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SPINY LOBSTER (*PANULIRUS INTERRUPTUS*) USE OF THE INTERTIDAL ZONE AT A
SANTA CATALINA ISLAND MPA IN SOUTHERN CALIFORNIA

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

Applied Marine and Watershed Science

by

Sean C. Windell


Fall 2015

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

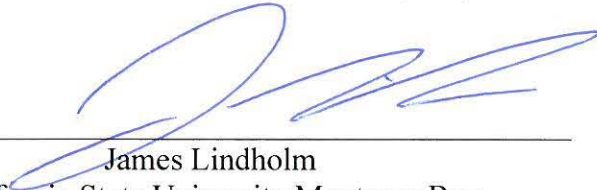
The Undersigned Faculty Committee Approves the

Thesis of Sean Windell:

THE VALUE OF HABITAT DIVERSITY IN MARINE RESERVES: SPINY
LOBSTER USE OF THE INTERTIDAL ZONE AT THE SANTA CATALINA
MPA



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Approval Date

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by

Sean C. Windell

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DEDICATION

For my parents, Terry Windell and Annick Therrien, and their love and support for me.

“There is nothing like looking, if you want to find something. You certainly usually find something, if you look, but it is not always quite the something you were after.”

- J.R.R. Tolkien, *The Hobbit*

ABSTRACT

Spin Lobster (*Panulirus interruptus*) Use of the Intertidal Zone
at a Santa Catalina Island MPA in Southern California

by

Sean C. Windell

Master of Science in Applied Marine and Watershed Science
California State University Monterey Bay, 2015

This study investigated spiny lobster (*Panulirus interruptus*) use of the intertidal habitat as an important and underappreciated foraging ground during the reproductive season, and the spatial scales over which lobsters interacted with this habitat at two locations off Santa Catalina Island, California. At Bird Rock and Big Fisherman Cove, there were significantly higher densities of lobsters within the intertidal zone at night compared to the adjacent subtidal zone, as well as a higher density of reproductively active (egg-carrying) females, suggesting the non-trivial use of this habitat. Spiny lobster density, size, sex ratio (in favor of females), and reproductive condition were also higher at Bird Rock, reflecting differences in the underlying intertidal habitat composition between locations. Percent cover of the California mussel (*Mytilus californianus*) exhibited a significant positive correlation with lobster density, and the elevated abundance of this preferred prey item might explain the enhanced lobster population metrics at Bird Rock. In addition, the spatial distribution of mussels on Bird Rock followed a clumped distribution with discrete patches at a sub-meter scale, which may influence the spatial scale of spiny lobster foraging behavior. The results of this study highlight a critical new dimension of spiny lobster management throughout Southern California, encouraging the consideration of the intertidal zone and the effects of prey distributions on foraging behavior.

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INTRODUCTION

Many organisms utilize multiple critical habitats throughout their life-cycle, either at different life-stages or for different behavioral purposes (foraging, reproduction, shelter, etc.) (Roberts 2000; Roberts et al. 2003). Ontogenetic shifts in habitat use typically differ between juvenile and adult stages for many marine species. For example, rearing juvenile flatfish occupy shallow coastal and estuarine nursery grounds while the adults reside in deeper offshore waters (Reichert and van der Veer 1991), and rearing juvenile tropical reef fish occupy seagrass beds or mangroves while adults reside on coral reefs (Cocheret et al. 2003). Behavioral shifts in habitat use commonly occurs temporally and cyclically, such as the seasonal outmigration of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) into the open ocean and the return of adults to freshwater to spawn (Williams 2006), and the migration of gray whales (*Eschrichtius robustus*) northwards in summer to forage in the Bering and Chukchi Seas and southwards in winter to calve offshore the west coast of Baja California (Rice et al. 1984). In order for a species to persist temporally and spatially, each critical habitat needs to be in a suitable condition that can support that particular life-stage or behavior. Temperate and tropical fish populations are harmed if nursery habitat is lost, Chinook salmon populations are negatively impacted if there is limited access to spawning grounds, and gray whale migratory patterns may change if their food source becomes unreliable. Such spatial and temporal shifts in habitat use are triggered by a multitude of factors, such as climate driven changes within the environment, periodic access to critical habitat, the availability of food, or the need for protection and energy conservation during reproduction.

The movement of a species between distinct habitats provides cross-system subsidies that allows a population to persist at higher densities than possible if it were in an isolated habitat (Polis and Strong 1996; Polis et al. 1997). This is particularly apparent in the movement of prey or consumers across habitats (Fagan et al. 1999). Krill (*Euphasea sp.*) move annually offshore from the Antarctic ice shelf into the open ocean, subsidizing their diet of algae with zooplankton (Smetacek et al. 1990), while also acting as a subsidized food source for migrating whales. In the West Indies, coral reef residing

parrotfishes (*Scarus sp.* and *Sparisoma sp.*) and surgeonfishes (*Acanthurus sp.*) will subsidize their diet through foraging diurnally in adjacent sea grass beds (Randall 1965). These cross-system movements and subsidies can maintain a species' population in a habitat too small or unproductive on its own, or provide additional resources during periods of high energetic demand, such as when reproducing (Polis 1997).

To comprehensively understand how the environment is influencing a species' behavior and distribution, it is important to consider the multiple spatial scales of species-environment interactions within each of the multiple habitats a species utilizes throughout its life-cycle, especially in regards to management intended to protect that species (García-Charton et al. 2000; Aíramé et al. 2003). Depending on the characteristics of certain important habitat features, such as the distribution of prey or the physical complexity of the landscape, a species interacts with its surrounding habitat across multiple spatial scales (Poff 1997; Garza 2014). The spatial scale of a particular habitat feature (or features) drives the spatial scale of a species' response, and varies with differences between habitats and between patches within habitats (Finlayson et al. 2008). For example, medium-sized marsupials in Australia (such as the burrowing bettong, *Bettongia lesueur*, brush-tailed button, *B. penicillata*, greater bilby, *Macrotis lagotis*, and bridled nailtail wallaby, *Onychogalea fraenata*) were observed to preferentially select particular macrohabitats to rest in during the day, and the spatial scale of this available resting habitat likely influenced the magnitude of competition between these species (Finlayson et al. 2008). Foraging habitat in particular influences a species' behavior through scale-dependent responses to the spatial distribution of its food source (Pinaud and Weimerskirch 2007). In the Pacific Ocean, the distribution of jellyfish drives the distribution of leatherback turtles (*Dermochelys criacea*), where leatherbacks are attracted to consistent hotspots of jellyfish presence in space and time (Houghton et al. 2006). Species can also respond to multiple habitat features within a particular environment in a hierarchical manner depending on the strength of influence of each feature. Knegt et al. (2011) showed that African elephants (*Loxodonta Africana*) prioritized searching for water over foraging for food, with the search for water occurring at a relatively finer spatial scale, thus revealing a hierarchical and scale-dependent response to the surrounding environment.

The California spiny lobster (*Panulirus interruptus*), though typically considered a subtidal species, will utilize multiple distinct habitats throughout its life-cycle, potentially interacting with each of these habitats at multiple spatial scales. Previous studies have documented spiny lobsters utilizing the intertidal zone on Santa Catalina Island (Robles 1987; Robles and Robb 1993; Robles et al. 2001), revealing that spiny lobster intertidal abundance peaks during the breeding season. These studies suggest that the intertidal may provide vital habitat to support the energetic requirements of lobster reproduction. The intertidal habitat supports mussel beds and algal turf communities that provide prey for spiny lobsters (California mussels, *Mytilus californianus*, shore crabs, *Pachygraspus crassipes*, limpets, *Collisella limatula* and *scabra*, and chitons, *Mopalia muscosa* and *Nuttallina californica*), potentially serving as a critical foraging habitat within the life-cycle (Robles and Robb 1993; Robles et al. 2001; Smith et al. 2008). Gut content analyses and *in situ* lobster exclusion experiments have demonstrated that spiny lobsters preferentially feed on the California mussel when available (Robles 1987; Robles et al. 2001), thereby acting as a keystone predator upon intertidal mussels at wave-exposed sites (Robles and Robb 1993). The spatial distribution of mussels could be influencing the spatial scale at which spiny lobsters are interacting with the intertidal habitat as a result of this directed change in their foraging behavior. Where mussels are absent in the intertidal, it is likely lobsters direct their foraging efforts towards their other prey source of algal turf communities, potentially producing a scale-dependent and hierarchical response depending on the distribution and availability of these habitat features.

