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LINKING HABITAT HETEROGENEITY TO GENETIC PARTITIONING IN THE ROCKY SUBTIDAL USING BLACK SURFPERCH (EMBIOTOCA JACKSONI).

A Thesis

Presented to the

Faculty of the

Division of Science and Environmental Policy

California State University Monterey Bay

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Coastal and Watershed Science and Policy

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by

Scott Robert William Toews

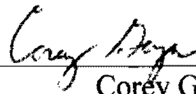
Fall 2012

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

The Undersigned Faculty Committee Approves the

Thesis of Scott Robert William Toews:

LINKING HABITAT HETEROGENEITY TO GENETIC PARTITIONING IN THE ROCKY SUBTIDAL USING BLACK SURFPERCH (EMBIOTOCA JACKSONI).



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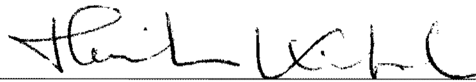

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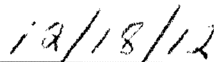

Approval Date

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by

Scott R.W. Toews

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DEDICATION

I would like to dedicate this work to my mother and father who, while not realizing it at the time, introduced me to my love of the water, all things in it, and inspired me to want to know what was going on below the surface. To my parents and my Aunt Verna who shared their values of education with me and without whose support I would not have had this opportunity.

ABSTRACT

Linking habitat heterogeneity to genetic partitioning in the rocky subtidal using black surfperch (Embiotoca jacksoni).
by
Scott Robert William Toews
Masters of Science in Coastal and Watershed Science and Policy
California State University Monterey Bay, 2012

Habitat composition and complexity can play an important role in structuring populations of marine organisms. However, the interactions between the physical and biological landscape and their combined effect on marine population dynamics are not well understood. In this study, I explored the role of habitat complexity (three-dimensional habitat structure) on habitat composition (abundance and distribution of habitat types) and their combined role in structuring genetic variation in populations of the black surfperch Embiotoca jacksoni, within Monterey Bay, California. Black surfperch have no pelagic larval stage, limited adult dispersal, and associate strongly with benthic habitat making them an excellent model system for this study. Structural complexity of subtidal habitat was calculated using digital elevation models of the sea floor. Habitat composition was estimated from photoquadrats of the subtidal benthos and collections of benthic algal samples, which were sampled for the surfperch's major prey sources in order to calculate prey biomass and distribution. Surfperch were collected for tissue samples and their stomach contents were analyzed for prey categorization (species and size distribution). We used 10 microsatellite markers to generate allele frequencies. GIS and spatial statistics were used to visualize and analyze the relationship between subtidal landscape variables and genetic diversity in black surfperch populations. This approach can provide rigorous quantitative estimates on the relationship between subtidal landscape complexity and genetic diversity in nearshore marine organisms.

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Nothing worth doing is worth doing without a mascot and to my credit I have had the fortune of having the best mascot possible. Loki has been a great partner who got me outside when I needed it and reminded me it was not all about me. I am thankful for the opportunities to ask these questions and follow my wonder knowing that wisdom begins in wonder.

1 INTRODUCTION

The physical and biological habitats of many marine species, especially low mobility and sessile species can be discontinuous with high spatial variation in the complexity and composition of their habitat. This landscape heterogeneity may in turn lead to populations of a species becoming subdivided in sub-assemblies with differing population dynamics and selective pressures (Endler 1991). These differing selective pressures can in turn lead to genetic pools that are heterogeneous across their distributional range (Burton 1983; Reeb and Avise 1990; Borsa et al. 1997; Neigel 1997). The resulting genetic heterogeneity may be due to several non-random factors including; selection through local adaptation (Hedgecock 1986; Knowlton and Keller 1986), genetic drift through barriers to connectivity (Gaggiotti et al. 2009; Galarza et al. 2009), or demography and life history (Hemmer-Hansen et al. 2007; Gaggiotti et al. 2009). Understanding genetic structuring of populations gives us insight into the processes involved in creating and maintaining genetic diversity. However, understanding the process and patterns of gene flow and local adaptation requires a greater understanding of landscape characteristics and how they might influence population structure. This understanding is critical for improving ecological knowledge of and improving management of genetic diversity of populations (Moritz 2002; Manel et al. 2003).

Genetic diversity is defined as any measure that quantifies the magnitude of genetic variability within a population and is a fundamental source of biodiversity. Biodiversity has become an important measure of ecosystem health used by conservation and resource managers (Thompson and Starzomski 2007). There is accumulating evidence from terrestrial, freshwater, and marine systems to suggest that sustainable ecosystem services depend upon biodiversity (Mcgrady-Steed et al. 1997; Tilman et al. 2006; Worm et al. 2006; Stachowicz et al. 2007; Hughes et al. 2008). Genetic diversity provides the raw material upon which evolution acts and is therefore crucial to a species' ability to adapt to its environment (Fisher 1930). Historically, research on genetic diversity has focused on its importance in evolutionary processes, though studies in evolutionary biology, agronomy and conservation biology indicate that genetic diversity can have important

ecological effects (Zhu et al. 2000; Leimu et al. 2006). Genetic diversity is closely linked to ecosystem function and evolution (Neuhauser et al. 2003; Hughes and Stachowicz 2004; Hughes et al. 2008) and is an important means of estimating adaptive evolution and population persistence (Holderegger et al. 2006). However, we have a poor understanding of the role that both the physical and the biological habitats play in generating and maintaining genetic diversity.

Understanding landscape effects on genetic structuring provides insights into fundamental ecological processes such as metapopulation dynamics, speciation, and ultimately the formation of species distributions (Keyghobadi et al. 1999; Roach et al. 2001; Manel et al. 2003; Storfer et al. 2006), each of which are important in the development of conservation, fisheries, and spatial management strategies. With an increasing emphasis on ecosystem-based management, better tools are required to quantify biodiversity and assess linkages to environmental drivers that may increase or decrease biodiversity (Arkema et al. 2006). To do this a landscape approach to ecological relationships between organisms and the environment may help determine influences of habitat on the distribution of genetic variation in a species.

The field of landscape ecology has advanced our understanding of how landscape heterogeneity affects ecological processes (Turner 1989) and provides a spatially explicit framework for understanding the relationships between ecological patterns and processes that can be applied across a range of scales (Turner 2005). More specifically, landscape ecology examines the development and dynamics of spatial heterogeneity, interactions across heterogeneous landscapes, the influence of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity. The structure of a landscape can be described by the composition and spatial arrangement of the habitat patches that make up ecosystems (Turner 1989). This structure has been quantified using a number of metrics (O'neill et al. 1988) including composite indices (e.g., habitat diversity) and measures of configuration (e.g., patch size) and context (size, spatial arrangement and composition of surrounding habitat patches) (Turner 1989). Understanding how landscape structure may influence the creation and maintenance of genetic diversity is critical for understanding ecosystem level functions.

Landscape genetics (Manel et al. 2003) seeks to understand the influence of ecological processes (Turner 1989) on genetic variation by quantifying the relationship between landscape variables, population genetic structure, and genetic variation. Landscape genetics has provided a framework for examining how the physical landscape affects genetic characteristics of populations. Understanding how landscape heterogeneity influences genetic diversity and populations structure requires the combination of high-resolution genetic markers and population genetic theory with spatial data and a variety of statistical methods (Storfer et al. 2006).

Traditionally, population genetic studies have been limited to tests of isolation-by-distance for making spatial inferences to estimate genetic structure (i.e., how genetic variation is distributed in space) and gene flow. Gene flow is a measure of organismal dispersal or the movement of genes alone and can provide a direct measurement of functional connectivity among populations (Holderegger et al. 2007). Landscape genetics provides a framework for examining the relative influence of landscape and environmental variables on gene flow, genetic discontinuities, and genetic population structure (Manel et al. 2003; Holderegger and Wagner 2006). One of the drivers for the growing theoretical and empirical interest in landscape genetic analyses is a shift by ecologists and conservation biologists to landscape scale analyses (Stork & Waits, 2010).

Landscape genetics has been used in a range of systems using different landscape parameters to predict genetic structuring, including plant cover type (Spear et al. 2005), habitat fragmentation (Spear and Storfer 2008), stream distance (Roach *et al.* 2001), and water flow rates (Michels et al. 2001). While landscape genetic approaches have been increasingly applied to examining the impact of environmental heterogeneity on the population structure of terrestrial and aquatic organisms, there has been limited application of landscape genetics in marine systems. Those studies that have focused on marine systems have generally focused at the scale of the seascape by examining the influence of ocean currents on population dynamics (Galindo et al. 2006; Hansen and Hemmer-Hansen 2007; Selkoe et al. 2008; Galindo et al. 2010). These studies assess the role that large-scale oceanographic variables play in structuring populations and measure connectivity as a function of larval dispersal (Selkoe et al. 2008). However, these large-scale approaches ignore the potential impact of fine scale, landscape based factors, which

may in fact fragment populations of low mobility marine populations and subsequently increase genetic variation. Furthermore, diversity as measured at a local scale may in fact arise from environmental factors that range across multiple scales (Garza 2008). An underlying assumption of seascape scale studies is that with increasing pelagic larval duration (PLD), connectivity will increase and there will be a concurrent decrease in population structuring. However, Weersing and Toonen's (2009) meta-analysis of the effect of PLD on genetic connectivity demonstrated only a weak relationship between the two variables. Similarly, previous studies of marine species with relatively low dispersal have shown unexpectedly fine scale genetic structuring of a few meters (Johannesson 1988; Andrade and Solferini 2007). Thus, there is a need for studies that can incorporate variation of scale and determine the scales at which the drivers responsible for genetic diversity become ecologically significant in the marine realm (Balkenhol et al. 2009). This is a significant knowledge gap when attempting to apply an ecosystem-based approach to marine conservation and management.

The focus on seascape scales is, in part, due to the great potential for larval dispersal that characterizes the majority of marine species. This life history pattern has led to a paradigm that considers marine populations open, where reproductive output is decoupled from recruitment of juveniles in local populations for reef fishes. This has led to a theoretic focus on larval dispersal and recruitment in reef fish ecology (Cowen and Sponaugle 2009). However, at local scales the influence of the environment on juveniles and adults might play a greater role in determining the scales, rates, and patterns of demographic and genetic connectivity among populations. Recent studies of larval dispersal patterns and genetic population structure suggests that local reef fish populations is less open than previously thought (Warner and Cowen 2002; Buonaccorsi et al. 2004; Cowen et al. 2006; Bay et al. 2008). This suggests that species with reduced scales of larval connectivity or without larval dispersal, the relationship of adult individuals with the local habitat at fine spatial scales might have important population level consequences (i.e. demographic and genetic connectivity).

Habitat composition, the abundance and distribution of the biological components of a habitat, can be driven by the variation in the structural complexity of the habitat. Structural complexity has been shown to be important in predicting abundance and

distribution in a diverse array of taxa including birds (Macarthur and Macarthur 1961), lizards (Reagan 1991), bighorn sheep (Sappington et al. 2007) and invertebrates (Beck 1998). In marine habitats, the distributions of adult reef fish, like most other adult organisms, are related to spatial variation in habitat composition and complexity (Grober-Dunsmore et al. 2007; Grober-Dunsmore et al. 2008). Structural complexity can influence habitat composition and is an important habitat characteristic with many ecological roles. Increased complexity provides habitat structure, promotes species richness, and alters boundary-layer flow over the bottom (Butman et al. 1994; Green et al. 1998). Along the seafloor, the interaction of current flow and substrate complexity can affect settlement of larvae and algae (Hills et al. 1999; Lapointe and Bourget 1999) and subsequent population performance because it controls delivery of nutrients, oxygen, and chemical cues (Weissburg and Zimmer-Faust 1993; Leonard et al. 1998; Lenihan et al. 1999). Complexity is an important habitat characteristic that serves many ecological roles (i.e. often correlated with species richness) and provides refuge from predators and physical stress (Pittman et al. 2009; Zawada and Brock 2009).

