the finer scale geomorphic classes are sufficiently ubiquitous and simply capturing hard bottom sufficed for capturing these higher resolution seafloor structure differences as well. In addition, the variation in the abundance of the fine-scale categories appears to occur at large geographic scales. Therefore, by distributing these large MPAs across the geographic variation in these finer scale features, the network captured that variation representatively.

Conversely, when the substrate cover predicted in the design process of the MLPA was compared to the substrate coverage derived from the seafloor data at the scale of individual MPAs, there are much larger discrepancies in the representation of habitat, such as the under-representation of rock in the predicted substrate maps of the Piedras Blancas MPA (Figure 3-4). These can be very important differences with respect to both the design and effectiveness of the MPA network. A key goal of the network is to ensure that young produced in one MPA contributes to the larval replenishment of populations in adjacent MPAs. This “larval connectivity” is a key element of MPA networks (Saarman et al. 2013). For populations to contribute to such a network, sufficient habitat to support those populations needs to be included in enough replicate MPAs that contribute to the network. The MLPA design process used cumulative species-area relationships to identify the minimum area of habitat to contribute to a network (where 90% of the species richness of a community is included in the minimum area; (MLPA 1999). The results from the replication analysis show that, although there were some large discrepancies in the area of habitat within individual MPAs compared to the predicted coverage of those habitats, there is adequate replication of three of the four habitats across the network to meet the design guidelines of the MLPA. The only habitat that is not adequately replicated is sediment habitat in the 30-100m depth range. This result is likely due to the unavailability of reliable proxies for predicting habitat coverage in the deeper depth ranges when designing the central coast network of MPAs.

The analyses in this study only look at finer scale features and variations across rocky reefs. Previous studies; however, have shown that there are ecologically important variations in sediment habitats where rippled scour depressions (RSDs) occur (Hallenbeck et al. 2012). RSDs are features that contain coarser grained sediment and are depressed relative to the surrounding sediment. Davis et al. (2013) showed that these sediment features are adequately represented across the central coast MLPA region.

Because of the inability of traditional, vessel-based seafloor mapping to collect data in the shallow (0-5m) surf zone in the nearshore environment along the coast, the use of seafloor data to estimate the distribution of habitats may be an under-representation of the rocky reef in the 0-30m depth class. Moving inshore, data collection is usually terminated at the point of unsafe navigation or the inability of the boat to move in further due to navigational hazards such as the presence of emergent rocks, thick kelp canopy, or unsafe wave environment. Most of these impediments to surveying are usually indicators of subsurface rock. Therefore, most of the benthic maps for the state waters end slightly offshore from the coastline in many areas where there is most likely rocky habitat. The development of new sampling methods and platforms that allow mapping of these shallow nearshore habitats, or analytical tools that allow for accurate extrapolation of adjacent habitat into these zones, is critical because of the abundance and diversity of species in these habitats and the ecosystem functions and services they produce (Carr and Reed *in press*). Unfortunately, a number of kelp forest monitoring transects were conducted in shallow depths that do not overlap with the seafloor habitat data due to the reasons discussed above and, therefore, were not used in the analyses (~ 40%).

Seafloor structure is often correlated with changes in fish abundance (García-Charton & Pérez-Ruzafa 1998); therefore, the spatial design of MPA monitoring programs must capture this variability of structure to accurately estimate the demographic responses (e.g., abundance, size structure, larval production) of populations to establishment of MPAs (Westera et al. 2003, Hamilton et al. 2010, Starr et al. 2010). Within the MPAs, the kelp forest monitoring program captures the available structure in most of the MPAs. When comparing the MPA sites to their corresponding reference sites, however, there are miss-matches between the seafloor structures sampled. These differences could confound comparisons of population trajectories over time inside and outside of the MPAs and conclusions regarding species responses to MPA establishment. In fact, taking into account the variation in reef structure greatly alters abundance estimates of fish species compared to methods that assume all rocky reef provides the same quality of habitat (Chapter 2). The kelp forest monitoring program in the central coast could adjust the locations of transects to ameliorate the effect of habitat differences on estimates of species responses to MPAs. Spatial designs of future monitoring studies should capitalize on the availability of seafloor maps to enhance the statistical power of monitoring studies to detect population responses. Using seafloor habitat data to evaluate MPA performance does have some limitations that need to be considered. Seafloor structure of the benthos is only one type of variable that can influence the distribution and abundance of species across the region. Other variables such as biogenic habitat structure, variations in species assemblages, patterns of upwelling, and differing levels of swell exposure could also play an important role and should be considered when analyzing the overall performance of MPA networks (MLPA, 2008; Carr et al 2010). As stated previously, the classification of seafloor habitat is an important first step in evaluating the placement of MPAs and can be combined with other measures of habitat quality to create predictive models of species abundance across the region using the biological observation data collected during monitoring surveys.

3.6 Conclusions

As marine conservation continues to move in the direction of ecosystem-based management and the designation of marine protected areas, there is a need for the development of methods that help to choose areas that are likely to meet the goals of the conservation criteria (Ward et al. 1999). Because of the lack of complete information on the distributions of species and the processes that maintain diversity, populations, species, and ecosystems (Conroy et al. 1996), surrogates that are linked to the maintenance of biodiversity are used in place of complete information (Ward et al. 1999). The variables derived from multibeam bathymetry data used in this study (i.e. substrate type, depth, habitat complexity, etc.) have been shown to be important to many marine species and overall biodiversity and, therefore, can be used as a helpful and initial method of evaluating the design of MPA networks. In addition, the generation of species-habitat relationships with the derivatives of the multibeam bathymetry data can be used to further our understanding of how the variation in seafloor structure affects the distribution and population sizes of species for which MPAs are created to protect.