The importance of the intertidal habitat and the role of scale in driving habitat utilization was explored through *in situ* observations of the California spiny lobster at two separate locations on Santa Catalina Island. This study sought to characterize the extent to which lobsters utilized the intertidal zone, and to evaluate the scale at which lobsters interacted with particular habitat features at these two locations. It was hypothesized that lobster density, size, sex ratio (in favor of females), and reproductive condition would be greater within the intertidal zone when compared to the adjacent subtidal zone, and this pattern would reflect underlying differences within the intertidal habitat. The intertidal habitat composition was measured at a sub-meter scale resolution to quantify the

variability in percent cover of various habitat features (i.e. macroalgae, barnacles, bare rock, etc.), including potential prey sources (mussel beds, turf algae) between locations, and to estimate the scale at which lobsters were potentially interacting with those habitat features (sub-meter or greater).

METHODS

Study Area

The study area was located on Santa Catalina Island, about 20 nautical miles offshore of Los Angeles, California, at Big Fisherman Cove (33°26'37" N, 118°29'05" W) and Bird Rock (33°27'03" N, 118°29'15" W; Fig 1). The specific sites selected were based on previous studies of the intertidal at Catalina and built upon previous data sets (Robles 1987; Robles and Robb 1993; Robles et al. 2001). Big Fisherman Cove has been part of a marine reserve since 1988 and is home to the USC Wrigley Institute for Environmental Studies (WIES). Big Fisherman Cove is largely protected from swell, leaving it relatively calm with little wave action. Bird Rock, an islet located several hundred yards offshore, was open to fishing until the recently established Blue Cavern State Marine Conservation Area (SMCA) was designated by California's Marine Life Protection Act in 2012, fully protecting it (CDFW 2015). Three sites on Bird Rock were located on the west face and were more exposed to swell and wave action compared to the three sites located on the southern wall of Big Fisherman Cove (Fig 1). The Bird Rock sites also fell along an exposure gradient that was greatest at the northwest end, and smallest at the southeast end (Robles et al. 2001). Other potential sites within the reserve were considered, but these areas were ruled out due to the steep slope and narrow width of the intertidal bench, and were thus not comparable to the historically used sites.

Study Species

The southernmost distribution of spiny lobsters is along the coast of Baja California and within the Gulf of California, and extends northward to San Luis Obispo Bay. Multiple habitats are utilized throughout the spiny lobster's life-cycle, each playing a role in the success of the next life stage. Spiny lobsters spawn in deep water from December to March, and migrate into shallower waters inshore throughout April and

May, with female lobsters carrying anywhere between 50,000 to 800,000 eggs (Engle 1979). The eggs then hatch into planktonic larvae by late August, where they spend up to 8 months in the water column before settling out onto shallow rocky reefs as juveniles (Iacchei et al. 2013). Juvenile lobsters preferentially recruit into shallow nursery habitat that consists of thin-bladed, densely matted plant cover, such as surf grass (*Phyllospadix scouleri*), where they spend 2 to 3 years rearing before moving into deeper waters (Engle 1979). Spiny lobsters are an economically important fisheries species, both commercially and recreationally in Southern California, with a consistent commercial harvest weight of 660,000 lbs per season (Nielson 2011; Hackett et al. 2013). Spiny lobsters also hold an ecologically significant role within kelp forest communities as a keystone predator, predated upon and suppressing urchin populations, which allows kelp forests to thrive (Paine 1974; Dayton et al. 1998).

Intertidal/Subtidal Spiny Lobster Surveys

Intertidal and subtidal surveys of spiny lobsters were used to quantify (1) density, size, sex ratio, and reproductive condition (the presence or absence of eggs on females) in the intertidal zone relative to the subtidal, and (2) density, size, sex ratio, and reproductive condition (collectively referred to as population metrics from hereafter) between Big Fisherman Cove and Bird Rock. Surveys consisted of abundance counts and hand-collections during the peak of spring high tides, with two samples collected in 2012 and one sample collected in 2013. Each location consisted of 3 sites (A, B, and C) containing two fixed 20 m band transects; one positioned in the intertidal approximately 1.2 m above mean lower low water (MLLW), and the other in the adjacent subtidal at an approximate depth of 3 m. All surveys were conducted on SCUBA, with count surveys occurring within a 24 hour cycle for day and night comparisons, and hand collections occurring only at night when the lobsters were active. The width of each intertidal transect was determined by the high water mark and the edge where turf algae meets understory algae, an approximate width of 4 m, which was also the approximate width for each subtidal transect. Count surveys yielded lobster measurements of density, and hand collection surveys yielded measurements of size, sex, and reproductive condition. Samples were collected in June and July as previous work revealed that peak lobster foraging activity within the intertidal took place during the late spring and summer

months (Robles 1987; Robles and Robb 1993; Robles et al. 2001). Lobsters were assumed to be foraging within the intertidal due to evidence from previous studies confirming the consumption of intertidal prey through gut content analysis and *in situ* lobster exclusion experiments (Robles 1987; Robles and Robb 1993; Robles et al. 2001). Surveys were conducted during the night and day, to confirm that lobster activity occurred only at night due to their nocturnal behavior (Robles 1987).

Intertidal Habitat Composition Surveys

Intertidal habitat surveys were conducted to determine what benthic habitat features (biotic or abiotic characteristics) influenced lobster abundance, and the spatial scale at which these habitat features occurred. Intertidal habitat composition was classified and measured for both study years using digital photographic transects. Photographic transects were 20 m in length taken at an approximate height of 1.2 m above MLLW, the estimated upper limit of *Mytilus californianus* (Robles 1987). Each photograph within a transect consisted of a 1 m² quadrat delineated by four cones at each corner, taken approximately 1.5 m above the ground. A Total Station laser surveyor (TOPCON[®]) measured the X, Y, and Z coordinates of each cone of each quadrat (control points), thereby georeferencing each photograph to create a photographic representation of each intertidal transect within ArcMap 10.1. Cover type and species were classified at a resolution of 5 cm, as well as the percent cover of each classification. Mussels (*Mytilus californianus*), barnacles (*Tetraclita rubescens*, *Chthamalus fissus*) and macroalgae (*Silvetia compressa*, *Phyllospadix scouleri*) were classified down to species, and all algae that were under 5 cm tall were labeled as Turf. The use of photo transects within a Geographic Information System (GIS) allowed for the capability to capture more data at a high spatial resolution and shorter timeframe than traditional *in situ* approaches. This was especially beneficial considering the time constraints associated with conducting work in the intertidal zone. The use of GIS was also beneficial for the identification of spatial scales lobsters were potentially interacting with the intertidal habitat through the use of spatial statistic tools.

Traditional physical quadrats measured *in situ* were also conducted during 2013 to groundtruth what was identified within the photo transects and provided a comparison

in the measurements of each methodology. *In situ* quadrats were 121 cm² and percent cover of benthic taxa were recorded at every meter along each transect, giving a total of 20 quadrats per transect. Percent cover was estimated visually within each quadrat.

Vector Ruggedness Measure

Terrain ruggedness at the meter scale was measured for each photographic transect in ArcMap using the Vector Ruggedness Measure (VRM) tool. Terrain ruggedness is a measure of variation in the three-dimensional orientation of the grid cells within a specified neighborhood. The VRM tool captured the variability of aspect and slope into a single measure, allowing for the quantification of landscape ruggedness (Sappington et al. 2007). The Inverse Distance Weighted (IDW) tool was first used in ArcMap to interpolate the elevation values of the control points across the rest of the transect space at a resolution of 10 cm. The VRM tool was then run with a Neighborhood size of 3. These VRM values were averaged for each photo transect in order to be used as a predictor variable in the subsequent statistical analyses.