While most marine fishes are oviparous with pelagic larvae that disperse soon after hatching, Surfperch (*Embiotocidae*) are a notable exception and are viviparous having internal fertilization. Females give birth to multiple fully developed offspring that are free-swimming and that have been shown to form sibling groups immediately after birth (Sikkel and Fuller 2010). Adult surfperch have very limited dispersal capability, swim within a meter of the reef substrate, require rocky reef habitat to forage and use as refuge, and live in restricted territories.

Black surfperch (*Embiotoca jacksoni*) are a common nearshore fish species that lives in a narrow band of the marine littoral zone (approximately 3 to 20 m) (Hixon 1981; Bernardi 2000; Froeschke et al. 2007) which ranges from Fort Bragg in northern California to central Baja California in Mexico (Humann and Hall 1996). This species attains a maximum length of about 35 cm (Humann and Hall 1996), and is commonly observed swimming within a meter of the reef substrate and feeding on small benthic animals (Quast 1968; Schmitt and Coyer 1982). It is strictly diurnal, becoming inactive near the reef substrate at night (Ebeling and Bray 1976). It eats various species of small, sedentary invertebrates (mainly crustacea) that inhabit a diverse aggregate "turf of small

plants and colonial benthic animals covering much of the reef bottom (Quast 1968; Schmitt and Coyer 1982, 1983; Schmitt and Holbrook 1984; Holbrook and Schmitt 1992). The primary preys are tube-dwelling and free-living gammarid amphipods (detritivorous and planktivorous crustaceans averaging several millimeters in length) (Schmitt and Holbrook 1984).

Black surfperch life history, low dispersal, and strong habitat affinity suggests that populations are dependent on habitat composition at local scales. Biological habitat composition has also been shown to be associated with varying levels of habitat complexity in the rocky subtidal. Taken together they may drive not only patterns of distribution and abundance in these populations but, over time, influence patterns of genetic variation in these populations. Using mitochondrial markers Bernardi (2000) demonstrated population structuring of black surfperch populations at a sub-regional scale. Their limited dispersal capability and fine scale habitat affinity (Holbrook and Schmitt 1984; Schmitt and Holbrook 1990; Holbrook and Schmitt 1992; Schmitt and Holbrook 2007), might drive fine scale (100's – 1000's meters) population structure. Partitioning of populations may be a long-term response to habitat variation through space. The goal of this study is to determine if black surfperch populations are structuring at local scales and if this structuring is influenced by both habitat complexity (the 3D structural complexity of the seafloor) and habitat composition (the biological distribution of habitat types through space). I hypothesize that populations of black surfperch will demonstrate genetic partitioning at relatively small spatial scales. I also predict genetic diversity will be correlated with a suite of landscape parameters (e.g. topographic complexity, slope, habitat complexity, algal habitat distribution, and prey distribution) that are also scale dependent. I tested these predictions through a novel integration of population genetics and landscape ecological techniques to estimate how habitat complexity may drive genetic variation in a population that resides in subtidal rocky reef systems.

For this study, I used a landscape genetics approach to examine the role of fine scale landscape variation on the genetic composition of relatively low mobility marine organisms. Using highly variable microsatellite markers, short tandem repeat sequences (usually di-, tri-, or tetranucleotides) that are polymorphic Mendelian markers I generated

population specific allele frequencies. These allele frequencies were then used as part of a model comparison to determine genetic variability between populations and subpopulations. Specifically, this study documents 1) the relationship of the physical landscape to biological habitat distribution 2) prey availability as a response to algal habitat distribution 3)Prey consumption as a function of prey availability and 4) population structure of the black surfperch as a function of the physical landscape, habitat distribution, and prey availability. Finally, this study attempts to generate an understanding of the interaction between genetics and the physical and biological landscape for management and conservation in the nearshore marine environment. Applying population genetic theory in a landscape ecology framework can help managers identify constraints created by anthropogenic, habitat, or environmental factors that may increase reproductive isolation, demographic independence among populations, and the reduced likelihood of population persistence. Though a few recent studies have examined how fine scale landscape complexity in the subtidal realm influences the distribution and abundance of mobile marine species (Grober-Dunsmore et al. 2008; Hovel and Regan 2008), few studies have examined the linkage between genetic diversity and micro-scale landscape processes in marine systems. The goal of this project was to examine the ability of geospatial and genetic tools to determine the influence of physical and biological habitat on population structuring in a marine fish.

2 METHODS

2.1 Study site

This study focused on the development of geospatial methods that can be used to visually and quantitatively estimate linkages between landscape complexity in rocky subtidal reefs, benthic habitat composition, prey abundance, and finally genetic partitioning in a model population of marine fish. I chose four nearshore study sites along the Monterey Peninsula, California (Figure 1).

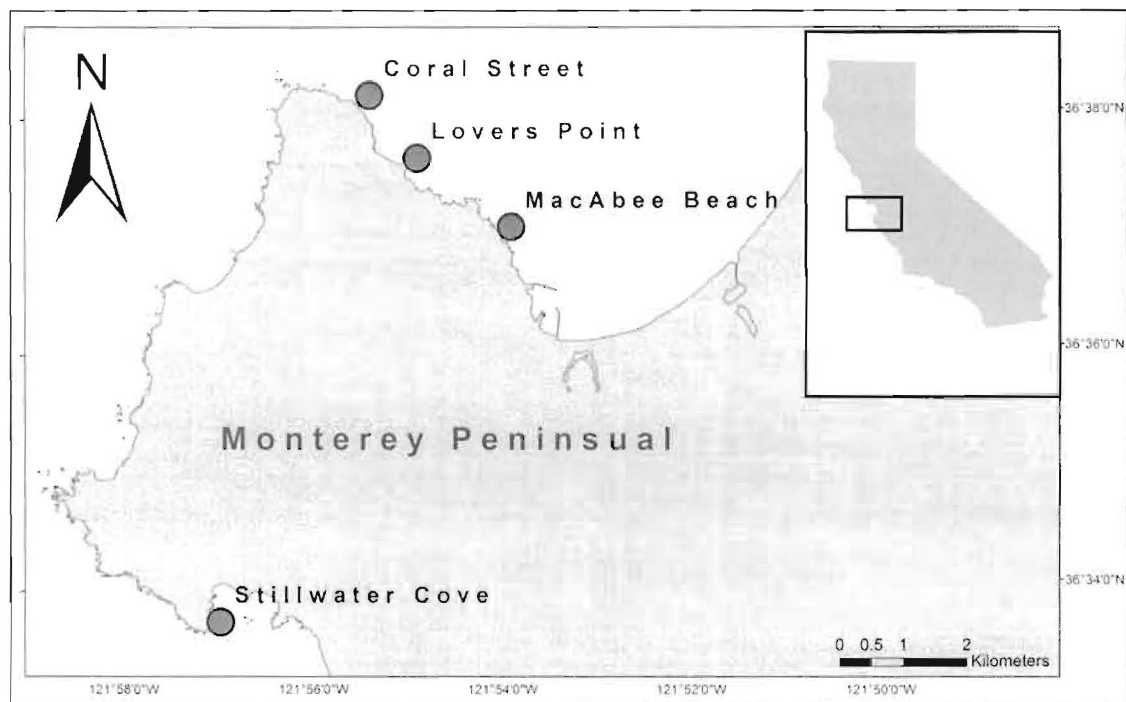

Figure 1: Map of research sites around Monterey Peninsula.

I used black surfperch habitat requirements to determine site locations that include rocky reef habitat between a depth of 5 and 20 meters. Using bathymetric data collected by the California Seafloor Mapping Program, I chose nearshore sites with depths between 5 and 15 meters with rocky reef habitat. Divers scouted the sites to ensure the presence and sufficient numbers of black surfperch at each site. Once site locations were selected, coordinates of site centers were chosen using ArcMap and uploaded to handheld GPS units (Table 1) to accurately revisit each site.

Table 1: Site locations with latitudes and longitudes

Site	Latitude	Longitude
MacAbee	36°37'4.579"	121°53'55.457"
Lovers Point	36°37'40.75"	121°54'48.38"
Coral Street	36°38'11.284"	121°55'20.364"
Stillwater	36°33'43.439"	121°56'58.362"

2.2 Field collections

2.2.1 Habitat Sampling

Photoquadrats (underwater images of a quadrat) were collected using a photoquadrat framer. The framer was constructed using PVC pipe and designed from a modified schematic from (Vroom et al. 2004). The dimensions of the photoquadrat used are 0.6 m by 0.45 m covering an area of 0.27-m^2. The framer was used to mount an Olympus Stylus Tough 6000™ housed in a pt -047 underwater housing with a sealife digital pro flash™.

For each site divers traveled by boat and navigated using a WASS enabled Trimble® GeoXT™ handheld GPS unit to find the site center. The boat anchor was dropped at the center point to anchor the boat and to be used as the central tether for subtidal transects. Divers descended along the anchor line to the seafloor. Once at the center point the dive assistant would clip a 50 meter transect tape on to the anchor and lay out the transect tape along a predetermined heading. At the end of the transect tape the photoquadrat was placed lengthwise along the center of the transect line and a photo of the substrate was taken by the lead diver (Figure 3). The photo number and time were recorded and the dive assistant would send a marker float to the surface using a diving reel.

At the surface, a support kayaker would paddle to the float and once on top of the float would record the position using the handheld GPS unit. No less than three positions were recorded for each waypoint and the time and sequential number of the waypoint were automatically recorded for each point. When the waypoint had been collected, the

kayaker would give three large tugs on the float for the dive assistant to reel the float back down. The divers would then move on to the next predetermined meter point along the transect tape while reeling in the transect tape. The predetermined meter marking was randomized for each ten-meter section for each transect. A total of sixteen transects were collected for each site for an approximate total of 97 photoquadrat points for each site.

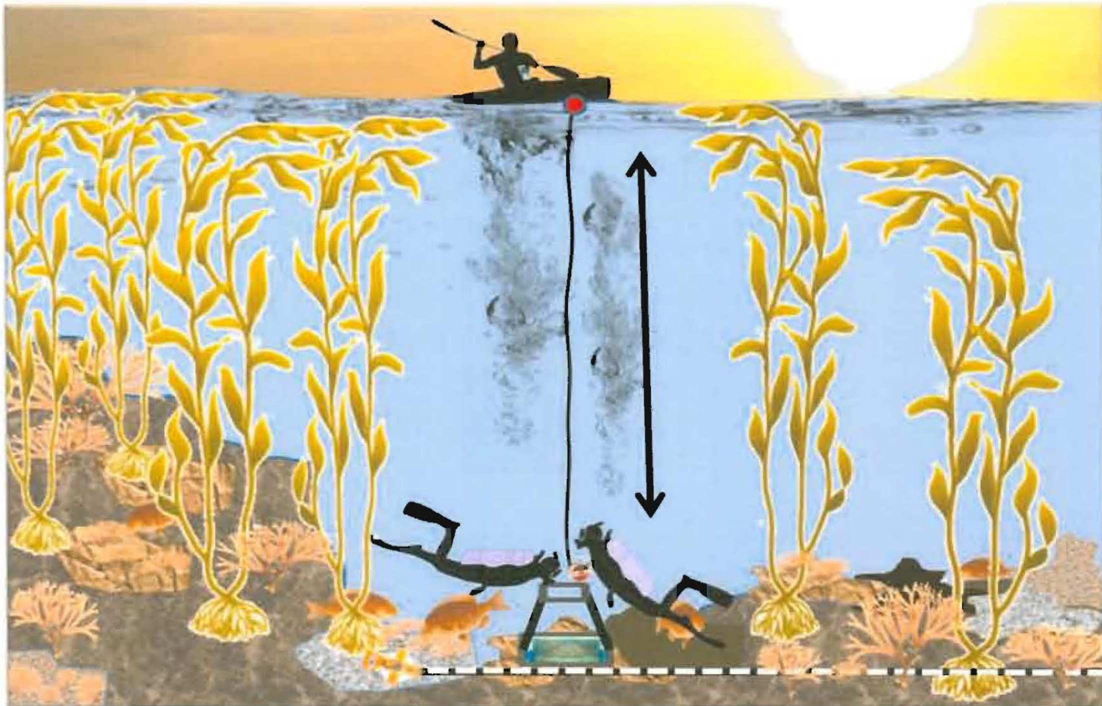

Figure 2: Schematic of photoquadrat collection and georeferencing.