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3.8 Figures

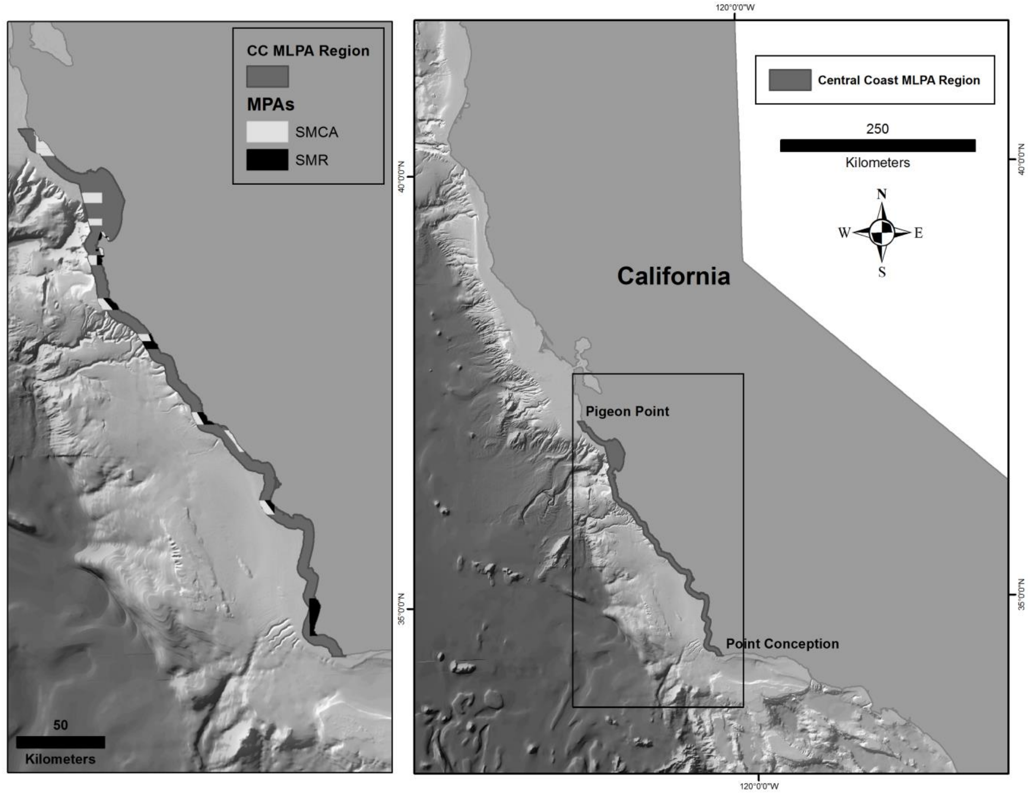

Figure 3-1: Central Coast MLPA Region. Image on the left is the Central Coast MLPA region along the Central Coast of California and the MPAs within the region. SMCA are State Marine Conservation Areas with limited allowable take, SMR are State Marine Reserves with no recreational or commercial take. The Central Coast MLPA Region extends three nautical miles (boundary of state waters) from shore. The image on the right shows where this region falls along the California coast.

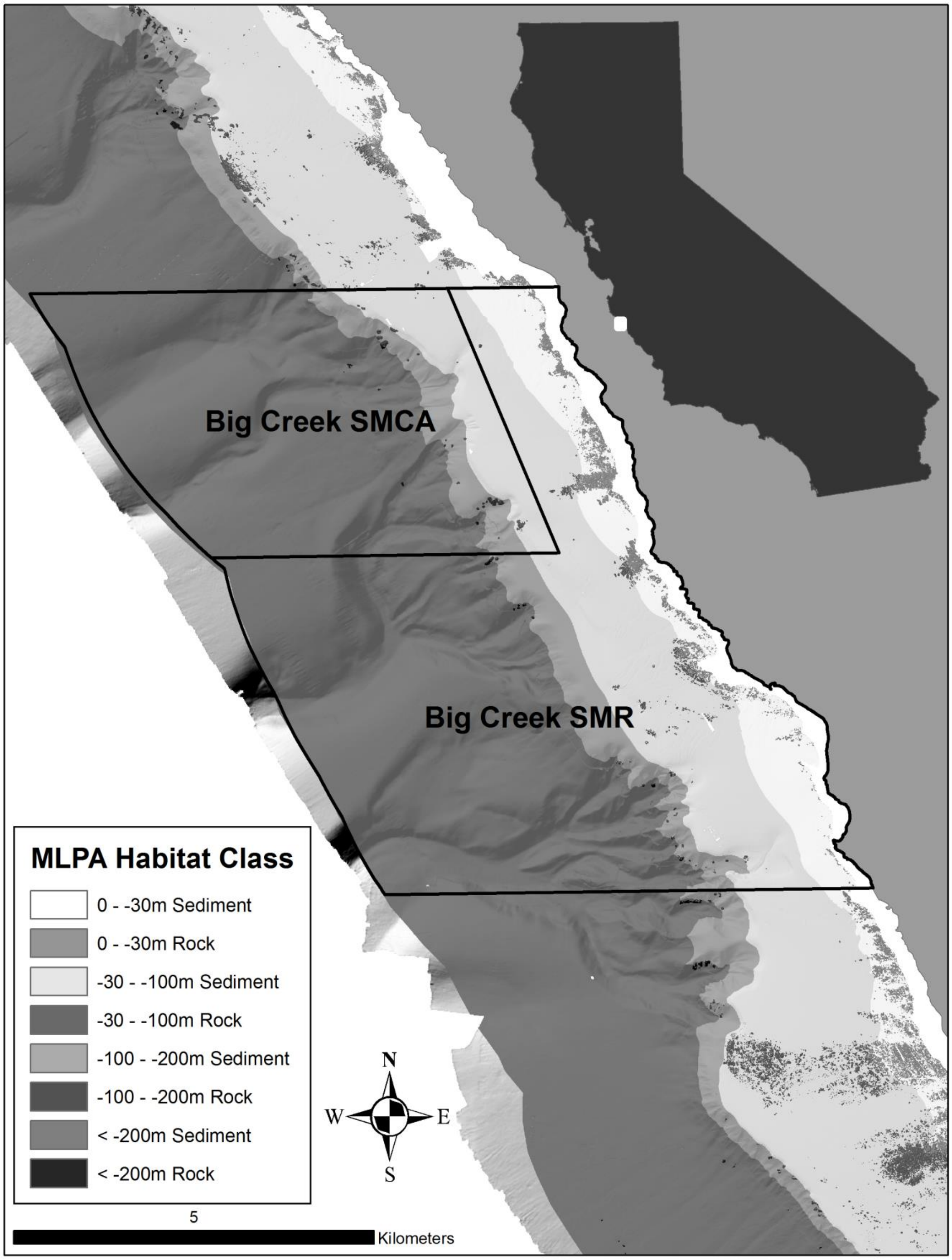

Figure 3-2: Example of results from the seafloor habitat classification within and around the Big Creek MPA. The different shades of gray represent the different substrate types and depth zones.