Statistical Analyses:

Spiny Lobster Migration, Use of Intertidal Zone, Density, Size, Sex Ratio, and Reproductive Condition

It was predicted that lobsters in the subtidal zone were migrating relatively short distances to forage in the adjacent intertidal zone. A two-way ANOVA tested for differences in lobster density between Time (Day vs Night) and Zone (Intertidal vs Subtidal), capturing when lobsters were most active and whether densities were comparable between Time or Zones.

Lobster use of the intertidal zone was determined by calculating the percent time available to forage in the intertidal habitat within a calendar year, during the breeding season (May through August), and when nocturnally active during the breeding season (between sunset and sunrise from May through August). Lobsters were considered to have access to the intertidal habitat during the period when a spring high tide cycle was between 1 m and 1.5 m or greater. Lobster access into the intertidal habitat was assumed to be restricted between sunset and sunrise since lobsters are nocturnal and actively

foraging at night. The total amount of time within these conditions was calculated using tide tables for the year 2013, which was then divided by the total time of one year, the length of the breeding season (all days between May and August), and the total time of the breeding season between only sunrise and sunset to yield percent use for these various periods of time.

A two-way ANOVA tested for differences in lobster density between the intertidal and subtidal zones and between the locations Big Fisherman Cove and Bird Rock. Kolmogorov-Smirnov (KS) two-sample tests tested for differences in lobster size-frequency between locations and between the zones for each location, resulting in a total of three tests. Chi-Square analyses of 2 x 2 contingency tables tested sex-ratio (male vs female) and reproductive condition (presence vs absence of eggs on females) between locations and between zones for each location, resulting in a total of six tests. If the expected cell frequencies were less than 5, a Fisher's exact test was used.

Intertidal Habitat Composition

Photographic transects were summarized and statistically compared with *in situ* 121 cm² quadrats using a Student's t-Test to assess the benefit of using geographically referenced photographs in the place of traditional physical quadrats. The magnitude of differences between methodologies shed light into the level of accuracy of intertidal habitat representation of each technique.

A non-metric multidimensional scaling (nMDS) analysis of the photographic transects tested for differences in intertidal benthic habitat composition between locations, providing interpretation of any differences within lobster population metrics between locations. The data were square-root transformed and then underwent a Wisconsin double standardization before the stress value was tested.

A linear mixed effects model tested which intertidal habitat cover types influenced intertidal lobster density, providing evidence for which cover types were driving differences within lobster population metrics between locations. The sites at each location were spatially close, and thus percent cover estimates were likely autocorrelated. Therefore, site was incorporated into the statistical models as a random factor to account

for any spatial autocorrelation that may have existed. The predictor variables used were percent cover of Turf Algae, *Mytilus californianus*, *Tetraclita rubescens*, *Chthamalus fissus*, *Silvetia compressa*, Foliose Red Algae, Bare Rock, and VRM. Each predictor was measured as percent cover and Arcsine transformed (except for VRM, which was averaged across each transect). Akaike's Information Criterion (AIC) then determined which model was the best fit to the data (Burnham and Anderson 2002). The value of AICc (AIC corrected for finite sample sizes) was used to determine the best fit model by selecting the AICc with the lowest value amongst all the models. Models that had a ΔAIC value ≥ 2 were considered significantly different from each other, and models that had a ΔAIC value < 2 were considered statistically indistinguishable. This analysis was conducted at a spatial scale of 80 m².

A Hot Spot analysis was performed within ArcMap 10.1 for parameters significantly correlated with lobster abundance to estimate whether lobsters were interacting with these habitat features at a sub-meter scale or greater, and if lobsters were interacting with the intertidal habitat at multiple spatial scales. The Getis-Ord G_i^* statistic with a Threshold Distance of 10 cm was calculated within ArcMap 10.1 for each significant habitat feature to determine if it exhibited any spatial clustering at a sub-meter scale, thereby informing the scale of lobster interaction with that habitat feature (sub-meter or greater). This analysis was paired with the results of a complimentary study determining the trophic interactions of the same lobsters using stable isotope analysis, providing inference into the potential spatial scale lobsters were interacting with particular prey items.

All statistical analyses were conducted using R statistical software (R Core Team 2012). All p-values were calculated with a significance threshold of $\alpha = 0.05$.

RESULTS

Spiny Lobster Migration

Lobster densities did not show a consistent trend for density in relation to time of day and zone (Table 1). During the day lobsters did not occur in the intertidal zone and

were found to only occupy the subtidal zone, often sheltering within the cracks and crevices of rocky habitat. In contrast, lobsters were active during the night in the intertidal and subtidal zones (Fig 2a). Lobsters were completely exposed from rocky sheltering habitat when active in the intertidal zone, and were generally foraging underneath macroalgae (surf grass, *Phyllospadix scouleri*, southern sea palm *Eisenia arborea*, and the invasive *Sargassum horneri*) when active in the subtidal zone. Subtidal lobster density decreased by 44% from day to night, while the intertidal zone experienced a large influx of lobsters. At night, intertidal lobster density was 26% greater than subtidal lobster density, and was 75% of the density of daytime subtidal lobsters.

Lobster use of Intertidal Zone

Intertidal habitat availability for lobster use, based on the conditions that access was possible when a tide cycle was between 1 m and 1.5 m or greater at night, was calculated in relation to an entire calendar year, the duration of the breeding season (May through August), and the duration of the breeding season between only sunset and sunrise. Lobsters had access to the intertidal zone for approximately 2.7% of the time of a calendar year, 7.9% of the time throughout the breeding season, and 46.6% of the time throughout the breeding season when focusing between sunrise and sunset. Considering all times of the day, the potential use of the intertidal zone was relatively small throughout the entire year and breeding season. When focusing the availability of the intertidal habitat to when lobsters were likely foraging during the breeding season (at night), the potential use of this habitat increased dramatically (46.6%).

Lobster Density

Lobster density at night was significantly higher within the intertidal zone compared to the subtidal zone at both locations (Table 2, Fig 2b). There were 48% more lobsters in the intertidal zone compared to the subtidal zone at Big Fisherman Cove, and 55% more lobsters in the intertidal zone compared to the subtidal zone at Bird Rock. This pattern was more pronounced at Bird Rock than in Big Fisherman Cove (Table 2, Fig 2b), revealing a significantly higher density of lobsters at this location. Lobster density within the intertidal zone was 67% higher at Bird Rock compared to Big Fisherman Cove, and total lobster density for both zones was 66% higher at Bird Rock.

Lobster Size

Lobster size distributions between locations were significantly different from each other, due to Bird Rock containing larger lobsters (2-sample KS test, $D = 0.23$, $p = 0.03$; Fig 2c). Lobsters at Bird Rock had an average carapace length of 8.83cm, while lobsters at Big Fisherman Cove had an average carapace length of 8.17 cm. Lobsters at Bird Rock were on average .66 cm larger in carapace length. Lobster size distributions were not significantly different between the intertidal and subtidal zones within each location.

Lobster Sex Ratio and Reproductive Condition

Lobster sex-ratio was more skewed towards females at Bird Rock compared to Big Fisherman Cove (Chi-squared test, $X^2 = 17.36$, $p < 0.001$; Fig 3a). Of the lobsters collected at Bird Rock 77% were female, while at Big Fisherman Cove 44% of lobsters collected were female. Lobster reproductive condition was also greater at Bird Rock compared to Big Fisherman Cove (Fisher's exact test, $X^2 = 0.09$, $p = 0.01$; Fig 3b). Of the collected female lobsters at Bird Rock 97% were carrying eggs, while at Big Fisherman Cove 78% of female lobsters were carrying eggs. Lobster sex ratio and reproductive condition were consistent between the intertidal and subtidal zones at both Bird Rock and Big Fisherman Cove. However, there was a higher abundance of total lobsters collected in the intertidal at both locations.