Two, 10 by 10 centimeter substrate scrapings were also collected along each transect for a total of 30 substrate samples from each site. Substrate and algae were scraped from the seafloor and placed into individually pre-marked Ziploc bags underwater. Substrate samples were brought back to the surface and stored in a cooler on the boat until they were transported back to the lab where they were stored at -20°C until processing. Substrate sample points were collected at select photoquadrat points and were dependent on the presence of surfperch habitat types. Samples were not collected from bare patches or patches without algal habitat types.

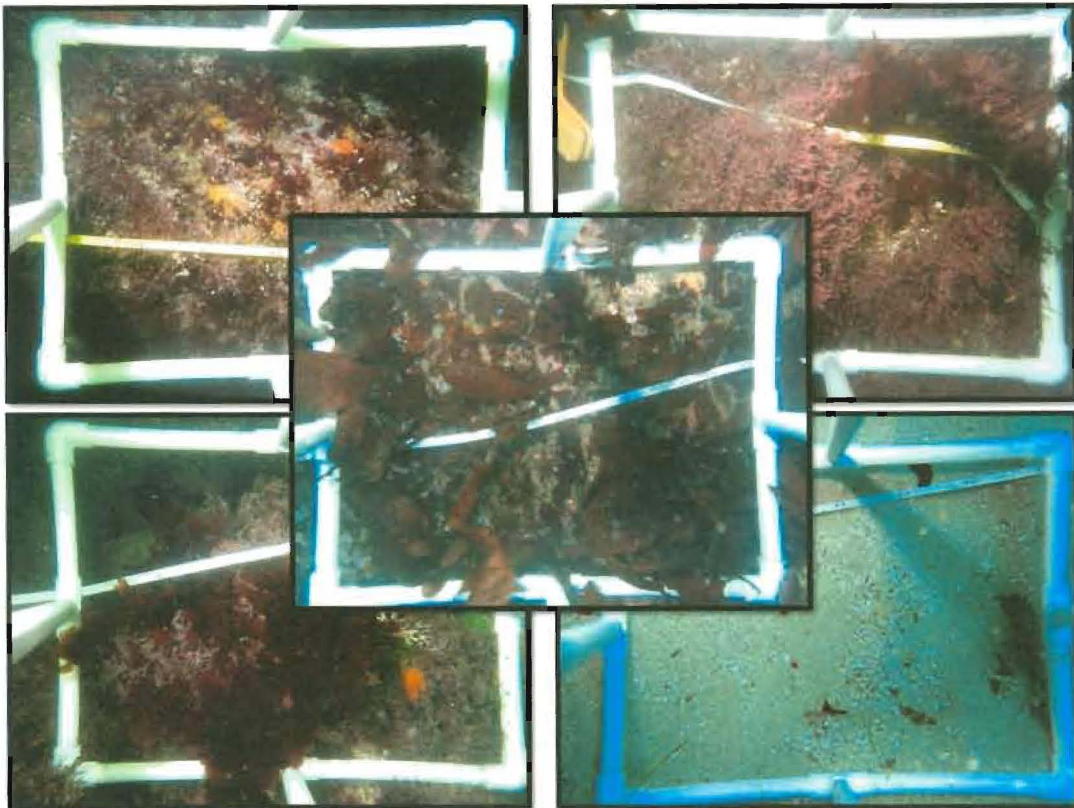

Figure 3: Mosaic of photoquadrats of substrate showing different levels of habitat diversity among photoquadrats.

2.2.2 Fish Sampling

Up to 20 black surfperch were opportunistically collected using pole spears by divers at each site. At each site, divers would patrol in an expanding circle from the center point and spear any black surfperch they encountered. When an individual was captured, the assistant diver would send up the marker float to the kayaker who would record the float position using the handheld GPS unit to record the waypoint with a minimum of three positions recorded for each waypoint. All fish were placed into individually pre-marked bags and the bag number and time was recorded by the lead diver. All fish were stored in a cooler in the field and then transported to the lab where they were stored at -20°C until processing.

2.3 Lab Processing

2.3.1 Benthic cover estimates

Photos from the camera were downloaded the same day that they were collected and organized by photo code and date. I used ACDsee™ photo editing and managing software to optimize photo quality for each quadrat. Optimization improved the contrast, brightness, and color of each photo for habitat classification. Optimized photos were then imported into the Coral Point Count with Excel extensions software package (CPCe) (Kohler and Gill 2006). I used CPCe to define the quadrat extent in each photo and place 100 random stratified points. The extent of the point distribution was delineated by manually creating a border that coincided with the area framed by the quadrat. For each photoquadrat, a stratified random point distribution using 100 points was created. CPCe stratified the points by dividing the photoquadrat into a grid of 10 boxes by 10 boxes with each box being ~27 cm^2, and 1 point was randomly placed within each box.

For each point, the habitat classification was recorded for the entire photo using a custom classification scheme based on nine habitat types, characteristic of the sites including habitat associations of black surfperch (Table 2). Classifications were processed at habitat level classification of algal groups and functional groupings for biogenic habitat. CPCe then was used to create excel tables that tabulated the percent cover of each habitat type for individual photos and grouped percent cover estimates for each Site. The habitat classification Other Algae was exclusively red foliose algae. Therefore, percent cover for the classification Rhodymenia and other algae were added together and used in all further analyses as a red algae habitat classification.

Table 2: Habitat groupings and codes for the percent cover estimation

Code	Habitat Type
T	Turf
LA	Laminarial
Rh	Rhodominia sp
ER	Erect Coralline
C	Encrusting Coralline
OA	Other Algae
OL	Biogenic Habitat
SAR	Sand,Artificial, rock
U	Unknowns
TWS	Tape, wand, shadow

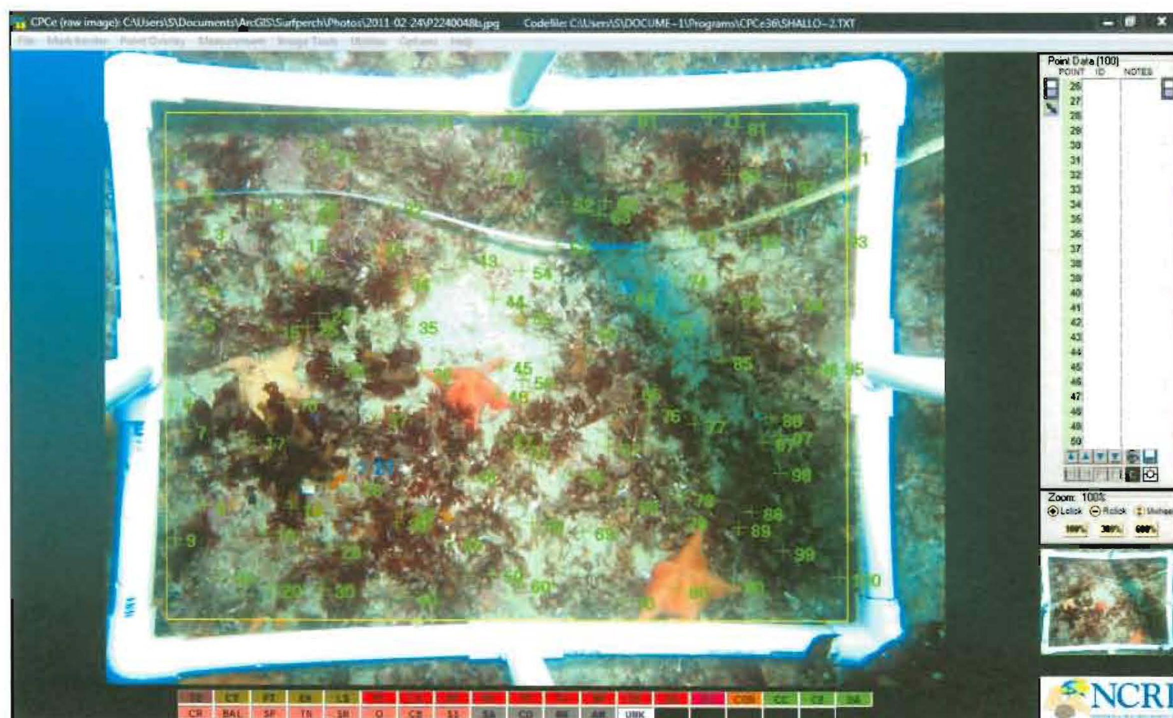

Figure 4: Photoquadrat from Lovers Point, February 24, 2011 with 100 stratified random points in CPCe (Kohler and Gill 2006).

2.3.2 Prey Estimates

Resource samples were thawed and following the protocols of Coyer (1979) invertebrates were separated from the algal materials. I identified all invertebrates to coarse taxonomic groupings (Table 2), counted all individuals, and measured the first 100 individuals from a group using an ocular micrometer (Schmitt and Coyer 1982). Length-weight relationships were used to estimate biomass for taxonomic groups (Coyer 1979).

Fish samples were thawed and dissected as soon as possible after collection. All prey items in the digestive tract of each fish was removed, identified, and counted using a dissecting microscope. A random sample of up to 100 individuals per taxon for each fish was measured using an ocular micrometer. I used the same length-weight relationship to estimate biomass for the fish samples as I used for the resource samples.

2.3.3 Genetics

Gill tissue from each fish was collected and stored in 95% ethanol at -20°C. Total genomic DNA was prepared from 75– 100 mg of tissue using a standard Proteinase K, chloroform extraction procedure (Sambrook et al. 1989).

For this study I used twelve (out of 21 tested) highly variable microsatellite loci (Table 3). These microsatellites were previously derived from a genomic library based on *Embiotoca jacksoni* DNA and analyzed (Bernardi 2008). Amplification of 50–100 ng of DNA followed standard reaction protocols, with cycling profiles of 45 s at 94 °C and 1 min at 54 °C, 45 s at 72 °C for 35 cycles, followed by 3 min at 72 °C.