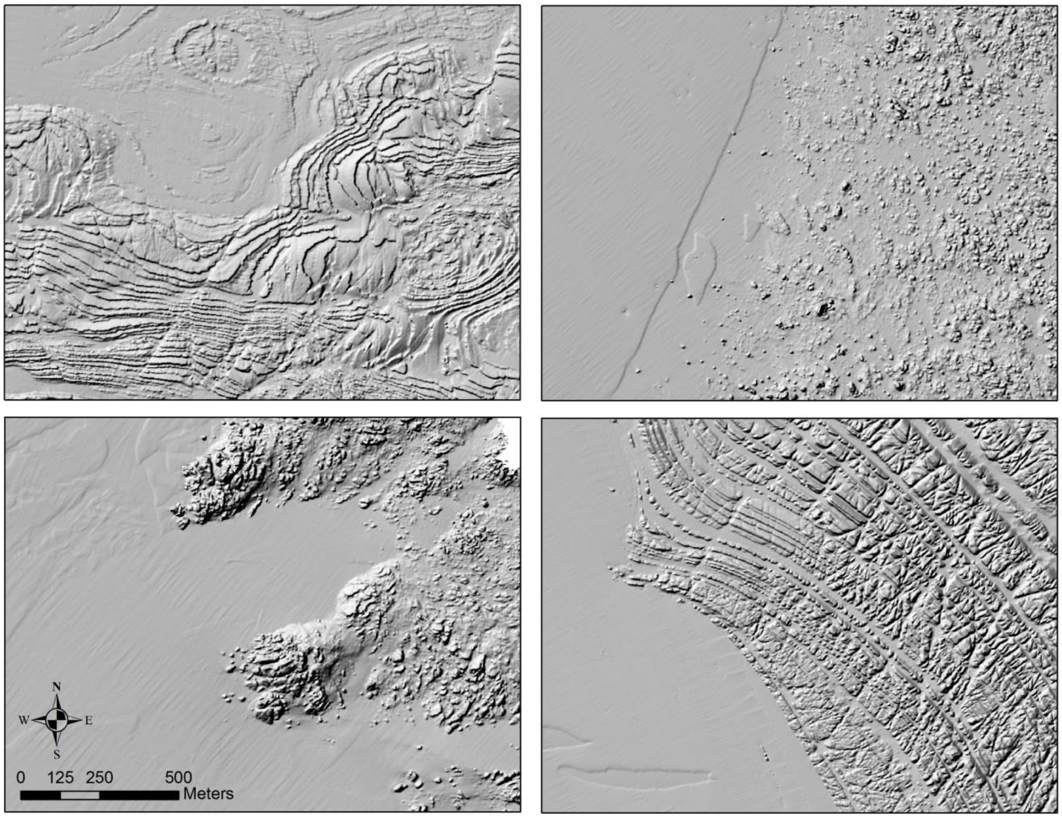

Figure 3-3: Shaded relief imagery of the seafloor produced from the digital elevation models (Sun Azimuth: 315, Sun Altitude: 45, Z-Factor: 3). These images show the ecologically relevant variation in the structure of rocky reef along the central coast of California.

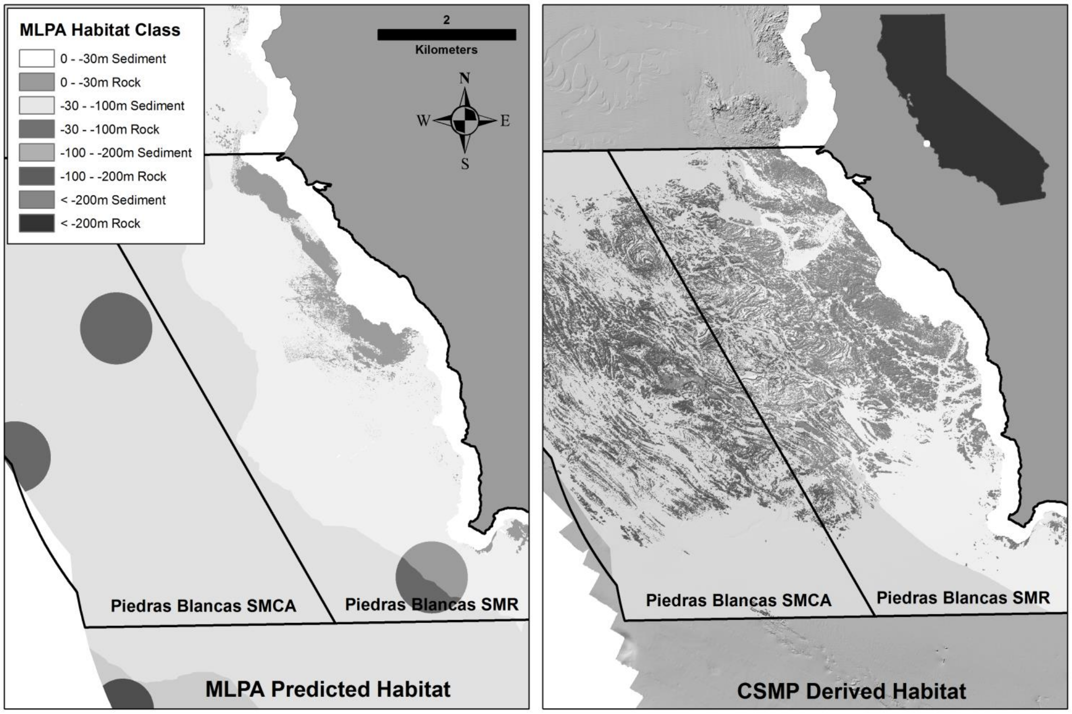

Figure 3-4: Comparison of the MLPA habitat classifications predicted using the best available data during the designation of the MPAs (left) and the habitat derived from the CSMP seafloor data (right) in the Piedras Blancas MPA.