Intertidal Habitat Composition

When comparing the accuracy of the *in situ* quadrats with the photographic transects, the *in situ* quadrats underestimated the presence of algae (Turf, $p = 0.004$ and *Silvetia compressa*, $p = 0.088$), and overestimated the cover of bare rock ($p = 0.047$). The higher resolution and greater spatial coverage of the photographic transects was also able to capture a higher percent cover of *Mytilus californianus* (4.2%) compared to the *in situ* quadrats (1%; Fig 4a), which only occurred on transect C of Bird Rock. Due to the small or non-existent cover of *Mytilus californianus* for each transect at both locations, there was not a statistically significant difference in percent cover estimates between photographic transects and *in situ* quadrats ($p = 0.46$). However, the broader coverage of the photographic transects was able to pick up the small *Mytilus californianus* cover while the *in situ* quadrats did not. On Bird Rock, the *in situ* quadrats underestimated turf

by 58%, and overestimated bare rock by 68% (Fig 4a). On Big Fisherman Cove, the *in situ* transects underestimated turf by 81% and *Silvetia* by 71%, and overestimated bare rock by 90% (Fig 4b).

The intertidal habitat cover types from the photographic transects were compared between Big Fisherman Cove and Bird Rock, revealing significantly distinct benthic compositions (nMDS, stress = 0.064; Fig. 5a). The intertidal assemblage at Big Fisherman Cove was composed more of macroalgae (*Silvetia compressa* and red foliose algae) and *Tetraclita rubescens*, whereas Bird Rock had a higher percent cover of turf algae, bare rock, and *Mytilus californianus* (Fig. 5b). Bird Rock contained 49% more turf algae and 62% more bare rock than Big Fisherman Cove, while Big Fisherman Cove contained 78% more *Silvetia* and 65% more *Tetraclita* than Bird Rock. Bird Rock was the only location to contain mussels at a cover of 4.2%.

A significant positive relationship between lobster density and the habitat feature *Mytilus californianus* (AICc = 97.26, Δ AIC = 0, df = 4, t = 6.78, p = 0.002) and a near significant negative relationship between lobster density and the Vector Ruggedness Measure (VRM) (AICc = 0.317, Δ AIC = 0, df = 4, t = -2.51, p = 0.066) were observed in the best fit model of the AIC test (Table 3). Lobsters were strongly positively correlated with *Mytilus californianus* on Bird Rock, with lobster density increasing with the presence of mussels (Fig 6). Lobsters were weakly negatively correlated with VRM, with lobster density increasing when terrain ruggedness (the variability of aspect and slope) decreased. Observationally, the intertidal bench at Big Fisherman Cove was steeper than Bird Rock.

The best fit model was statistically indistinguishable (Δ AIC \leq 2) from two other models that had slightly higher AICc values (Table 3). One model contained a significant positive relationship with the variable *Mytilus californianus* (AICc = 98.21, Δ AIC = 0.95, df = 4, t = 7.32, p = 0.002), while the other model also contained a significant positive relationship with *Mytilus californianus* (AICc = 0.302, Δ AIC = 0.09, df = 5, t = 6.88, p = 0.003) and a weak negative relationship with turf algae (AICc = 98.21, Δ AIC = 0.95, df = 4, t = 2.27, p = 0.086). Of all three indistinguishable models,

all of them contained a significant relationship with *Mytilus californianus*, and weak non-significant relationships if other variables were present (i.e. VRM and turf algae).

The spatial scale of the distribution of *Mytilus californianus* at Bird Rock was determined due to its significant strong positive correlation with lobster density. *Mytilus californianus* exhibited significant clustering at a sub-meter scale (Hot Spot Analysis, $-2.02 > Gi \text{ z-score} > -8.22$, $p < 0.004$; Fig 7), existing at fine-scale patches on the intertidal bench. Other habitat features, such as *Tetraclita rubescens*, *Chthamalus fissus*, and bare rock also exhibited fine-scale clustering, however none of these habitat features were significantly correlated with lobster density. Turf algae and *Silvetia compressa* did not display any clustering at a fine-scale distribution, but were evenly distributed across the entire length of each transect (at a scale of 10's of meters).

DISCUSSION

The intertidal habitat functioned as an important foraging ground for California spiny lobsters residing in the adjacent subtidal during their breeding season (May through August) on Santa Catalina Island, California. Spiny lobsters preferentially fed on the intertidal California mussel when present, likely subsidizing their diet through this cross-system migration to support the higher energetic demands of reproduction. Moving across systems to forage is common amongst marine species. The American lobster (*Homarus americanus*) migrates seasonally from deep offshore waters to shallower inshore waters in late spring (Childress and Jury 2009), where it then exhibits a similar diel pattern of moving from the subtidal to the adjacent intertidal to forage (Jones and Shulman 2008). Other common patterns of cross-system use are of nocturnally active grunts (*Haemulidae sp.*) and snappers (*Lutjanidae sp.*) that shelter in mangroves by day and forage in adjacent seagrass beds by night in the Caribbean (Verweij et al. 2006), and landlocked Arctic charr that migrate during spring to smaller, more productive lakes, growing faster and reaching maturity sooner than those that don't (Näslund 1990).

Spiny lobsters migrated short distances from the adjacent subtidal into the intertidal at night to forage. Although previous studies have documented that lobsters were capable of traveling long distances (at the scale of 100s of meters to kilometers;

Hovel and Lowe 2007), lobsters were also documented to move short distances depending on their surrounding habitat (Engle 1979; Stull 1991; Withy-Allen 2013). On Santa Catalina Island, lobsters were observed to have high site fidelity and short home ranges (Stull 1991), and would home to the same area for shelter (Engle 1979). Within the La Jolla Ecological Reserve in San Diego, Southern California, lobster movement patterns were directly dependent on habitat availability, with most lobsters traveling only a few meters from sheltering to foraging habitat (Withy-Allen 2013). On the New England Coast, American lobsters exhibited a similar migration pattern; after moving into shallow water during their breeding season, American lobsters were observed traveling short distances into the adjacent intertidal zone to forage on prey (Jones and Shulman 2008). The benefit of migrating short distances into the intertidal zone can allow spiny lobsters to conserve energy when foraging while simultaneously avoiding predators that have limited or no access to the intertidal habitat (such as leopard sharks and giant sea bass).

Spiny lobster access into the intertidal habitat was available for a small portion of time throughout a single calendar year (2.7%), initially seeming negligible. However, when focusing the availability of intertidal habitat for lobster foraging to the duration of the breeding season (May through August) and when lobsters were active (between sunset and sunrise), the proportion of potential use of this habitat increased dramatically (46.6%) and was likely crucial during this seasonal event. Despite access to the intertidal habitat being ephemeral and seasonally episodic, it plays a vital role as a prey source during the energetically demanding breeding season.

The non-triviality of spiny lobster utilization of the intertidal habitat was illustrated through the significantly higher density of lobsters occupying the intertidal zone at night compared to the adjacent subtidal at both locations. At Bird Rock, lobster size, sex ratio (in favor of females), and reproductive condition were significantly higher compared to Big Fisherman Cove, and this difference in population metrics was likely influenced by the differences in intertidal habitat composition between locations. The California mussel (*Mytilus californianus*) was the only habitat feature to exhibit a significantly strong positive correlation with lobster density and were significantly more

abundant at Bird Rock. Lobsters are historically known to preferentially feed on mussels at Bird Rock (Robles 1987; Robles et al. 2001) and their availability as a food source was potentially supporting the higher population metrics observed. The presence of mussels on Bird Rock and their absence within Big Fisherman Cove was likely a result of higher wave exposure and wave velocity facilitating mussel recruitment (Robles and Desharnais 2002).