Table 3: Microsatellite loci characteristics. Columns correspond to: microsatellite name (Locus), (F) forward and (R) reverse primer sequence, repeat motif, and amplification size of original clone (Amp. size), GenBank Accession numbers are EU781555 to EU781566

Locus	Primer sequence (5′–3′)	Repeat motif	size
EJ_C3	F: 5′-CGTCAATGATACTCATGTGAAC-3′ R: 5′-ATGTCCCCTTGGGATTAA-3′	(TAGA)4(TACA)8	113
EJ_B5	F: 5′-CCACCTGGGGCTAAACTG-3′ R: 5′-CACGGCAGACAGAGCAAC-3′	(CATC)15	112
EJ_B3	F: 5′-CATTTTCCATCCATCCTTCTG-3′ R: 5′-CAGCACAAGCATCACATTAGC-3′	(CATC)14	156
EJ_B1	F: 5′-ACTCGGACAGTAAAGCTGAGG-3′ R: 5′-AAAATGTCTCCTTGCAGGATC-3′	(CATC)14	180
EJ_A12	F: 5′-GAAAGAAGCTCAATGCAATCAC-3′ R: 5′-AGCAGCTCTCAGATCAGAGGTA-3′	(CA)24	232
EJ_A10	F: 5′-AACAAAAACTGCATCCAAGATG-3′ R: 5′-ACGAACTGTTCCATCCTCAAG-3′	(CA)15	228
EJ_A2	F: 5′-AGCAAAGGTCAAAGGTCAA-3′ R: 5′-TTGTGGCTGTTGTTTATGG-3′	(CA)20	235
EJ_A7	F: 5′-AATACCGTCGATGCTTTGTATC-3′ R: 5′-GCCTCTGATTATACGTCAGCTC-3′	(CA)15	245
EJ_A11	F: 5′-ACTTCCATGACAACAAAGTAGG-3′ R: 5′-CAAAATAAGCCAAGTGTGATG-3′	(CA)24	283
EJ_B8	F: 5′-GGTCGTATTTTGCAGTATGC-3′ R: 5′-AAGGATTCCCAACATCATG-3′	(CATC)30	266
EJ_A5	F: 5′-AACCGCTGAGTAAGTAAACATC-3′ R: 5′-TCATCCCCATCATATTTATAGC-3′	CA)30	275
EJ_D2	F: 5′-CCTCCCTTTACCCATCTTTATC-3′ R: 5′-AAGGATATTGAGTCACCACAGG-3′	(TAGA)6	283

2.4 Statistical Analysis

2.4.1 Site Characterization

Using ArcMap 10.1, I incorporated bathymetric digital elevation models of the near shore around the Monterey Peninsula. The Seafloor Mapping Lab at California State University, Monterey Bay, supplied all bathymetric seafloor data. From the elevation models, I used the Slope, Topographic Position Index (TPI), and Vector Ruggedness Measure (VRM) tool sets within ArcMap to generate raster models of slope, TPI, and VRM of the seafloor. Slope is the measure of the rate of change in depth from each cell. TPI is the difference between a cell elevation value and the average elevation of the neighborhood around that cell. Positive values mean the cell is higher than its surroundings while negative values mean it is lower. The positive and negative classification is then used to identify peaks, valleys, and plains (Jenness 2006). VRM measures habitat complexity as the variation in three-dimensional orientation of grid cells within a neighborhood (Sappington et al. 2007).

In ArcMap, I created 100 random points for each of the four sites and sampled the depth, slope, TPI, and VRM rasters respectively. The stored values for each variable for each point were used to test for differences among sites of the physical variables. I imported my photoquadrat GPS points into ArcGIS and following the same sampling procedure for the random points, I sampled the physical variable rasters. To determine if the sampled points were sufficiently random I used a linear model to compare pooled and among sites for differences between the random points and the photoquadrat points.

2.4.2 Spatial Autocorrelation

Most ecological data sets have a spatial component that can significantly influence statistical tests (Zuur et al. 2009). While everything may be related, things closer together tend to be more related to one another than they are to things at a greater distance. This is known as spatial autocorrelation, which can occur when an observation at one location positively or negatively affects the value of an observation at another point in space (Legendre 1993). Autocorrelation quantifies the degree to which spatial phenomena are correlated to itself in space, the level of interdependence between the variables, and the nature and strength of the interdependence (Cliff and Ord 1973, 1981). Spatial autocorrelation violates the assumption of independently and identically distributed errors of most standard statistical procedures (Anselin 2002), inflating type I errors, occasionally inverting the slope of relationships when not accounted for in the model (Kuhn 2007).

I examined the raw data and model residuals for the presence of spatial autocorrelation by plotting covariance against spatial lags between paired observations also known as correlograms (Legendre and Fortin 1989). Spatial covariance structures were estimated for each point and added as an explanatory variable in the models. I estimated the covariance structure by creating correlograms of multiple model runs with different covariance structures added. An exponential function was used for the correlation structure as it best describes the reduction of spatial autocorrelation of the data. Estimated covariance between two points was calculated from the fitted spatial autocorrelation model as a function of separation distance, calculated as the Euclidean distance between the two points. Creation and plotting of correlograms and modeling of

spatial autocorrelation were performed using the R statistical program (R Development Core Team 2011).

Moran's I is a commonly used method to measure spatial autocorrelation is and measures how similar a data point is to its neighboring points (Legendre and Legendre 1998). Moran's I was used to test for the presence of spatial autocorrelation in the variables used for the GLM model and to generate correlograms for both response and environmental variables. Moran's I usually varies between 1.0 and -1.0, where 1.0 indicates positive correlation (clustered) and -1.0 indicates negative correlation (dispersed) and zero indicates no spatial autocorrelation (random) (Diniz-Filho and De Campos Telles 2002). Correlograms, Moran's I coefficients plotted against the geographical distance class, were created to show the spatially lagged similarity between neighboring data points.

2.4.3 Modeling Approach

To examine the multiple variables and their respective influence I used a model comparison approach. Generalized linear models (GLM) are extensions of linear regression that are able to incorporate different distributions (e.g. the binomial distribution for binary and proportional data). These models also use a link function between the expected values of the response variable and explanatory variables that ensures that the fitted values are appropriate (e.g. larger than zero for count data, or between 0 and 1 for binary data) (Mccullagh and Nelder 1989).

I developed Generalized Linear Models to quantify the influence of the predictor variables on the response variables. Each model was developed in R statistical package using a backward deletion stepwise selection and the Akaike information criterion (AIC) to determine variable inclusion in the model (Chambers and Hastie 1993). Information theoretic approaches (Burnham and Anderson 2002) provide a nested framework to test each model against a simpler model to determine the most significant contributing factors in the model. Stepwise selection provides the opportunity to explore whether different variables are important and to measure their relative contributions to driving distribution patterns.

2.4.4 Habitat Distribution

There paucity of turf habitat in the photos dictated its exclusion from further analyses. For the remaining four habitat variables, I used arcsine transformed photoquadrat estimates of habitat percent cover to create linear models of each habitat group as a function of the three physical variables and site for a total of four saturated models.

$$M_1: Reds = \beta_0 + \beta_1 VRM + \beta_2 Slope + \beta_3 TPI + \beta_4 Spatial\ Covarience$$

$$M_2: Laminarials = \beta_0 + \beta_1 VRM + \beta_2 Slope + \beta_3 TPI + \beta_4 Spatial\ Covarience$$

$$M_3: Articulate\ Coraline = \beta_0 + \beta_1 VRM + \beta_2 Slope + \beta_3 TPI + \beta_4 Spatial\ Covarience$$

$$M_4: Biogenic\ Cover = \beta_0 + \beta_1 VRM + \beta_2 Slope + \beta_3 TPI + \beta_4 Spatial\ Covarience$$

I used an information-theoretic approach (Burnham and Anderson 2002) to select these hypotheses in terms of the likelihood that each model gave rise to the data. Each hypothesis was compared using evidence ratios derived from AIC. I conducted a backwards stepwise regression to determine the best model using AIC.

2.4.5 Prey Distribution

I calculated total numbers of all prey groups from the resource samples and looked at proportion of each group as a function of the total number for each sample, pooled for each site and pooled across sites. I then repeated the same calculations for the fish gut samples as were done for the resource prey samples. I selected a sub-group of prey items, amphipods and crabs, which made up the highest proportion of fish diets and all subsequent analyses, were done using these two taxonomic groupings.

I compared average biomass of resource prey to fish diet prey and did a regression analysis between the two to detect differences in prey selectivity in fish from resource availability. I conducted a two-way t-test to determine if there was a difference between average prey biomass from the resource samples and the fish diet samples. I used model

comparison to determine the influence of biological and physical variables on prey availability in the environment and in fish diets.

I used a logarithmic transformation on all biomass data and arcsine transformations for the percent cover data for model comparisons. To determine the influence on habitat availability on prey biomass I compared prey biomass as a function of habitat availability with the spatial covariance structure to account for the spatial autocorrelation.

$$M_R\!: Resource\ Prey = \beta_0 + \beta_1 Spatial\ Covarience + \beta_2 Reds + \beta_3 Laminarials + \beta_4 Articulate\ Coraline + \beta_5 Biogenic\ Habitat + \beta_6 VRM + \beta_7 TPI + \beta_8 Slope$$

$$M_F\!: Fish\ Prey = \beta_0 + \beta_1 Spatial\ Covarience + \beta_2 Reds + \beta_3 Laminarials + \beta_4 Articulate\ Coraline + \beta_5 Biogenic\ Habitat + \backslash\beta_6 VRM + \beta_7 TPI + \beta_8 Slope$$

2.4.6 Genetic analysis

I ran the microsatellites on an automated sequencer ABI 310 and scored them using the software Gene Mapper version 3.7 (Applied Biosystem). Raw scores were then binned and tabulated and the potential presence of null alleles was controlled with Microchecker (Van Oosterhout et al. 2006). I analyzed within-sample deviations from Hardy–Weinberg (HW) expectations using an exact test of HW proportions for multiple alleles (Guo and Thompson 1992) using GENEPOP version 3.2 (Raymond and Rousset 1995). I used Arlequin (Excoffier et al. 2005) to examine the data conformance to HW expectations, and to estimate expected and observed heterozygosities (HE and HO). Finally, to analyze the independence of the microsatellite loci, I conducted an exact test for linkage equilibrium in Arlequin 3.5.

I assessed population structure using both classical FST calculations including GST, Analysis of Molecular Variance (AMOVA), as well as more recently derived estimates of population differentiation, namely jost's D and G''. Using highly polymorphic microsatellite markers the GST-value cannot reach its maximum value of 1. Even when populations share no alleles at all, GST-values remain low. To calculate 'real' genetic differences between populations, it has been suggested that a different method using the differentiation index D and the bias-corrected estimator D_{est} is more accurate

(Jost 2008). These indices are based on the effective number of alleles resulting in a more meaningful perception of differentiation (Heller and Siegismung 2009; Jost 2009).

I estimated genetic differentiation among populations with *Fst* (Weir and Cockerham, 1984; calculated by Arlequin) using 95% confidence limits. An Analysis of Molecular Variance (AMOVA) was done using the software package Arlequin (Schneider et al., 2000). As a fixation index, *Fst* does not accurately measure the magnitude of genetic differentiation among populations when heterozygosity is high and/or variable among sampling locations (Hedrick 2005; Jost 2008). Thus, I compared the estimates of *Fst* with estimates of actual genetic differentiation, D*est*, using the program SMOGD (Jost 2008; Crawford 2010) To test for isolation by distance in the samples I conducted a MANTEL test using linear pairwise F_{ST} values and pairwise distance (km) among samples as implemented in GENEPOP (10,000 permutations).

Finally, to test for influence of the environmental parameters I conducted a MANTEL test using pairwise environmental values as well as pairwise distance parameters among all samples. Variation in F_{ST} values for each population relative to fish density and landscape complexity was analyzed using a generalized linear model using the GESTE (genetic structure inference based on genetic and environmental data) analytical program (Foll and Gaggiotti 2006). The GESTE program implements a hierarchical Bayesian approach to estimate population-specific F_{ST} values and which local environmental factors likely contribute to observed genetic structures. The model is based on a GLM structure using MCMC's to estimate posterior distributions. Local FST, a site-specific metric of allelic differentiation, was calculated with a maximum likelihood approach in the program GESTE (Foll & Gaggiotti 2006) with all sampling sites included. I compared the Pairwise genetic data (Fst and Dest) with euclidean and oceanographic distance metrics. Correlations were tested with mantel tests.