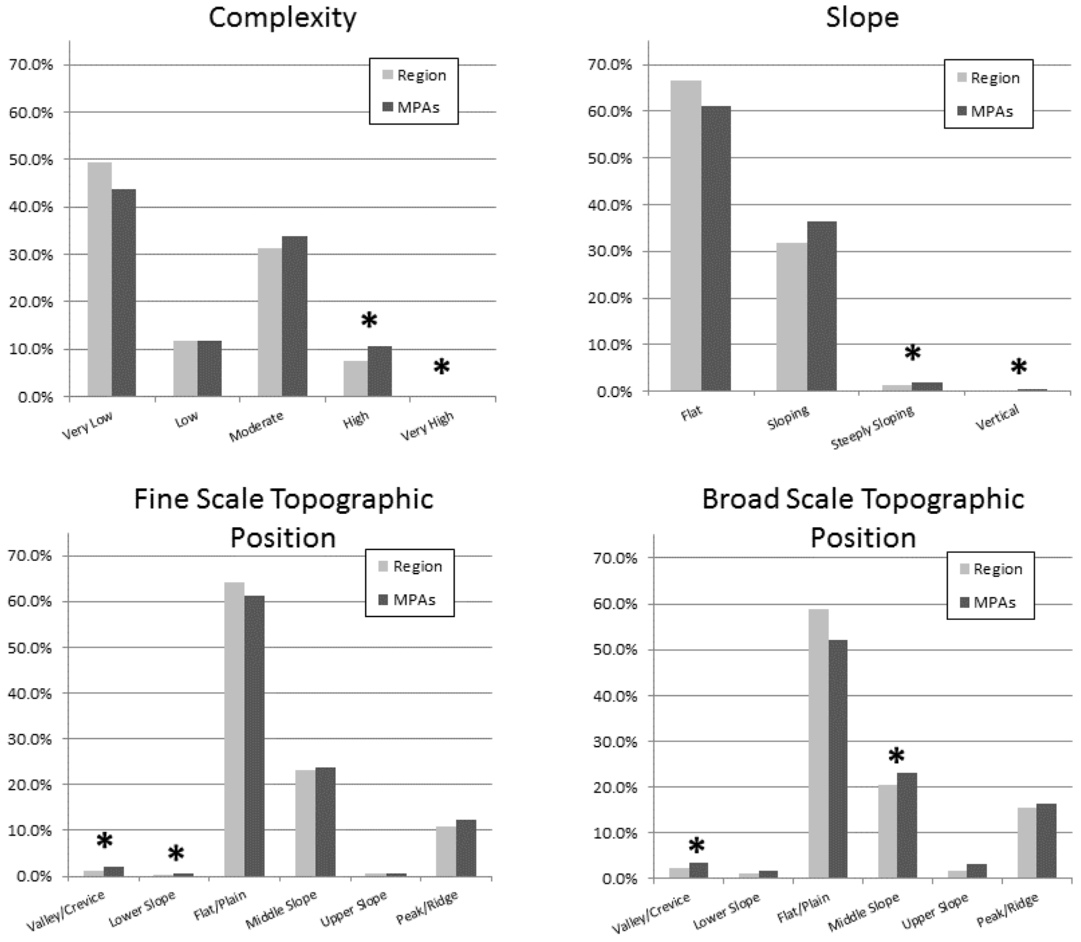

Figure 3-5: Comparison of the percentage of habitat classes derived from the CSMP data across the region (light gray) and within the MPAs (dark gray). The asterisks (*) above the bars represent those pairs that fell outside the 20% threshold of similarity.

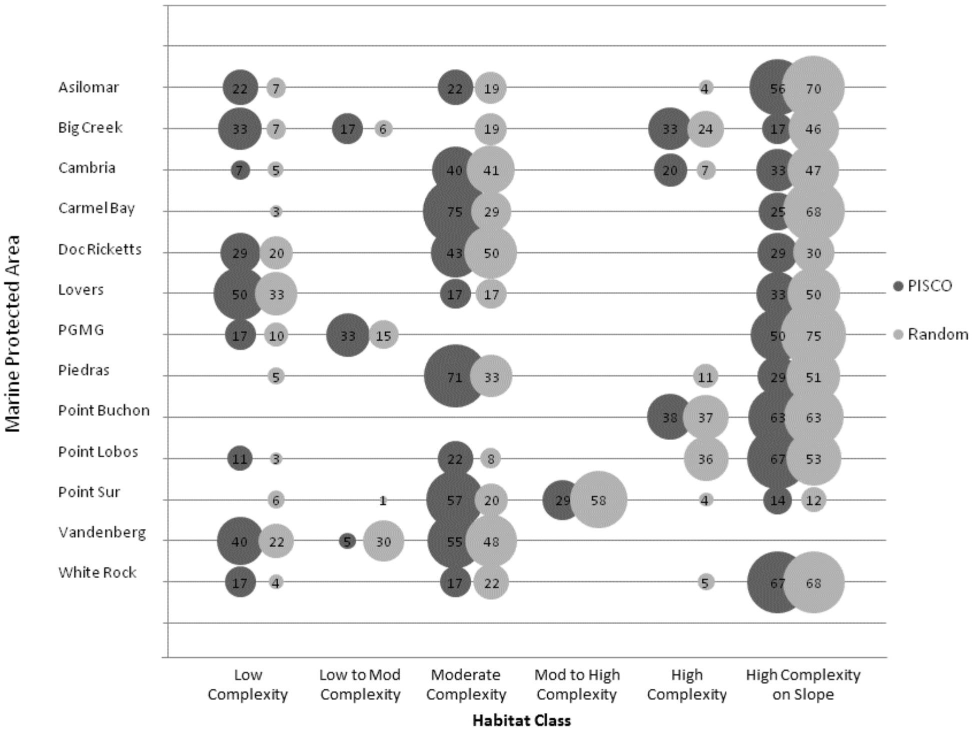

Figure 3-6: Comparison of the total percentage of each of the habitat classes derived from the cluster analysis within each of the 13 MPAs used in this analysis (light gray) and the percentage of PISCO transects that fell in those habitat classes (dark gray). The size of the circles represent the percentage of transects in each of the corresponding habitat classes and are labeled with the percentage value. The red asterisks represent those habitat classes that were not well-represented by the monitoring transects based on the 20% deviance threshold.