A partnered study conducted on the same lobsters within the same locations and timeframe provided further supportive evidence that lobsters preferentially fed on mussels. McCormick (2015) used stable isotope analysis to determine the gut composition of intertidal and adjacent subtidal lobsters at Bird Rock and Big Fisherman Cove, observing lobster diet on Bird Rock to be comprised largely of mussels (75% or greater). A Manly selectivity analysis revealed that when mussels were available lobsters would selectively prey upon them. Mussels also contained a higher C:N ratio within their muscle tissue, a proxy for lipid content, when compared to other prey types such as limpits (*Collisella limatula* and *C. scabra*) and shorecrabs (*Pachygraspus crassipes*), and therefore were likely higher in nutrition and more energetically beneficial. At Bird Rock, 77% of lobsters observed were female and 97% of those females were carrying eggs, whereas at Big Fisherman Cove 44% of lobsters observed were female and 78% of those females were carrying eggs. This higher reproductive potential at Bird Rock was likely supported by the availability of mussels as a prey source.

The spatial distribution of mussels on Bird Rock existed as discrete patches at a sub-meter scale, and was potentially directly influencing the scale of spiny lobster foraging behavior. The occurrence of small-scale hotspots, such as the clustering of preferred prey, can drive the behavior of a predatory species that feed upon them (Houghton et al. 2006; Piatt et al. 2006; Finlayson et al. 2008). Lobsters on Bird Rock were likely targeting mussels as their preferred prey source, and therefore were directed by the mussel's fine-scale distribution within the intertidal zone. It was also possible that lobsters were interacting with the intertidal habitat at various spatial scales depending on the availability of mussels and other prey types within algal turf communities. Depending on the characteristics and distribution of certain habitat features, such as

various prey types, a species may interact with its surrounding habitat in a scale dependent and hierarchical manner (Knecht et al. 2011). When mussels were unavailable, lobsters likely foraged within algal turf communities (the other primary intertidal prey source; Robles 1987), which existed at a much broader spatial distribution (10s of meters), thereby directing lobster foraging behavior at a broader spatial scale. However, this study did not directly evaluate the spatial scale of lobster foraging activity and it is worth further investigation to determine the potential scale-dependent and hierarchical influence mussels and algal turf communities may have on lobster foraging behavior.

Mussels are a common intertidal prey source and influence the upshore movement of certain subtidal species that prey upon them. The American lobster on the Atlantic coast of the United States exhibits a similar behavior as the California spiny lobster, moving into the intertidal zone from adjacent subtidal habitat to forage mainly on blue mussels (*Mytilus edulis*) and the shorecrab *Carcinus maenasi* (Jones and Schulman 2008). The seastar *Pisaster ochraceus* is considered an intertidal keystone predator upon California mussels within the Pacific Northwest (Paine 1969), and foraging behavior has been positively correlated with mussel recruitment, revealing the seastar's preference for mussels as a prey source (Robles et al. 1995). Subtidal predatory fish, such as the banded wrasse (*Notolabrus fucicola*) and spotted wrasse (*Notolabrus celidotus*), were observed to feed heavily on small intertidal mussels (*Mytilus galloprovincialis* and *Xenostrobus pulex*) in New Zealand, so much so that the level of predation intensity accounted for much of the variation in intertidal mussel recruitment (Rilov and Schiel 2011). California spiny lobsters have also been observed to feed upon the invasive Asian mussel *Musculista senhousia* in Mission Bay, California, and were considered one of the primary factors of resistance of the mussel's establishment (Cheng and Hovel 2010). The importance of mussels as an intertidal prey source for subtidal species is apparent from these studies, but is an area that is still currently understudied.

Historically, mussel density was much higher on Bird Rock. Over the last several decades, mussel density has decreased dramatically to the remnant sub-meter patches that existed at the time of this study. The loss of mussels was potentially influenced by the El Niño events of 1987-1988 and 1997-1998 (C. Robles and C. Garza, personal

communication). El Niño weather patterns may have reduced upwelling and increased water temperatures, therefore decreasing productivity and planktonic food sources for mussels. The decline of mussels on Bird Rock may have also been exacerbated by the preferential predation of spiny lobsters. Continued monitoring of Bird Rock in 2014 has revealed that the remnant population of mussels is now completely gone (C. Garza and M. McCormick, personal communication) and further study would provide valuable insight into how lobster foraging behavior and the population may change with the recent absence of this prey source.

Researching other habitat features, such as the distribution of subtidal rocky habitat and surfgrass, is necessary to provide a more comprehensive understanding of the spiny lobster's interaction with the intertidal habitat and is recommended for future studies at Bird Rock and Big Fisherman Cove. The condition and abundance of adjacent subtidal habitat may be important in determining the strength of intertidal-subtidal trophic interactions (Rilov and Schiel 2006). It was visually apparent that Bird Rock contained more adjacent subtidal habitat than Big Fisherman Cove, and may contribute to the higher population metrics observed there. The abundance of surfgrass, which acts as a nursery habitat for juvenile lobsters (Engle 1979), may also influence lobster density within the intertidal, and a higher abundance of this habitat feature was also observed at Bird Rock. Future studies should incorporate the linkages and influences of the adjacent subtidal habitat upon lobster interactions with the intertidal habitat.

The use of the intertidal habitat as an important foraging ground by subtidal species is an understudied topic, and an increased understanding could benefit protective management practices that target certain subtidal species. Around the world marine protected areas (MPAs) have shown to be an effective management tool towards the protection and recovery of lobsters (Cox and Hunt 2005; Shears et al. 2006; Babcock et al. 2007), including Southern California (Iacchei et al. 2005; Kay et al. 2012). However, the incorporation of the intertidal zone and the habitat features that provide a valuable prey source (mussel beds and algal turf communities) could strengthen the efficacy of an MPA that targets lobsters in California. The use of the intertidal habitat is directly linked to the lobsters' reproductive life-stage, and deserves to be considered within the range of

critical habitats that require representation within management that targets this species. The intertidal habitat in relation to other subtidal species, such as the American lobster of New England and certain fishes (such as the banded and spotted wrasses of New Zealand), warrants consideration as well, potentially being an important linkage for subtidal communities and fisheries around the world.

It is becoming well recognized that for an MPA to be effective, the range of multiple habitats a targeted species utilizes throughout its life-cycle, as well as the multiple spatial scales that species interacts within each of those habitats, needs to be considered and incorporated into the design process (García-Charton et al. 2000; Halpern 2003; Gerber and Heppell 2004; Pilkitch et al. 2004; Deither and Schloch 2005; Leslie 2005). Typically, species-habitat interactions were looked at over broad spatial scales, such as the distribution of kelp forests or coral reefs (Jones 2002; Friedlander et al. 2003), and was likely due to a targeted species being mobile with wide coverages of distance, or the jurisdictional scale of management driving the classification of habitat representativeness (Jones et al. 1992; Stevens 2002). However, species often interact with their habitat at relatively finer scales than their distribution as a result of the distribution of their food source or other habitat features (Houghton et al. 2006; Pinaud and Weimerskirch 2007; Scott et al. 2012), and these interactions can often be overlooked in the management process (de Roos et al. 1998; Fauchald et al. 2000). It is important to understand the variability of the spatial scale of influence a particular habitat has upon the behavior of a species that utilizes it, and how these interactions change over time when designating an area for protective management.

This study illustrated the value of using contemporary innovative technologies, such as surveying total stations, digital photography, and GIS for intertidal sampling. This methodology measured the benthic intertidal habitat composition of the entire transect, as opposed to sub-sampled estimates of standard *in situ* quadrats. The total census coverage, in combination with the high resolution of the photographs, detected the subtle differences in mussel abundance between locations and the significant positive relationship between mussels and lobsters. This crucial relationship would not have been identified if the study solely relied on *in situ* quadrat estimates of percent cover. Another

benefit of this methodology was the relative rapidity in data collection and the ability to post-process the data within a GIS with spatial statistical capabilities. It is encouraged for future intertidal research to consider utilizing such innovative technologies to improve upon data collection and analysis.