3 RESULTS

3.1 Site Characterization

All sites were statistically different for all but one of the physical habitats estimated from seafloor map derivative data sets. Vector Ruggedness Measure, Slope, and Depth were all significantly different among sites (Figure 5). However, Topographic Position Index was not significantly different among sites. I tested an equivalent number of random points from each site and modeled against photoquadrat points to detect sampling bias in site characterization. The t-test detected no difference among the random and photoquadrat points for any of the habiat characteristic variables. The spatial autocovariance included in the models accounted for the site effect and was included in all models.

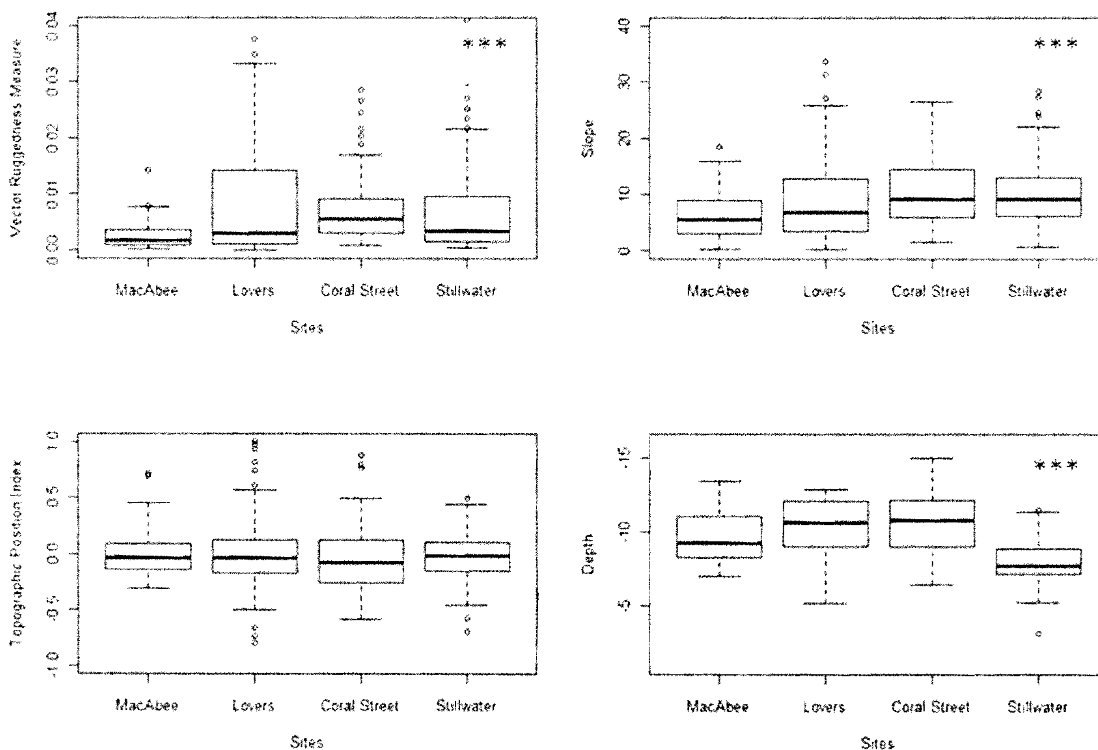

Figure 5: Boxplots of physical habitat variables from 100 random sampling points per site; a) Vector Ruggedness Measure, b) Slope, c) Topographic Position Index, d) Depth. * denotes significant differences among sites.**

3.2 Spatial Autocorrelation

There was significant positive spatial autocorrelation for composition, complexity, and prey availability variables (Table 4). The auto covariance of both physical and biological habitat variables was positive at relatively small spatial scales (~ 5 meters) and dissipated quickly as the scale increased (Figure 6). This suggests that samples close to one another were more similar than by chance but that this relationship disappeared quickly at only slightly larger scales where most of the samples were taken in relation to one another. Including spatial autocovariance in the models reduced the spatial autocorrelation residual values. The quick dissipation of the autocorrelation suggested that an exponential model was required to model the spatial autocovariance structure within the GLM's for the subsequent model selection.

Table 4: Spatial autocorrelation table showing observed and expected Moran's I with associated standard deviation and p-value for significant autocorrelation.

	VARIABLES	Observed Morans I	Expected Morans I	sd	p-value
Complexity	**VRM**	0.170	-0.003	0.010	0
	TPI	0.071	-0.003	0.010	4.54E-13
	Slope	0.105	-0.003	0.010	0
Composition	**Reds**	0.294	-0.003	0.010	0
	Laminarial	0.130	-0.003	0.010	0
	Articulate Coralline	0.578	-0.003	0.010	0
	Biogenic	0.048	-0.003	0.010	5.53E-07
Prey	**Total Prey Resource**	0.172	-0.009	0.033	4.51E-08

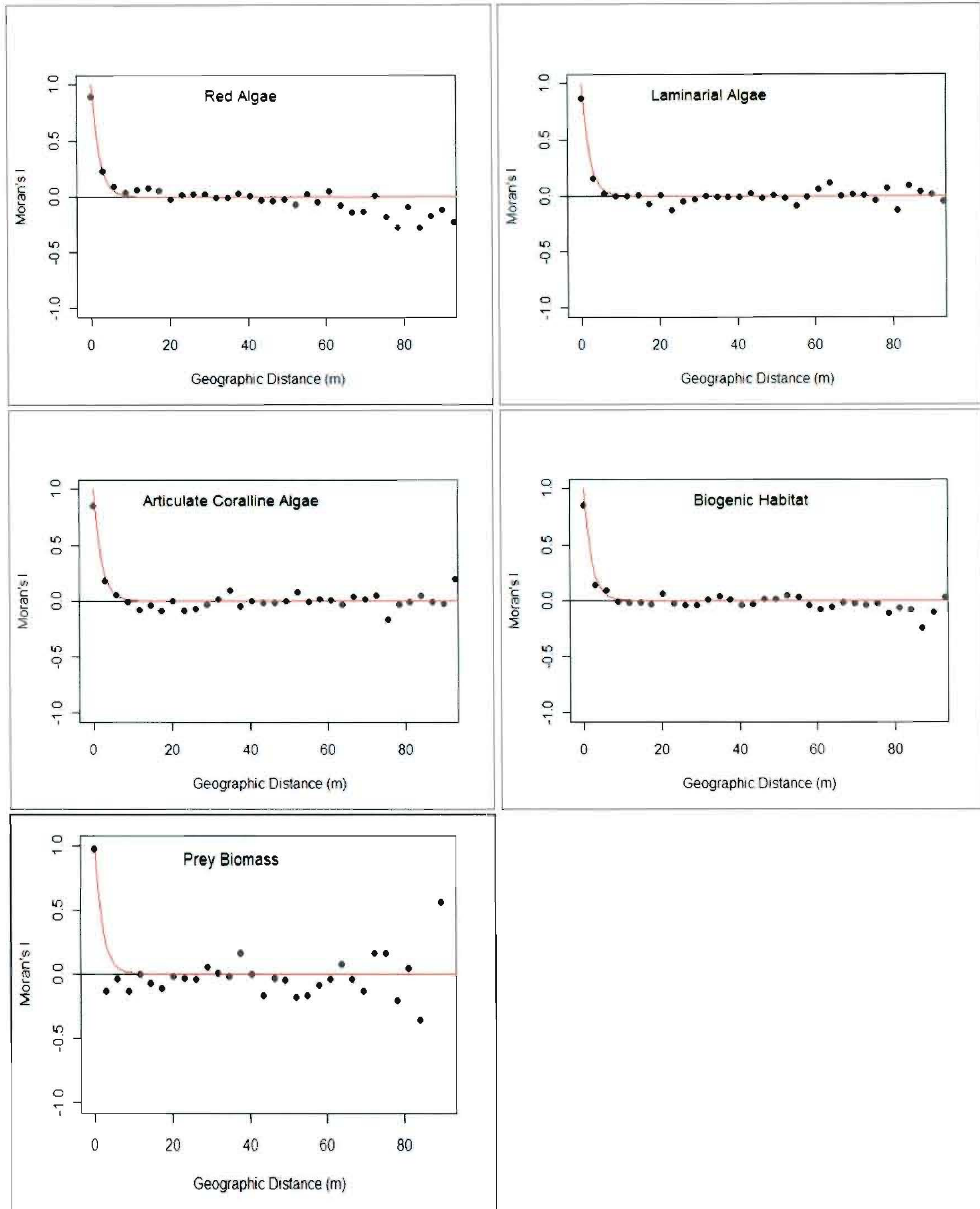

Figure 6: Correlograms for the biological habitat variables a) Red Algae b) Laminarial Algae c) Articulate Coralline Algae d) Biogenic Habitat e) Prey Biomass

3.3 Habitat Distribution

A total of 400 photoquadrats were collected from the four sites and used to estimate percent cover estimates of benthic habitat. Habitat availability varied greatly within and among sites (Figure 7). Within sites, patchy mosaics exist at the scale of several meters as can be seen in the raster maps created for each habitat type for Lovers Point. These rasters show the percent cover of each habitat type interpolated across the site from the photoquadrat data collected (Figure 8) with red being high percent cover and blue low percent cover. Among sites, differences were significant as all model selections of the possible models for habitat type as a function of physical variables and site kept site as a significant variable.

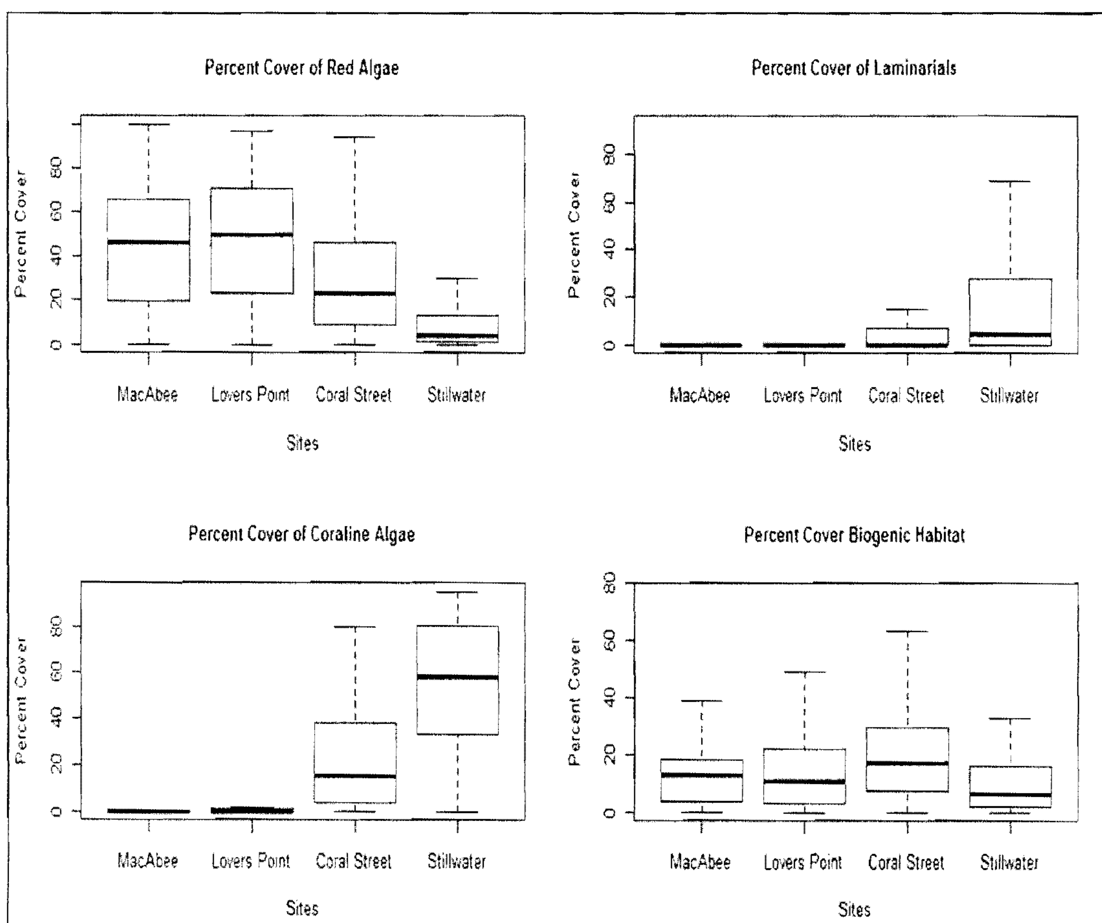

Figure 7: Boxplots of percent cover of habitat types from 100 random sampling points per quadrat; a) Red Algae, b) Laminarial Algae, c) Articulate Coralline Algae, d) Biogenic Habitat. ***denotes significant differences among sites.