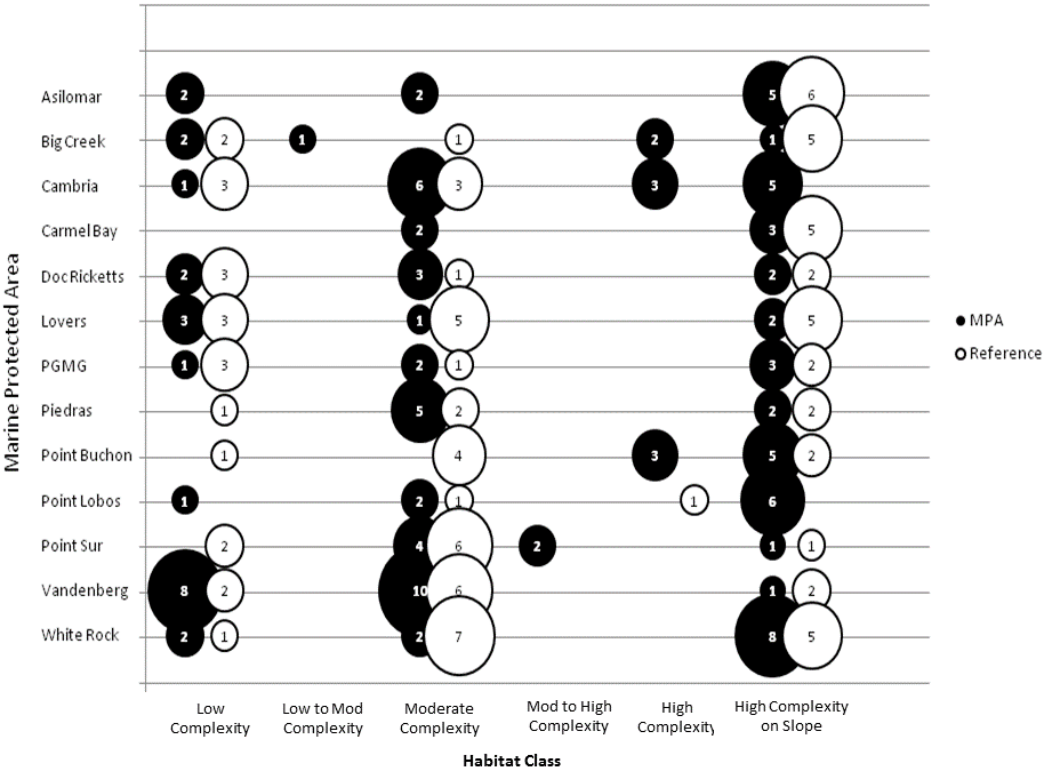

Figure 3-7: Comparison of the habitat represented in the MPA monitoring transects (black) and the habitat represented in the reference site transects (white) for each of the 13 MPAs looked at for this analysis. The size of the circles represent the number of transects in each of the corresponding habitat classes and are labeled with the number value. *Note: the transects represented in this figure are only those containing fish data. The invertebrate and algae transects were excluded from this analysis.

3.9 Tables

Table 3-1: Percentage of each habitat type across the central coast region and within the Central Coast MPAs predicted by the MLPA Science Advisory Team (SAT) in the design process and the values derived from the CSMP seafloor habitat classification, along with percent deviations between those values for the region and the MPAs. The bold text identifies those habitat categories whose differences exceeded the 20% deviation threshold and also those habitat categories predicted to exist in the design process but was not detected in the CSMP seafloor data.

Habitat	MLPA Predicted Habitat in CC Region	CSMP Derived Habitat in CC Region	Percent Deviation between predicted and derived habitat in the CC Region	MLPA Predicted Habitat inside CC MPAs	CSMP derived Habitat inside CC MPAs	Percent Deviation between predicted and derived habitat in the CC MPAs
0-30m Sediment	24%	21%	-12.5%	20%	20%	0%
0-30m Rock	6%	5%	-16.7%	8%	8%	0%
30-100m Sediment	49%	51%	4.1%	43%	42%	-2.3%
30-100m Rock	4%	4%	0%	6%	5%	-16.7%
100-200m Sediment	**5%**	**7%**	**40%**	**7%**	**9%**	**28.6%**
100-200m Rock	**1%**	**0%**	**n/a**	**3%**	**0%**	**n/a**
>200m Sediment	**9%**	**12%**	**33.3%**	**11%**	**15%**	**36.4%**
>200m Rock	**1%**	**0%**	**n/a**	**2%**	**0%**	**n/a**

Table 3-2: Percentage of each substrate type within the individual MPAs in the Central Coast region predicted by the MLPA Science Advisory Team (SAT) ("Predicted") compared to the values derived from the CSMP seafloor substrate classification ("Observed"). Those deviation values highlighted in bold represent those values that exceed the 20% threshold of dissimilarity.

MPA	Substrate					
	Rock			Sediment		
	Predicted (%)	Observed (%)	Deviation (%)	Predicted (%)	Observed (%)	Deviation (%)
Año Nuevo SMCA	28.4	39.5	**39.1**	71.6	60.5	-15.5
Greyhound Rock SMCA	10.4	10.6	1.9	89.6	89.4	-0.2
Soquel Canyon SMCA	22.4	1.4	**-93.8**	77.6	98.6	**27.1**
Portuguese Ledge SMCA	32.0	5.1	**-84.1**	68.0	94.9	**39.6**
Pacific Grove Marine Gardens SMCA	74.3	55.1	**-25.8**	25.7	44.9	**74.7**
Asilomar SMR	71.5	59.9	-16.2	28.5	40.1	**40.7**
Lover's Point SMR	35.9	26.9	**-25.1**	64.1	73.1	14.0
Edward F. Ricketts SMCA	31.5	17.9	**-43.2**	68.5	82.1	19.9
Carmel Pinnacles SMR	83.4	75.8	-9.1	16.6	24.2	**45.8**
Carmel Bay SMCA	43.0	33.2	**-22.8**	57.0	66.8	17.2
Point Lobos SMCA	33.7	5.6	**-83.4**	66.3	94.4	**42.4**
Point Lobos SMR	39.2	44.1	12.5	60.8	55.9	-8.1
Point Sur SMR	55.3	36.2	**-34.5**	44.7	63.8	**42.7**
Point Sur SMCA	18.6	11.0	**-40.9**	81.4	89.0	9.3
Big Creek SMCA	1.2	0.3	**-75.0**	98.8	99.7	0.9
Big Creek SMR	4.9	2.5	**-49.0**	95.1	97.5	2.5
Piedras Blancas SMR	12.5	33.6	**168.8**	87.5	66.4	**-24.1**
Piedras Blancas SMCA	6.4	27.7	**332.8**	93.6	72.3	**-22.8**
Cambria SMCA	22.8	29.5	**29.4**	77.2	70.5	-8.7
White Rock (Cambria) SMCA	38.5	48.4	**25.7**	61.5	51.6	-16.1
Point Buchon SMR	17.2	21.4	**24.4**	82.8	78.6	-5.1
Point Buchon SMCA	6.1	3.2	**-47.5**	93.9	96.8	3.1
Vandenberg SMR	8.1	5.6	**-30.9**	91.9	94.4	2.7