The concept of multiple scales of use across multiple habitats within a species life-cycle has largely focused on vertebrate organisms, and this study provided one of the first examples applying this concept to a mobile invertebrate. The intertidal habitat was an important foraging ground for breeding spiny lobsters within Big Fisherman Cove and Bird Rock, providing prey subsidies to the adjacent subtidal habitat. The difference within the composition of the intertidal habitat between locations was also likely influencing the density and spatial scale at which lobsters interacted with it. This study can help inform lobster management within Southern California, as well as other subtidal species across the world, through encouraging the consideration of the intertidal zone and the habitat linkages associated with it, as well as the effects of prey distribution on predator foraging behavior.

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APPENDIX A: FIGURES AND TABLES

Table 1. Two-way ANOVA; Zone tested the Intertidal vs Subtidal, and Time tested Day vs Night with lobster density as the response variable.

Source	df	SS	MS	F	P
Zone	1	0.992	0.992	14.98	<0.001*
Time	1	0.117	0.117	1.76	0.189
Zone x Time	1	2.503	2.503	37.80	<0.001*
Residuals	<u>68</u>	<u>4.503</u>	0.066		
Total	71	8.115			

Table 2. Two-way ANOVA; Zone tested the Intertidal vs. the Subtidal, and Location tested Big Fisherman Cove vs. Bird Rock with lobster density as the response variable.

Source	df	SS	MS	F	P
Zone	1	0.172	0.172	8.07	0.008*
Location	1	0.464	0.464	21.79	<0.001*
Interaction x Zone	1	0.042	0.042	2.00	0.167
Residuals	<u>32</u>	<u>0.681</u>	0.021		
Total	35	1.36			

Table 3. AIC table showing the best fit model with lobster density as the response variable. The best fit model (model 5) contained the parameters ‘mussel’ and ‘VRM’. ‘Mussel’ was significantly positively correlated with lobster density ($p = .002$) and VRM was weakly negatively related to lobster density ($p = 0.066$). Models with a ΔAIC less than 2 were statistically indistinguishable. All models indistinguishable with the best fit model contained a significant positive relationship with the parameter ‘mussel’ (model 1, $p = 0.002$; model 3, $p = 0.002$; model 4, $p = 0.003$).

Model #	Model	K	AIC	AICc	ΔAIC	AICw	
1	m(1)	1	91.63	97.35	0.09	3.02E-01	1 Mytilus californianus
2	m(2)	1	108.63	114.58	17.32	5.49E-05	2 turf algae
3	m(3)	1	106.85	112.57	15.31	1.50E-04	3 VRM
4	m(1+2)	2	88.21	98.21	0.95	1.97E-01	4 Tetraclita rubescens
5	m(1+3)*	2	87.25	97.26	0	3.17E-01	5 Chthamalus fissus
6	m(1+4)	2	91.96	101.96	4.7	3.01E-02	6 Silvetia compressa
7	m(1+5)	2	92.31	102.31	5.06	2.53E-02	7 red foliose algae
8	m(1+6)	2	90.38	100.38	9.13	6.64E-02	8 bare rock
9	m(1+7)	2	91.36	101.36	4.1	4.07E-02	
10	m(1+8)	2	93.44	103.44	6.18	1.44E-02	
11	m(1+2+3)	3	88.64	105.44	8.18	5.30E-03	
12	m(1+2+3+6)	4	90.63	118.64	21.38	7.22E-06	

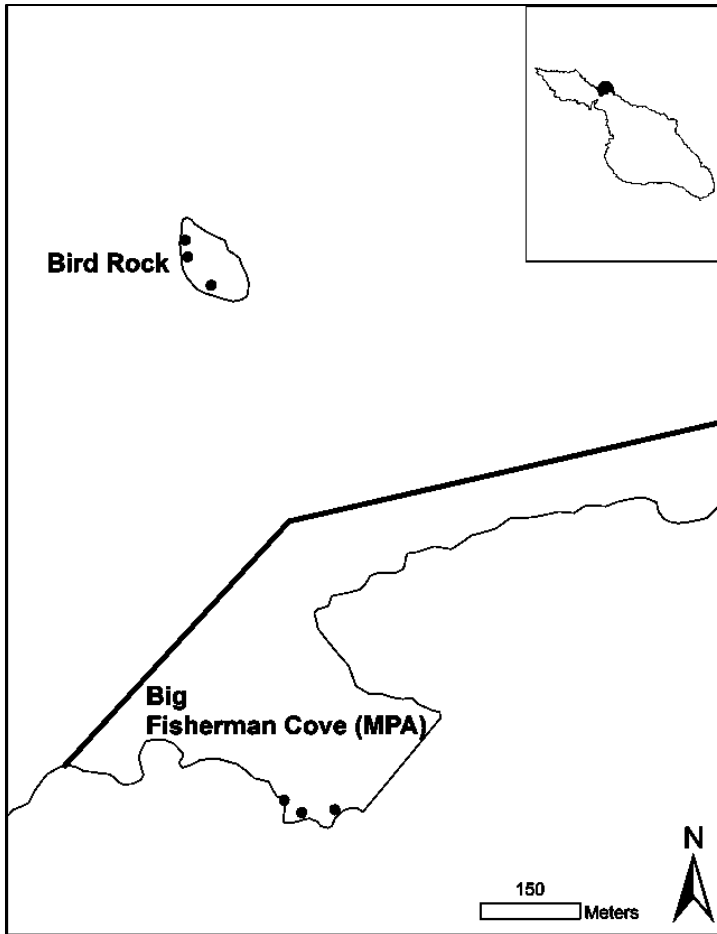


Figure 1. Map of study area on Santa Catalina Island. The points depict the study sites and the black line indicates the border of the WIES MPA.