All models included the spatial autocovariance structure to address the spatial autocorrelation (Table 5). Model comparisons for red algae showed VRM and TPI to be important predictor variables. However VRM alone is important variable (AIC_w 0.24, er 1.01) while TPI makes up a smaller contribution to the availability of red algae. The null model for laminarial algae was the strongest model and showed that spatial covariance is the only strong predictor of percent cover of laminarial species. Articulate coralline algae were best predicted by TPI measurements while the null model with spatial covariance best described biogenic habitat percent cover.

Table 5: AIC tables for model comparison of habitat availability for red algae, laminarials, articulate coralline algae, biogenic habitat.

	Model	df	AIC	AICc	delAIC	AICw	er
M0	glm(Reds ~ Spatial Covar)	3	104.2276	104.2889	2.145677	0.083664	2.923667
M1	glm(Reds~Spatial Covar+VRM+TPI+Slope)	6	103.8944	104.1103	1.967135	0.091476	2.673979
M2	**glm(Reds~Spatial Covar+TPI+VRM)**	**5**	**101.9893**	**102.1432**	**0**	**0.244606**	**1**
M3	glm(Reds~Spatial Covar+TPI+Slope)	5	104.4832	104.637	2.493848	0.070297	3.479624
M4	glm(Reds~Spatial Covar+VRM+Slope)	5	103.8746	104.0284	1.885251	0.095299	2.566712
M5	glm(Reds~Spatial Covar+VRM)	4	102.071	102.1733	0.030135	0.240948	1.015181
M6	glm(Reds~Spatial Covar+Slope)	4	104.5345	104.6368	2.493576	0.070306	3.47915
M7	glm(Reds~Spatial Covar+TPI)	4	103.7629	103.8652	1.721993	0.103405	2.365516

	Model	df	AIC	AICc	delAIC	AICw	er
M0	**glm(Laminarials~Spatial Covar)**	**3**	**3291.036**	**3291.098**	**0**	**0.352997**	**1**
M1	glm(Laminarials~Spatial Covar+VRM+TPI+Slope)	6	3296.163	3296.379	5.281211	0.025175	14.02169
M2	glm(Laminarials~Spatial Covar+TPI+VRM)	5	3294.37	3294.524	3.426617	0.063634	5.547285
M3	glm(Laminarials~Spatial Covar+TPI+Slope)	5	3294.165	3294.319	3.221749	0.070498	5.007188
M4	glm(Laminarials~Spatial Covar+VRM+Slope)	5	3294.897	3295.05	3.952942	0.04891	7.217229
M5	glm(Laminarials~Spatial Covar+VRM)	4	3293.03	3293.132	2.034783	0.127621	2.76597
M6	glm(Laminarials~Spatial Covar+Slope)	4	3292.904	3293.007	1.909073	0.1359	2.597466
M7	glm(Laminarials~Spatial Covar+TPI)	4	3292.396	3292.498	1.400333	0.175264	2.01408

	Model	df	AIC	AICc	delAIC	AICw	er
M0	glm(ArtCor ~ Spatial Covar,data=dat)	3	-85.16056	-85.09933	1.122697	0.184719	1.753035
M1	glm(ArtCor~Spatial Covar+VRM+TPI+Slope)	6	-82.88888	-82.67294	3.549087	0.054907	5.897587
M2	glm(ArtCor~Spatial Covar+TPI+VRM,data=dat)	5	-84.48313	-84.32928	1.892748	0.125689	2.576351
M3	glm(ArtCor~Spatial Covar+TPI+Slope)	5	-84.48714	-84.33329	1.888736	0.125941	2.571188
M4	glm(ArtCor~Spatial Covar+VRM+Slope)	5	-81.90204	-81.7482	4.473833	0.03458	9.36441
M5	glm(ArtCor~Spatial Covar+VRM)	4	-83.21385	-83.11155	3.11048	0.068371	4.736224
M6	glm(ArtCor~Spatial Covar+Slope)	4	-83.57675	-83.47445	2.74758	0.081973	3.950293
M7	**glm(ArtCor~Spatial Covar+TPI)**	**4**	**-86.32433**	**-86.22203**	**0**	**0.323819**	**1**

	Model	df	AIC	AICc	delAIC	AICw	er
M0	**glm(Biogenic Habitat~Spatial Covar)**	**3**	**-4015.971**	**-4015.91**	**0**	**0.384941**	**1**
M1	glm(Biogenic Habitat~Spatial Covar+VRM+TPI+Slope)	6	-4010.211	-4009.995	5.914571	0.020001	19.24566
M2	glm(Biogenic Habitat~Spatial Covar+TPI+VRM)	5	-4012.177	-4012.023	3.887162	0.05512	6.983717
M3	glm(Biogenic Habitat~Spatial Covar+TPI+Slope)	5	-4012.204	-4012.05	3.860017	0.055873	6.889569
M4	glm(Biogenic Habitat~Spatial Covar+VRM+Slope)	5	-4012.018	-4011.864	4.045827	0.050916	7.56032
M5	glm(Biogenic Habitat~Spatial Covar+VRM)	4	-4013.995	-4013.893	2.016864	0.140423	2.7413
M6	glm(Biogenic Habitat~Spatial Covar+Slope)	4	-4014.013	-4013.91	1.99973	0.141631	2.717914
M7	glm(Biogenic Habitat~Spatial Covar+TPI)	4	-4014.142	-4014.04	1.870359	0.151095	2.547671

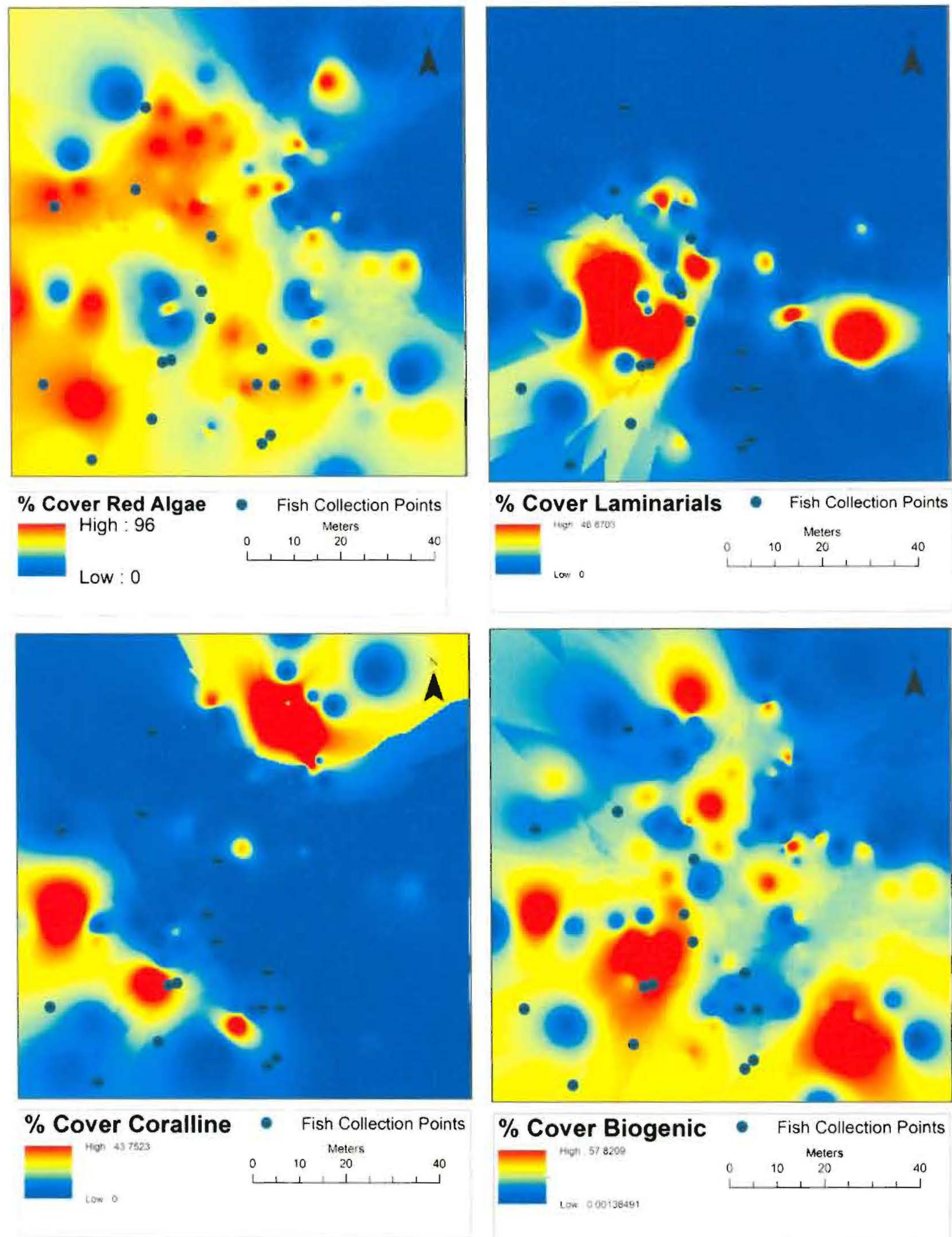

Figure 1: Interpolated raster models of percent cover of the four habitat variables a) Red Algae b) Laminarial Algae c) Articulate Coralline Algae d) Biogenic habitat at the Lovers Point research site. Each raster has the mapped points of fish caught at each site.

3.4 Prey Distribution

A total of 111 benthic samples were collected from all sites. There were 22 taxonomic groups that were identified and 51,465 individuals were counted. The majority were gammarid amphipods, which totaled 21,247 individuals. The total proportion of prey by taxon was dominated by gammarid amphipods (Figure 2). Fish diet data had a higher proportional number of gammarid amphipods (Figure 3). Dissections of fish showed that some individuals would have fewer amphipods in there stomach but would have several crabs. The crabs were significantly larger than amphipods and appeared to be a significant prey source in terms of biomass when available. As this trend was consistent across sites subsequent analysis of prey availability is restricted to crab and amphipod prey groups with the other prey groups excluded from analyses.