Table 3-3: Linear distances for the habitat types in the 0-30m depth range (rock, sediment and kelp) and areas of habitat types in the 30-100m depth range (rock and sediment) within each MPA along the Central Coast MLPA region. Those percentages that do not meet the criteria to be considered a replicate as specified in the MLPA (1.8 kilometers for 0-30m rock, sediment and kelp; 0.52 km^2 for 30-100m rock; 26 km^2 for 30-100m sediment) are in bold typeface. "n/a" indicates a depth range is not present in an MPA and, therefore, that habitat is not present in the MPA.

MPA	Linear Distance Rock in 0-30m depth range (km)	Linear Distance Sediment in 0-30m depth range (km)	Linear Distance Kelp in 0-30m depth range (km)	Rock Area in 30-100m depth range (km^2)	Sediment Area 30-100m depth range (km^2)
Lovers PointSMR	**0.1**	**1.2**	**0.0**	n/a	n/a
Piedras Blancas SMR	4.6	5.4	3.3	1.390	**5.823**
Piedras Blancas SMCA	n/a	n/a	n/a	6.080	**16.270**
Carmel Pinnacles SMR	n/a	n/a	n/a	0.763	**0.287**
E.F. Ricketts SMCA	**0.3**	**1.1**	**0.2**	n/a	n/a
Carmel Bay SMCA	2.5	2.2	4.1	**0.322**	**0.922**
Point Lobos SMR	4.1	**1.5**	4.5	3.583	**5.314**
Point Lobos SMCA	n/a	n/a	n/a	0.557	**0.211**
Ano Nuevo SMCA	5.9	3.7	0.0	2.030	**4.241**
P.G.M.G. SMCA	2.0	**0.9**	**1.7**	**0.251**	**4.241**
Asilomar SMR	2.3	**0.8**	1.8	**0.156**	**0.061**
Soquel Canyon SMCA	n/a	n/a	n/a	**0.350**	38.143
Portuguese Ledge SMCA	n/a	n/a	n/a	**0.337**	**4.177**
White Rock SMCA	3.5	2.0	5.3	**0.256**	**1.043**
Cambria SMCA	5.2	4.3	7.4	**0.002**	**0.378**
Point Sur SMR	7.0	4.7	8.1	2.471	**7.541**
Point Sur SMCA	n/a	n/a	n/a	2.832	**22.397**
Point Buchon SMR	4.4	**0.7**	3.5	1.229	**11.809**
Point Buchon SMCA	n/a	n/a	n/a	0.837	**20.991**
Greyhound Rock SMCA	4.3	**0.7**	**0.0**	**0.090**	**22.302**
Big Creek SMR	2.6	6.8	5.6	**0.151**	**8.212**
Big Creek SMCA	n/a	n/a	n/a	**0.020**	**2.612**
Vandenberg SMR	3.4	19.6	**0.0**	**0.219**	26.724

Discussion

Through this dissertation, I demonstrated the application of concepts developed within the field of landscape ecology to understanding what drives the distribution, abundance, structure and dynamics of populations and communities and how this knowledge can be applied to conservation and management. As conservation biologists continue to move away from the single species approach to management and shift the emphasis towards ecosystems and landscapes (Franklin 1993), the application of landscape ecology techniques towards preserving biodiversity is becoming more common (Barbault 1995). The field has progressed in this direction past simple descriptions to more spatial modeling and simulations using GIS and sound methodology (Hobbs, 1997), allowing for the ability to create maps and other figures to communicate results to other disciplines and planners (Antrop 2001).

The application of landscape ecology to the understanding of terrestrial systems has been aided by the ability to map out large areas of the habitat using optical remote sensing technologies (Brown et al. 2011). The application of these technologies to the mapping of the ocean floor is limited to only those depths that light can penetrate and; therefore, greatly decreases the area of seafloor habitat that can be mapped using these technologies (Brown et al. 2011). More recently, acoustic technology has allowed for increasing the depth range of seafloor mapping at resolutions that are comparable or better than those collected in the terrestrial realm (Hughes Clarke et al., 1996; Lurton, 2002; Mayer, 2006; Brown et al. 2011). Currently only 5-10% of the seafloor is mapped at comparable resolution to terrestrial maps (Wright and Heyman 2008; Brown et al. 2011) but that area continues to grow (Brown et al., 2011). If not for the seafloor habitat maps provided through the CSMP, I could not derive many of the landscape metrics outlined in this dissertation. Moving forward, we can take into account the effect of the landscape on the distributions of species and communities to better understand metapopulations, species distributions, and how management actions affect the marine environment.

To fully understand the interaction of species with their habitat, complete knowledge of the environment is necessary, which includes the seabed and the water column both spatially and temporally (Brown and Blondel 2009). Unfortunately, many oceanographic measures are collected at much coarser resolution (meters to tens of kilometers) (Kenny et al. 2003) than the acoustically or laser acquired seabed information (tens of centimeters to tens of meters) (Brown et al. 2011). Those habitat mapping studies that rely on oceanographic variables are usually conducted at much broader scales (Kostylev and Hannah 2007; Brown et al. 2011). Through this dissertation, I was able to apply some aspects of the water column to understanding the distributions of the species and populations but there is still a lot of progress to be made in the incorporation of oceanographic variables. Without acknowledging the third dimension in our application of landscape ecology, we are missing those attributes that are important to the supply of food, nutrients, gametes, and new recruits within the ecosystem (Brown et al. 2011).