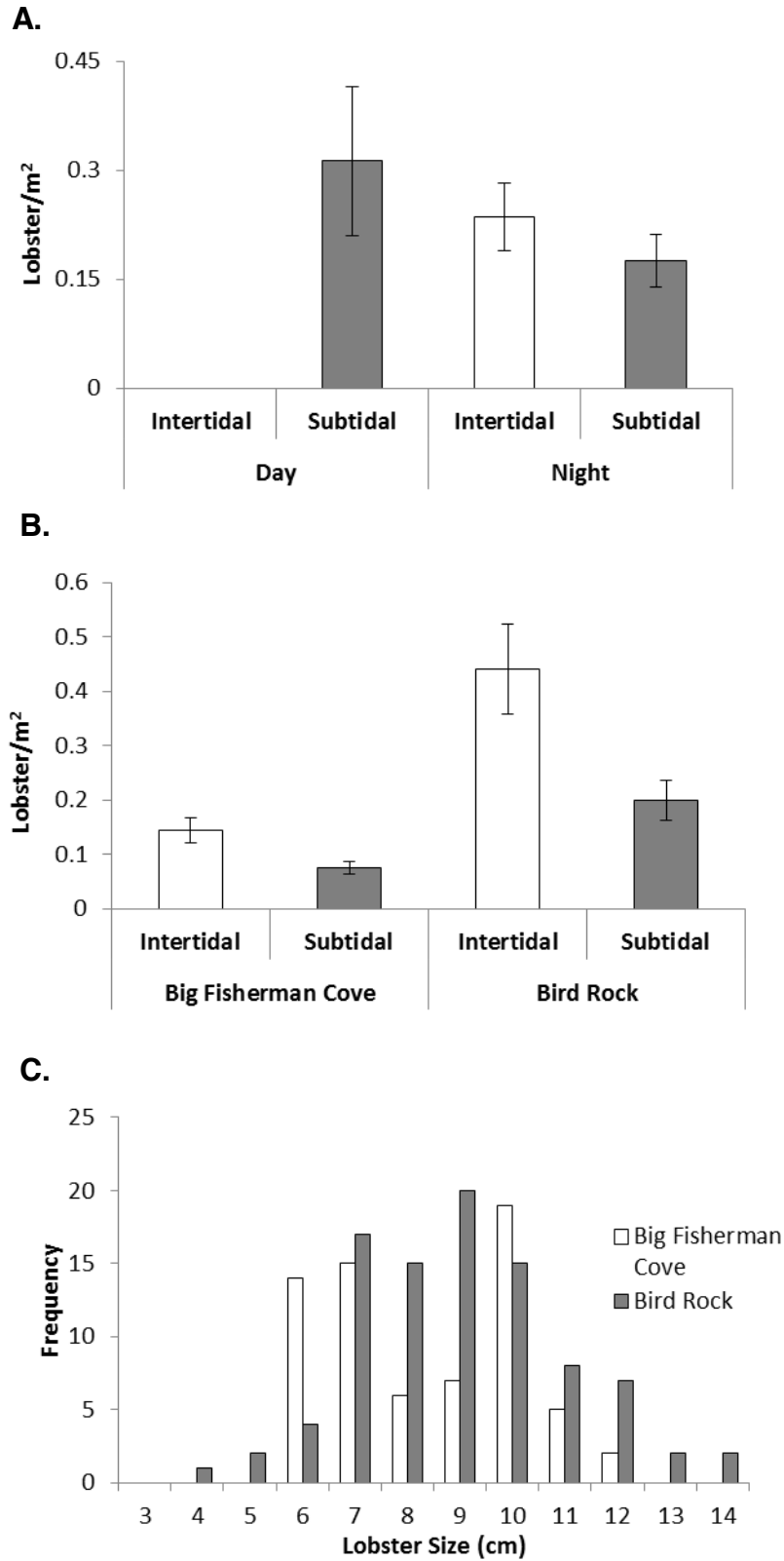


Figure 2. a) Mean lobster density by Zone and Time of Day. b) Mean lobster density by Zone and Location. c) Size frequency of Big Fisherman Cove vs. Bird Rock.

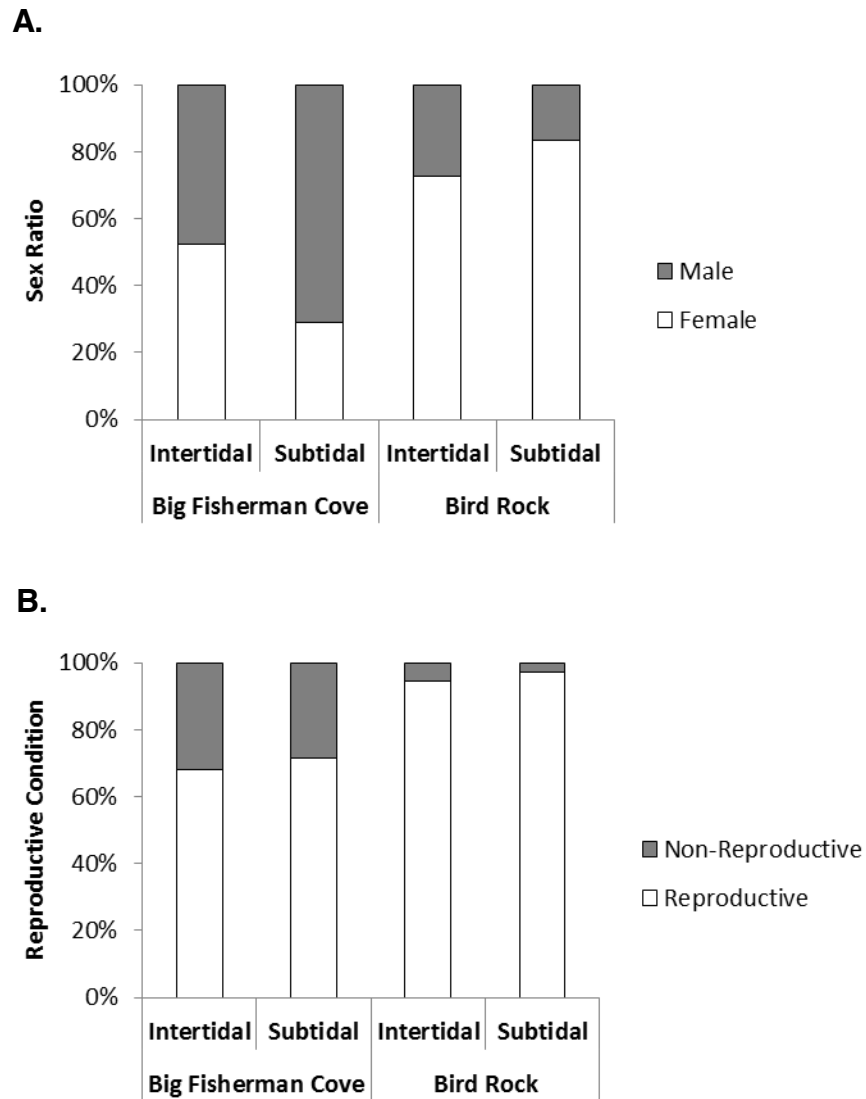


Figure 3. a) Proportional comparison of sex between Bird Rock and Big Fisherman Cove. B) Proportional comparison of reproductive condition (presence or absence of eggs on females) between Bird Rock and Big Fisherman Cove.

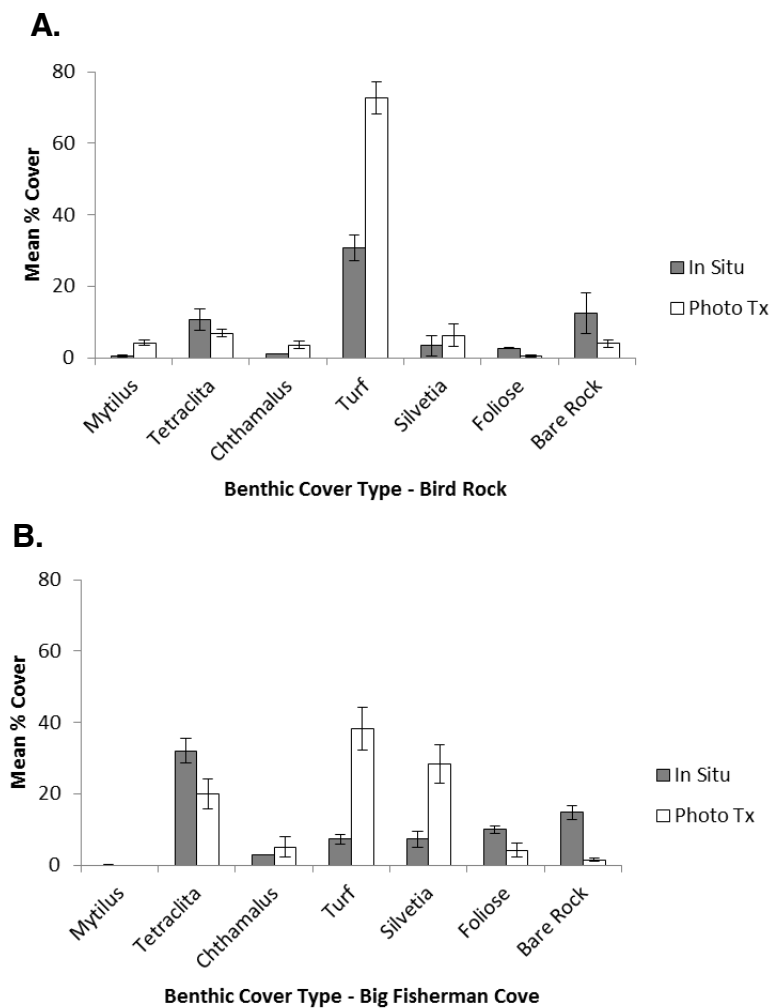
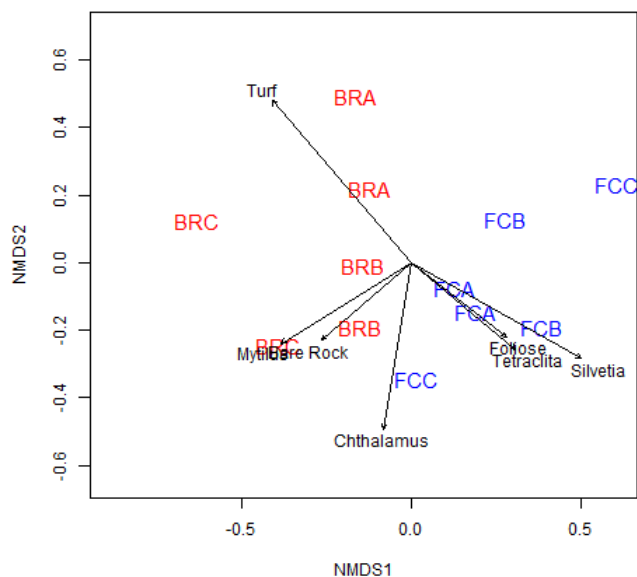


Figure 4. a) *In situ* quadrat surveys vs. photographic transect percent cover measurements for Big Fisherman Cove, b) *In situ* quadrat surveys vs. photographic transect percent cover measurements for Bird Rock.