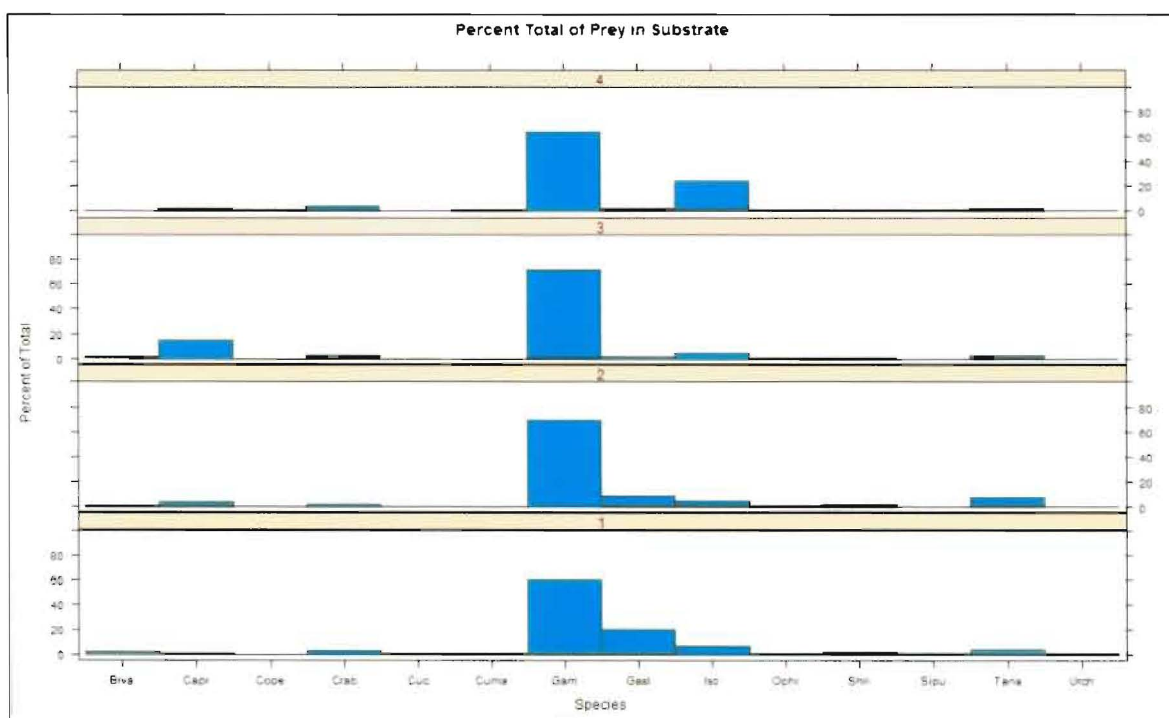

Figure 2: Proportion of prey by number in resource samples

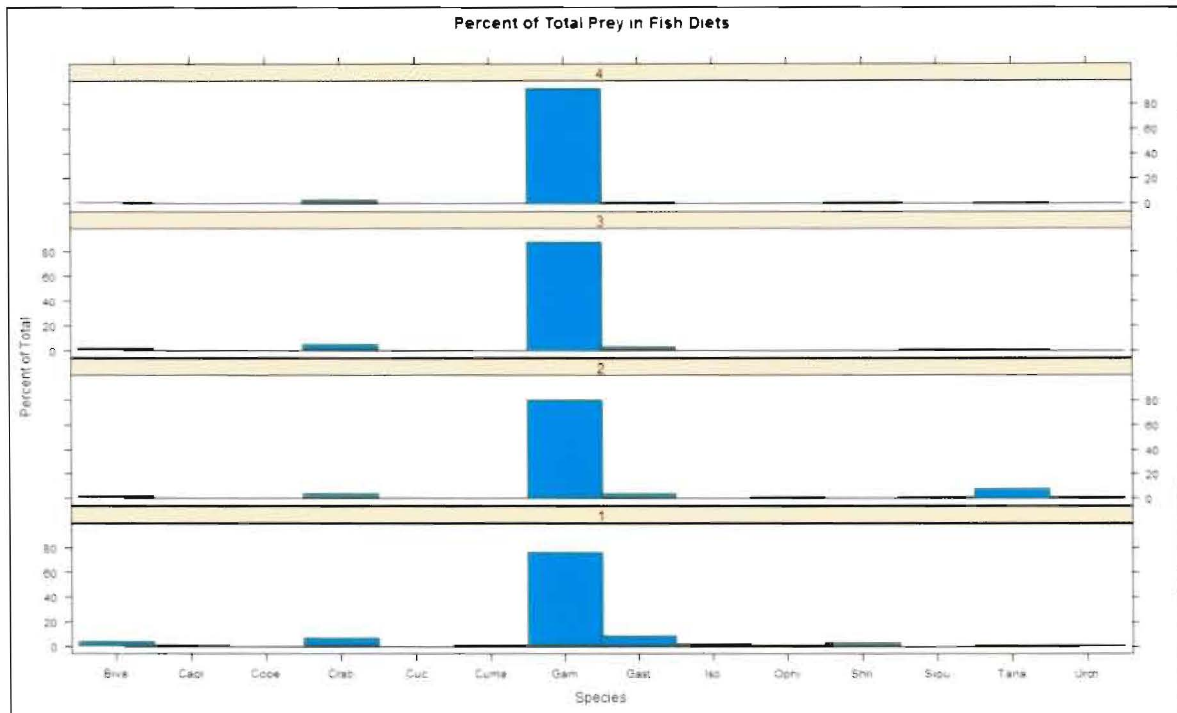

Figure 3: Proportion by number of prey items from a) resource samples and b) fish gut analysis.

Across sites, fish selected a similar proportion of crabs and amphipods in their diet. MacAbee had the greatest variation in diet among individuals and this variation among individuals' declines with successive sites sampled. Fish diets were increasingly dominated by Amphipods as sites were sampled from site 1 to site 4 (**Error! Reference source not found.**). Fish selected prey items that were on average larger than prey collected in the environment (**Error! Reference source not found.**).

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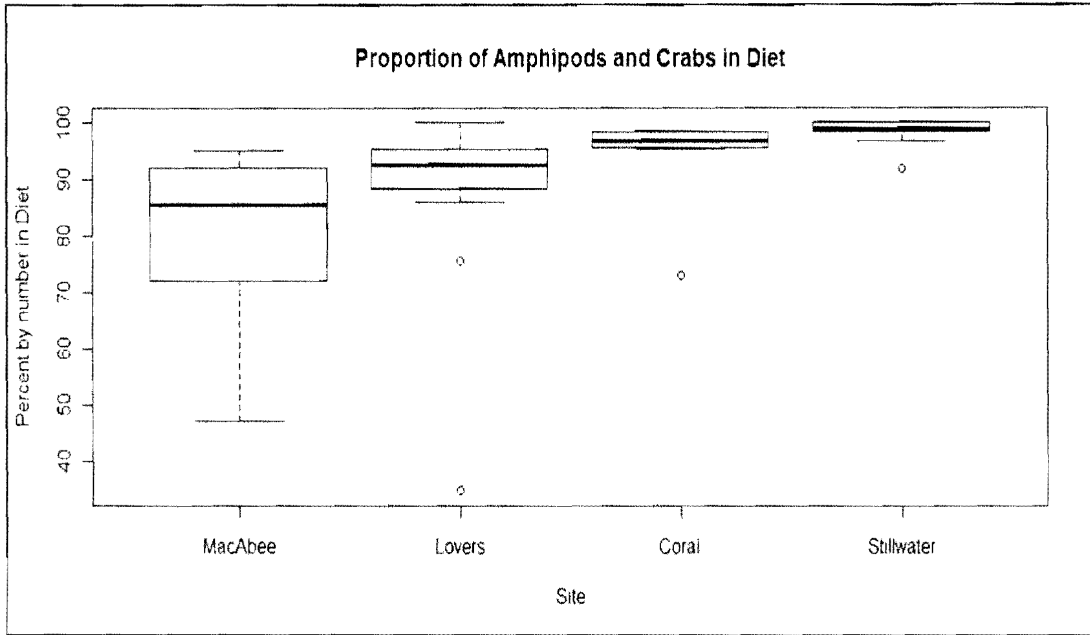

Figure 11: Proportion of gammarid amphipods and crabs in surfperch diet across research sites.

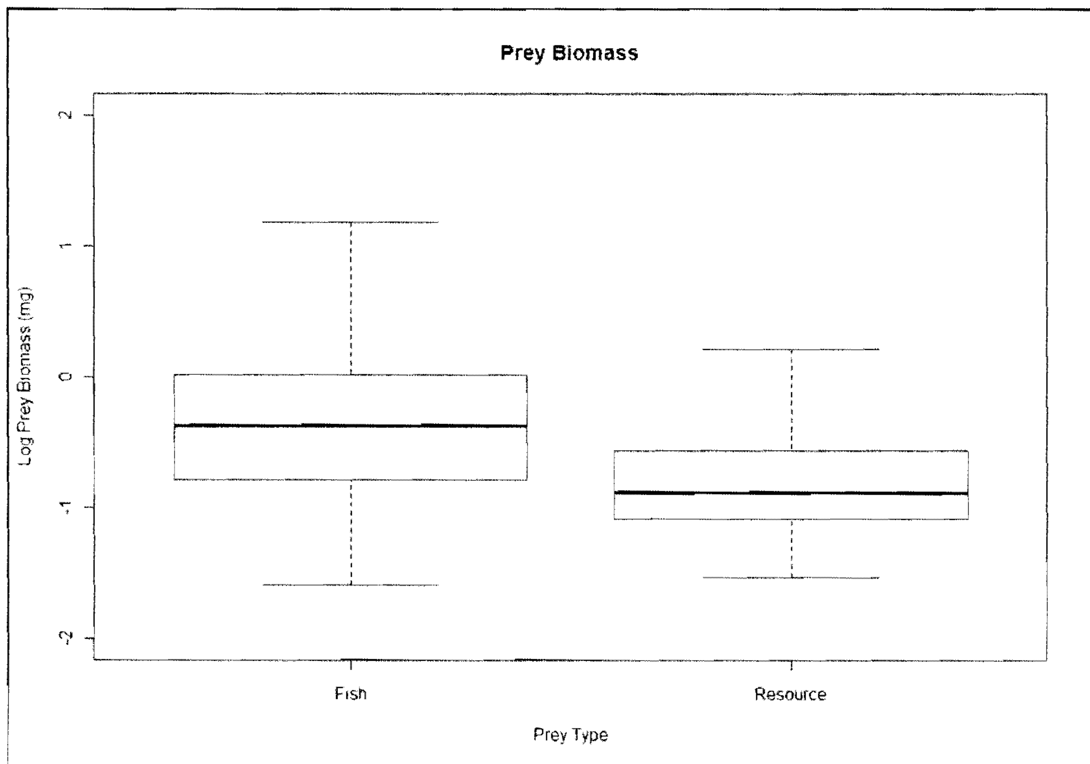

Figure 12: Mean differences in log transformed prey biomass between fish diets and resource availability.

For the resource prey availability model the stepwise regression demonstrated that red algae, VRM, and slope were significant contributors.

$$M_F: Resource\ Prey = \ Red + VRM + Slope$$

3.5 Genetic analysis

Multi-locus genotypes (11 loci) were obtained from a total of 64 individuals: 8 from Coral Street, 20 from Lovers Point, 18 from MacAbee Beach, and 18 from Stillwater cove. No evidence of linkage disequilibrium was found between any pair of loci, indicating independent segregation of alleles. Following correction for multiple tests, no significant departure from Hardy-Weinberg expected proportions was found in each sampled site. The microsatellite loci had relatively low levels of variation (i.e. 1–6 alleles per locus; mean allelic richness ranged between 1 and 5.3 alleles per locus), although moderate levels of expected heterozygosity were found (i.e. mean HE ranged between 0.2 and 0.9).