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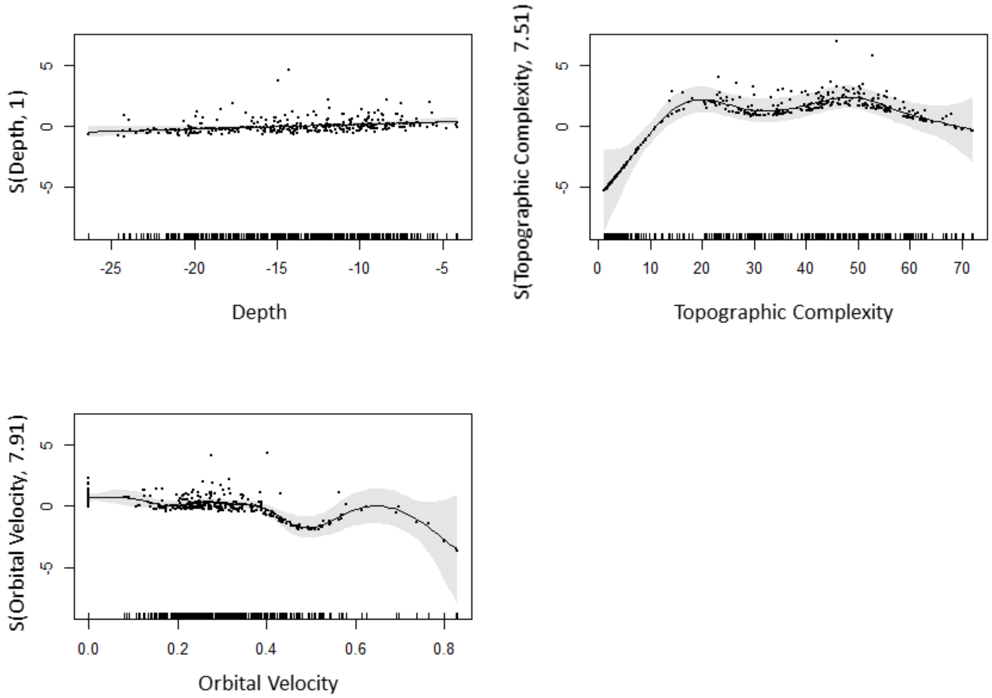
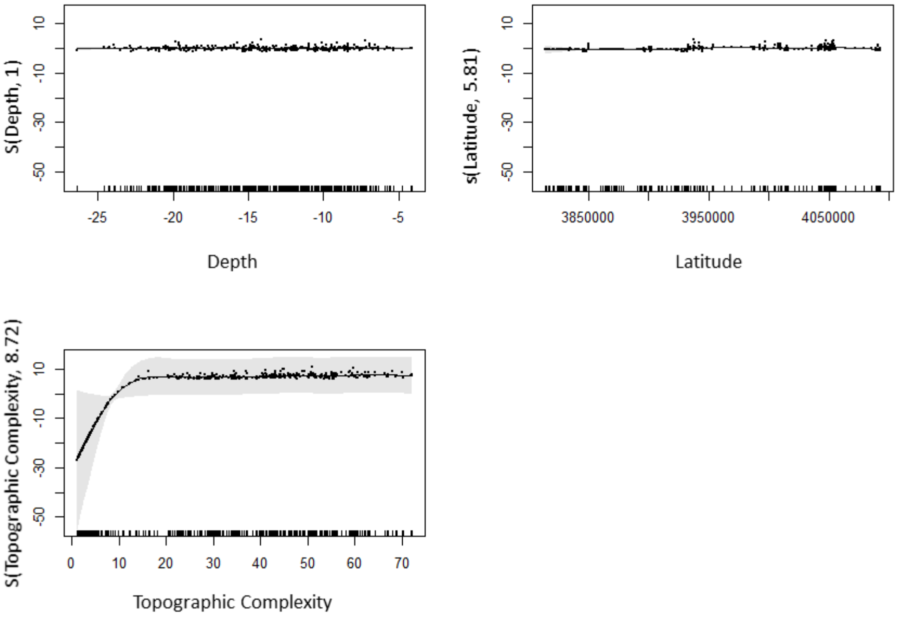
Appendix A: Relationships of densities with environmental variables for (a) E. lateralis, (b) E. jacksoni, (c) S. serranoides, (d) S. atrovirens, (e) S. carnatus, (f) S. chrysomelas, and (g) S. melanops.

The x-axes show the explanatory variables and the range of values of those explanatory variables and the y-axes are the smooth functions along with the degrees of freedom.

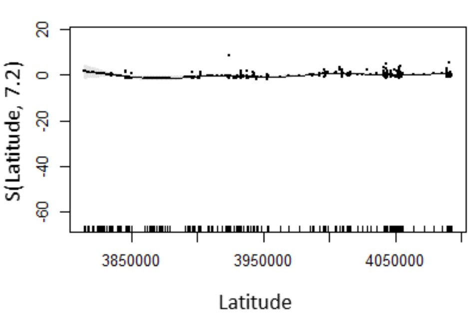
a) *Embiotoca lateralis*:

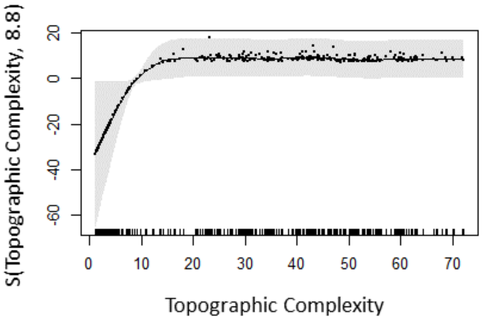


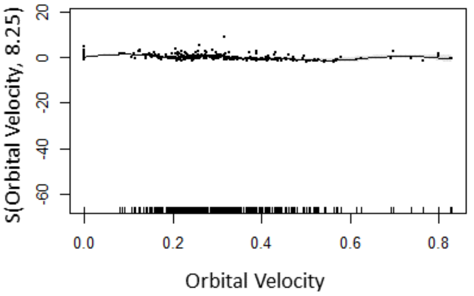
b) Embiotoca jacksoni



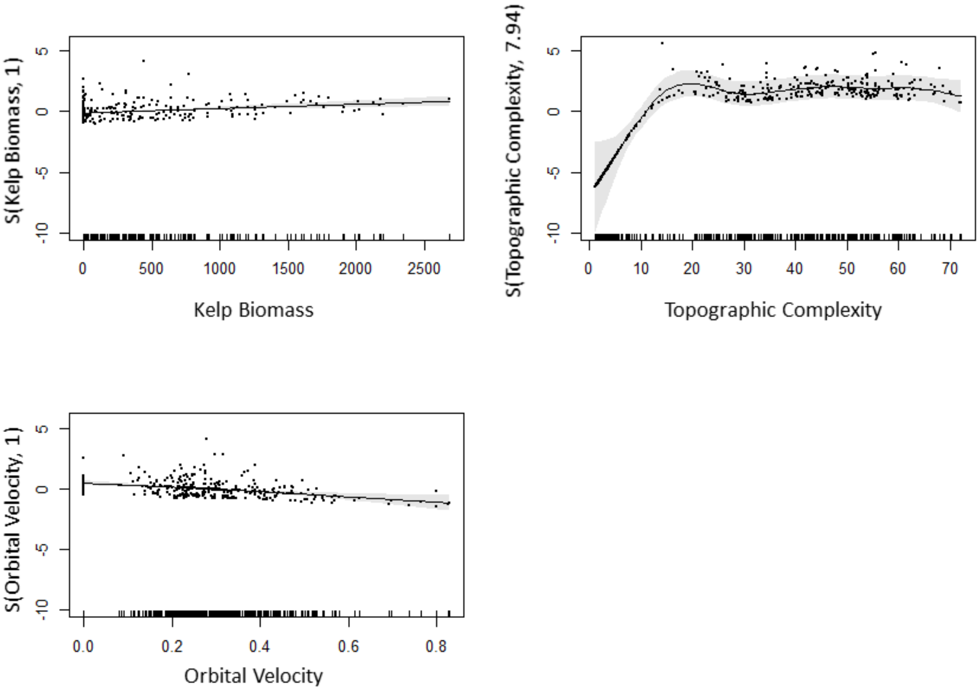
c) Sebastes serranoides



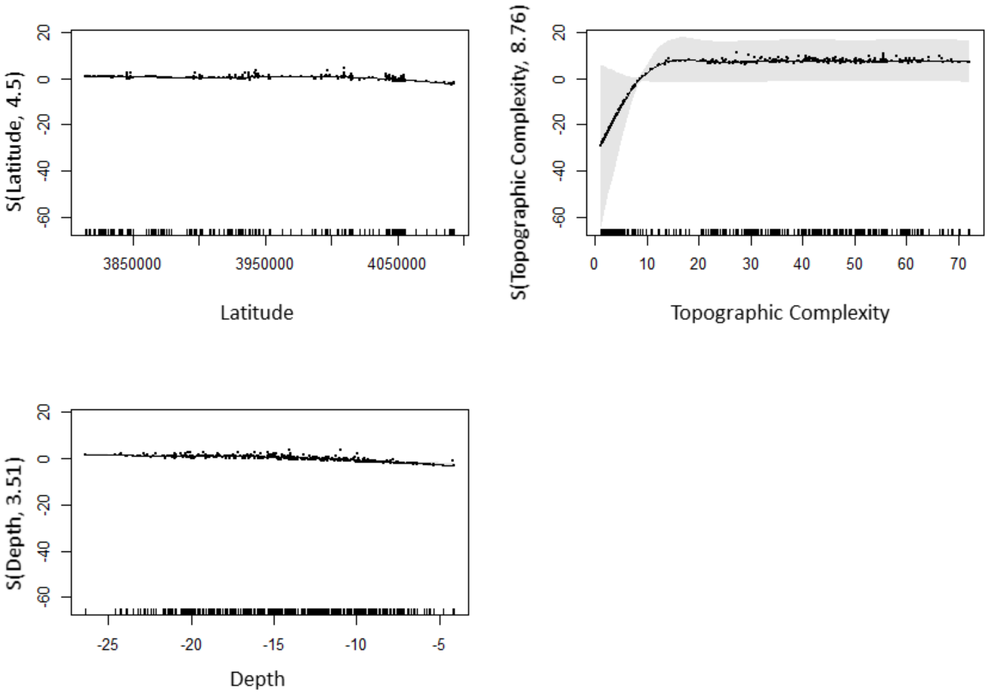




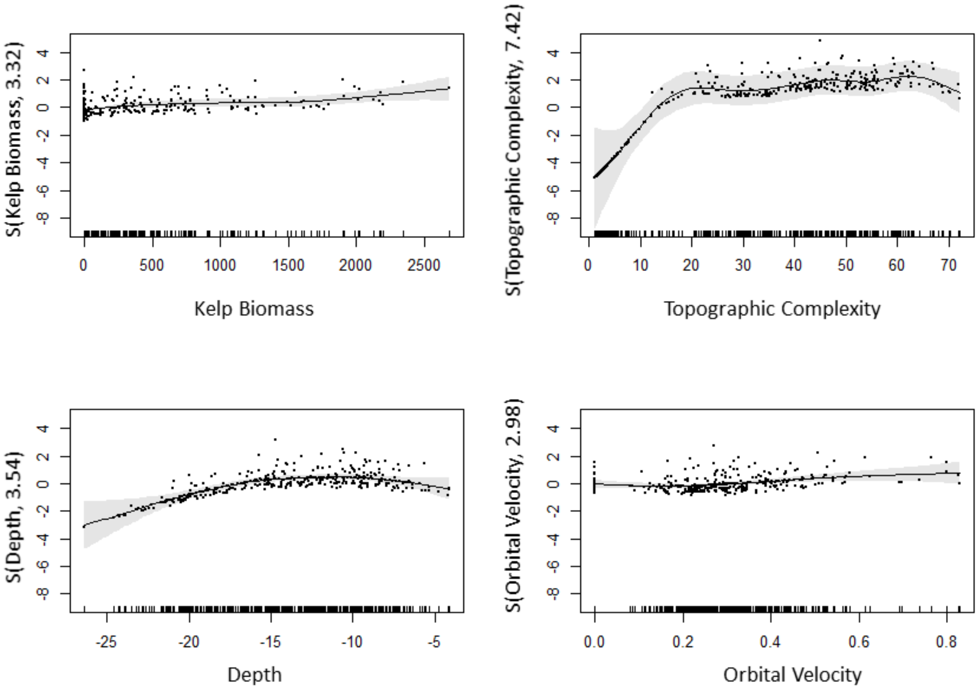
d) Sebastes atrovirens



e) Sebastes carnatus



f) Sebastes chrysomelas



g) Sebastes melanops