A.



B.

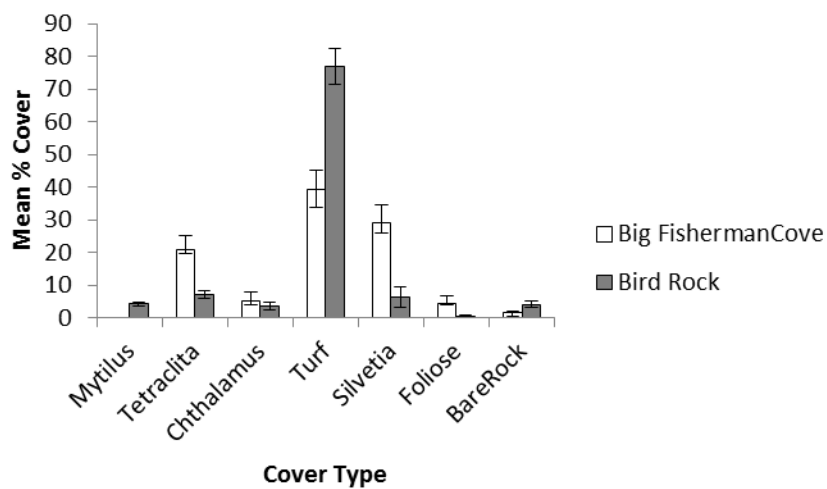


Figure 5. a) Non-metric multidimensional scaling analysis revealing significantly distinct intertidal compositions between Big Fisherman Cove and Bird Rock (Note: *Mytilus californianus* and Bare Rock are overlapping). b) Mean percent cover of habitat features for Big Fisherman Cove and Bird Rock.

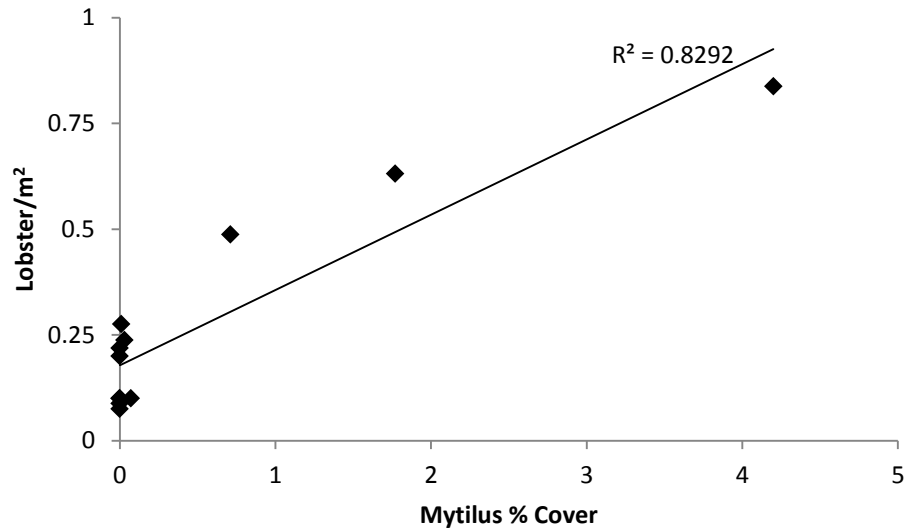


Figure 6. Lobster density was strongly correlated with mussel presence (note: this figure does not represent the best fit model, but shows the direct relationship between mussels and lobster density).

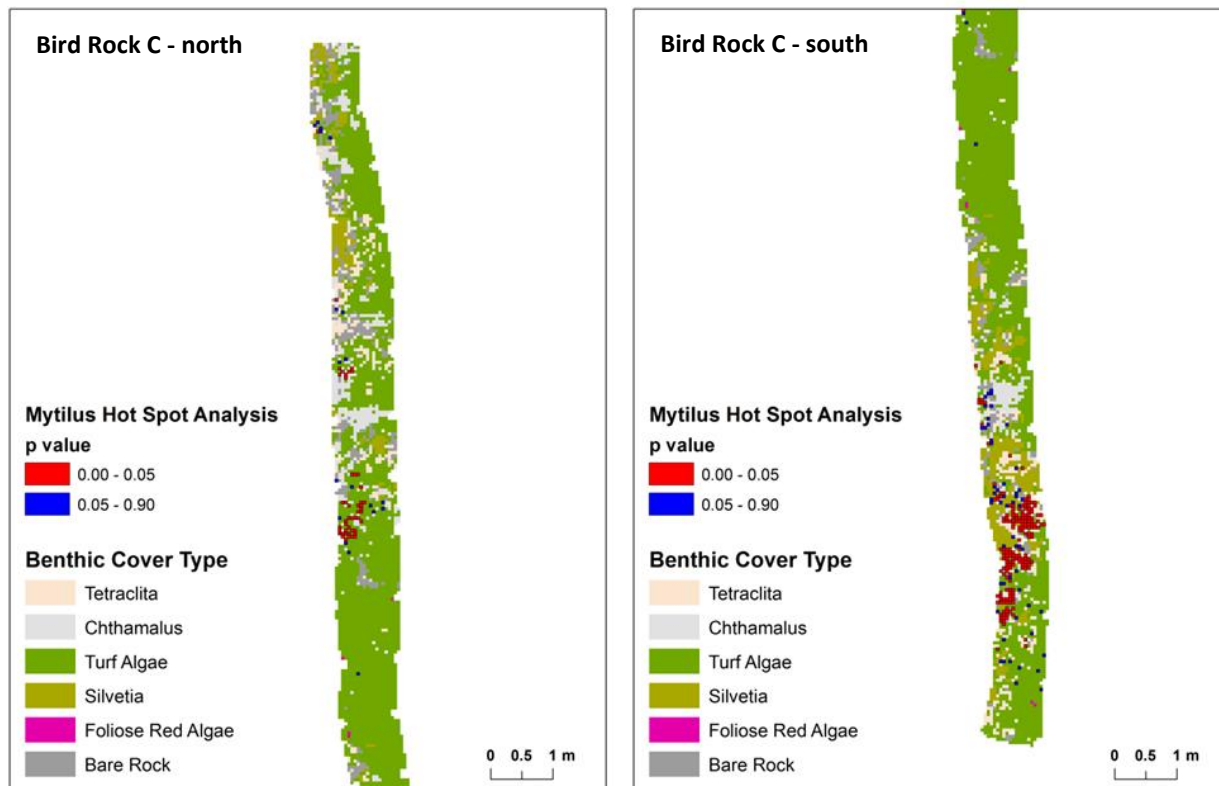


Figure 7. North and south terminuses of transect Bird Rock C showing where *Mytilus californianus* is significantly clustered ($p \leq 0.05$) at a sub-meter scale as a result of the Hot Spot Analysis tool in Arcmap 10.1.