Fst values for the among and within population comparisons show no significant structuring among the four sites (Table 6). Splitting the sites into two regions, the Monterey region and the Carmel region, also did not show any structuring. *D* estimates were also non-significant and low for among sites and among regions comparisons.

Table 6: AMOVA table of within and among differences showing no among site differences.

AMOVA	Components	Sum of Squares	Varience Components	Precentage Variation
	Among populations	6.328	0.00061	0.02727
	Within populations	238.321	2.21894	99.97273
	Total	244.649	2.21955	

The site-specific GESTE *Fst* values were low (Table 7) and there was no significant structure among populations. GESTE analyses indicated that all combinations of factors received low posterior probability.

Table 7: Geste generated *Fst* values for research sites

Fst statistics

	mean	mode	95% HPDI
Coral Street	4.19E-22	4.19E-22	[4.19e-22-4.19e-22]
Lovers Point	3.08E-22	3.08E-22	[3.08e-22-3.08e-22]
MacAbee	2.43E-22	2.43E-22	[2.43e-22-2.43e-22]
Stillwater	2.98E-22	2.66E-22	[2.66e-22-3.61e-22]

4 DISCUSSION

The main goal of this study was to examine the linkages between the structural complexity, biogenic composition of the seafloor, and the population structuring of black surfperch populations using geospatial and genetic tools. This study demonstrated that the measures of structural complexity, VRM, TPI, and Slope, are useful for describing the distribution of both red algal and articulated coralline algal habitats. Red algal habitats were best described by VRM and TPI and articulated coralline algal habitats were best described by TPI alone. In this study, black surfperch were selective in prey choice with a significant preference for amphipods and crabs, which made up the largest proportion of prey in their diet. Surfperch also showed size selectivity choosing larger than average prey items from their environment. Models that included a combination of structural complexity and habitat composition, specifically red algal habitat cover, TPI and slope best described the density of both amphipods and crabs. However, there was no significant genetic differentiation detected among the different research sites. Model comparisons using differentiation measures were not successful in finding a non-trivial solution compared against the physical and biological variables. All models of genetic differentiation were significantly similar to one another and no single model was significantly better than any other model.

Structural complexity and habitat composition

Coarse scale habitat categorizations (i.e. rock and sand) are commonly used for subtidal systems such as for MPA designation for the Marine Life Protection Act (MLPA) process in California. The linkage of habitat composition to the structural complexity demonstrated in this study suggests that the underlying seafloor structure plays an important role in the distribution of biological habitat at a finer scale not captured by coarse habitat categorizations such as the one used in the MLPA process. This suggests that the likelihood of capturing targeted habitats in MPA's within a spatial region is dependent on the structural complexity of the underling seafloor not just the presence or absence of coarse habitat type alone, such as rocky reefs. Not all rock is equal as is implied by the broad

categorization of habitats that have been commonly used to date and the scale that an organism interacts with the environment drives the relationship between structural complexity and ecological patterns.

Structural complexity is an important habitat characteristic with many ecological roles. Increased complexity provides habitat structure, promotes species richness, and alters boundary-layer flow over the bottom (Butman et al. 1994; Green et al. 1998). The interaction of flow and substrate heterogeneity can affect settlement of larvae and algae (Hills et al. 1999; Lapointe and Bourget 1999) and subsequent population performance because it controls delivery of nutrients, oxygen, and chemical cues. VRM as an estimate of fine scale rugosity, and TPI as an estimate of coarser scaled peaks and valleys, together were useful for describing multiple scales of structural complexity and describing their influence on red algal species distribution. These measures of complexity together suggest that red algae are strongly linked to the seafloor structure at both coarser and finer scales.

In this study, the percent cover of red algae differed among sites with greater percent cover at the MacAbee and Lovers sites with percent cover declining significantly at Coral Street and Stillwater Cove sites. Wave exposure was not incorporated in this study; however, it likely plays a significant role in the differences among sites in the observed cover of red algae. Red algae may require a minimum amount seawater current flow along the seafloor for both optimal establishment and growth while over a certain threshold may reduce percent cover through physical disturbance. In contrast, articulated coralline algae may require flow dynamics that are opposite that of red algae, which require greater current flow for optimal establishment and growth. Peaks and valleys may provide a refuge or alter flow regime, increasing it in areas, preferred by articulated corallines. However, at sites with high exposure in may decrease flow rates offering refuge for reds and at sites with lower exposure in may increase flow rates for reds.

Vector ruggedness measure was most strongly linked to red algae. This suggests that finer scaled habitat complexity was important to the red algae group. This may be due to the increased surface area a highly complex seafloor has for algal attachment. It may also play part in the importance of current flow regimes important to red algae. The seafloor current flow pattern may become more dynamic with a more structurally complex seafloor. This has implications to not only red algal species but also other species that are

dependent on complex flow patterns for larval settlement, nutrient, oxygen, and chemical cue flow dynamics.

Percent cover of articulated coralline algae was best predicted by TPI alone. TPI is a measure of peaks, valleys, and plains. This measure may indirectly measure areas of high or low seafloor current flow. While TPI may relate to high or low flow areas, the sites overall exposure will best describe seafloor current patterns. As current flow is important to formation of articulated coralline patches and this study did not include measures of current flow at research sites we may have missed important ability to predict. However, being able to detect differences using TPI alone demonstrates that peaks and valleys may play an important role in finer scale hydrodynamics and therefore may play and indirect roll in abundance of articulated corallines or similarly dependent seafloor communities. In this study, there was an obvious difference among sites with an increase in coralline algae with an increase in exposure of the sites. Both Coral Street and Stillwater showed significantly greater amounts of articulate coralline than either MacAbee or Lovers (Figure 7) and both were relatively exposed sites that received greater ocean swell on average throughout the year (pers. Obs) with greater intensity and duration of high swell periods.

Two of the habitat types, laminarials, and biogenic habitat were best described by spatial autocovariance alone suggesting that the spatial patterns of sampling were tightly linked to the spatial distribution of Laminarial cover. Laminarials were relatively rare and occurred in clusters when they were found. This strong spatial structuring of occurrence likely overwhelmed all of the other predictor variables included in the models. At the other end of the spectrum, the biogenic habitat classification was a coarse categorization with distribution patterns being moderately common and evenly spread throughout all of the research sites. This category may have been too broadly distributed to detect links to any of the physical variables. Breaking this group into subcomponents may assist in generating patterns that would provide a better comparison within the models used in this study.

Black surfperch are generalists but will be selective when able to choose preferred prey. They winnow food, taking large chunks of the seafloor, spitting out inorganic material and taking in the rest. There were large amounts of shell and sand debris in the stomach contents. Analysis of surfperch diets demonstrated that gammarids were the dominant prey species by number of individuals but that some individual fish

supplemented their diets heavily with crabs, which were fewer in number but significantly larger and likely greater nutritional value. A few crabs were the equivalent of many amphipods by weight. While other species were present in their diets, there was no single group that appeared consistently among individuals or varied greatly across sites.

Average prey biomass was not significantly different among sites while fish selected prey items were larger on average than the prey available in the environment. The pattern of distribution of prey species was similar among sites with some small differences in proportion of prey with gammarid amphipods dominating the prey groups. Percent cover of red algae, VRM, and slope best described prey availability. However, red algae cover is linked to VRM, which suggests colinearity. This makes interpretation difficult as the predictor variables are not independent of one another and the relative influence hard to determine. However, it is appropriate to say that prey availability can be described by the abundance of red algae, VRM, and slope and that red algae can be described by VRM and TPI. This demonstrates the importance of the physical parameters measured in this study to the abundance and distribution of prey items for black surfperch.

Understanding genetic structuring of populations can provide insight into the processes involved in creating and maintaining genetic diversity. This understanding is critical for improving ecological knowledge of and improving management of genetic diversity of populations (Moritz 2002; Manel et al. 2003). Furthermore, identifying subpopulations among what are assumed to be single populations also have significant implications in the management of many marine species. Accurate predictions of species habitat relationships allow for potential mapping of individual species' distributions and justify the increasing use of habitat-based management approaches (Stoner et al. 2001; Valavanis et al. 2004) and the use of habitat classifications for marine park planning (Ward et al. 1999). Black surfperch give birth to live young have low mobility as adults and population structuring has been demonstrated at relatively small spatial scales (km's). I postulated that I should be able to detect structuring among my research sites, separated by 16km's broken up by stretches of sandy beaches that are not suitable habitat for this species. However, the genetic data demonstrated that population structuring was not occurring at the scale at which this study examined local black surfperch populations. This unexpected result may point to greater movement of black surfperch and suggests that

stretches of inhabitable sand may not be a barrier. Hixon (1981) demonstrated that this species had small home ranges (50m) with movement between adjacent reefs while Bernardi (2000) demonstrated that significant stretches of sandy seafloor, such as Santa Monica bay, can act as a barrier to migration. This study demonstrates that at a local scale contiguous stretches of rocky reef allow these fish to move more frequently and further distances on average than expected. While it is important to note that a single individual per generation, migrating from one population to another, will swamp a detectable genetic signal of population structuring between the two areas, this appears to be occurring across both sandy stretches and at distances thought to act as barriers. This may be the result of enough rocky pathways throughout the region that relatively rarer migration events across uninhabitable stretches are more likely to occur. Black surfperch have short life spans meaning that this movement occurs more regularly than previously thought. Having a more balanced sampling design between each side of the Monterey peninsula may have strengthened my ability to determine genetic differences among the areas. The maximum geographic distance between populations was 15 km while three of the four sites were within 4km of each other. It only takes one migrant per generation to swamp out the ability to detect genetic structuring and a greater spatial scale may be necessary to detect ongoing genetic structuring. The barriers along the Monterey peninsula may not have been significant enough to prevent small spatial scale movement of individuals at a generational temporal scale.

Discontinuities and spatial variation in the structural complexity and biogenic composition are important in the ecological dynamics that may result in population structure at local scales. However, understanding the scale at which population structure can be detected compared with the scales at which the population dynamics that lead to structuring is critical to estimate any linkages between the environment and populations. Landscape heterogeneity may lead to populations of a species becoming subdivided in sub-assemblies with differing population dynamics and selective pressures (Endler 1991) but determining the scales that this occur is a difficult task. Differing selective pressures may lead to genetic pools that are heterogeneous across their distributional range (Burton 1983; Reeb and Avise 1990; Borsa et al. 1997; Neigel 1997) but detecting the breaks between these pools requires sampling across a number of pools at scales both at the organismal

level and across local scales. The resulting genetic heterogeneity may be due to several non-random factors including selection through local adaptation (Hedgecock 1986; Knowlton and Keller 1986), genetic drift through barriers to connectivity (Gaggiotti et al. 2009; Galarza et al. 2009), or demography and life history (Hemmer-Hansen et al. 2007; Gaggiotti et al. 2009).Understanding genetic structuring of populations give us insight into the processes involved in creating and maintaining genetic diversity. However, understanding the process and patterns of gene flow and local adaptation requires a greater understanding of how landscape characteristics influence population structure. This understanding is critical for improving ecological knowledge of and improving management of genetic diversity of populations (Moritz 2002; Manel et al. 2003)

This study has demonstrated that indexes of complexity created from fine scale bathymetric data can be used to describe biological habitat distributions. These in turn can be used to describe prey availability for black surfperch. This study has also demonstrated a methodology to take landscape genetics into the nearshore marine environment and begin to ask questions about the importance of the landscape itself on marine populations by measuring genetic structuring. The landscape component of this study has demonstrated the linkages between biological composition and structural complexity and that this relationship is dependent ecological requirements and physical dynamism of areas chosen.

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