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Multiscale Habitat Use and Effects of Resource Availability on California Spiny Lobster (*Panulirus interruptus*) Population

Taylor Eddy

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MULTISCALE HABITAT USE AND EFFECTS OF RESOURCE
AVAILABILITY ON CALIFORNIA SPINY LOBSTER (*PANULIRUS*
INTERRUPTUS) POPULATION SUCCESS

A Thesis

Presented to the

Faculty of

Moss Landing Marine Laboratories

California State University Monterey Bay

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Marine Science

by

Taylor Eddy

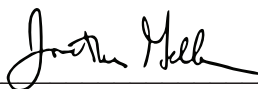
Spring 2021

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

The Undersigned Faculty Committee Approves the

Thesis of Taylor Eddy:

MULTISCALE HABITAT USE AND EFFECTS OF RESOURCE
AVAILABILITY ON CALIFORNIA SPINY LOBSTER (*PANULIRUS*
INTERRUPTUS) POPULATION SUCCESS



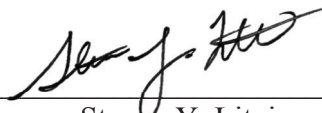
Jonathan Geller, Chair
Moss Landing Marine Laboratories



Corey Garza
California State University Monterey Bay



Scott Hamilton
Moss Landing Marine Laboratories



Steven Y. Litvin
Monterey Bay Research Institution, Moss Landing, CA



Daniel Shapiro, Interim Dean
Associate VP for Academic Programs and Dean of Undergraduate and Graduate Studies

May 26, 2021

Approval Date

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ABSTRACT

Multiscale Habitat Use and Effects of Resource Availability on
California Spiny Lobster (*Panulirus interruptus*) population
success

by

Taylor Eddy

Masters of Science in Marine Science
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Habitat use can affect ecological and biological processes, such as resource use, survival, and reproduction. For many species, habitat use can vary with season as their energetic needs change, for example increasing foraging area in the energetically costly reproductive season. In this study, I sought to understand the seasonal and temporal scales of spiny lobster (*Panulirus interruptus*) habitat use in a southern California ecosystem by integrating habitat surveys using GIS (Global information system), lobster demographic surveys, and diet analysis using stable isotopes. I focused on the California spiny lobster (*Panulirus interruptus*) because the species uses a variety of habitats at different seasonal and spatial scale and is economically and ecologically important. My two study sites on Santa Catalina Island, California, Bird Rock and Big Fisherman Cove, were characterized by rocky substrate and high algal cover, but exhibited differences in the cover of mussels. Results indicated that Bird Rock had a higher density of lobsters than Big Fisherman Cove and intertidal habitat recorded higher density of individuals than subtidal habitat at both sites during nocturnal high tides. At Bird Rock, the proportion of females was 25% higher, and their reproductive condition was 43% greater than that at Big Fisherman Cove. I detected a distinct seasonal change in the diet of spiny lobsters, such that a higher diversity of prey resources was consumed in the summer, when nighttime high tides permit movement and foraging from the subtidal to the intertidal, compared to the winter, when high tides rarely overlap with nocturnal foraging behavior and winter storms can make it inaccessible. Stable isotope results indicated that lobsters at Bird Rock foraged on the mussel beds that are present at the site, while no mussel consumption was detected at Big Fisherman Cove. Seasonal foraging in the intertidal habitat acts as a diet subsidy for the spiny lobsters during the reproductive season, a time of high energetic cost. Observed differences in the reproductive condition of the lobster population are likely due to the presence of the mussel bed at Bird Rock. Understanding fine scale spatial and seasonal habitat needs of target species can help create better protected areas, not only for the spiny lobster, but other critically important species.

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INTRODUCTION

Species habitat use can affect many ecological and biological processes such as resource use, growth, survival, and reproduction. Some marsh birds have shown habitat preference when selecting nesting locations in western New York (Lor & Malecki 2018). For piping plover (*Charadritus melodus*), reproductive success is dependent on the available habitat (Prindiville Gaines & Ryan 1988). For some species, habitat use can change because of changes in environmental conditions, to meet their energetic needs, or prey and other resource availability. Perry et al. (2019) reported that adult Antarctic krill exhibit seasonal cross shore migrations from shelf to open ocean habitats, and the inverse is true of the juveniles. This habitat partitioning decreases intraspecific competition in foraging and may also be driven by prey size ranges. Seasonal migrations frequently align with the reproductive season, a time of increased energetic needs (Prindiville, Gaines and Ryan 1988, Donovan et al. 1995, Norris et al. 2004). One well known example of this is the salmon migration to freshwater rivers to spawn, with juveniles returning to the open ocean (Williams 2006). Changes in habitat use can also occur on a smaller scale, such as observed in the sea star, *Pisaster ochraceus*. This species moves during the nocturnal high tides from the lower intertidal to the upper intertidal to forage on mussel beds – a prey resource otherwise inaccessible to the sea star (Garza & Robles 2010).

The utilization of resources from outside of a species' primary habitat is called a spatial subsidy. Resources from one habitat (e.g., prey, detritus, and nutrients) being used in a second habitat can lead to increases in population productivity in the receiving habitat (Polis et al. 1997). Spatial subsidies can be achieved through many vectors.

Nutrients can be carried in the movements of water masses through processes like upwelling, currents, and tidal movement (Polis & Hurd 1996, Polis et al. 1997).

Upwelling in coastal ecosystems leads to increases in productivity throughout the food web (Croll et al. 2005). Kelp wrack transported via ocean currents are an important subsidy for near-shore terrestrial ecosystems (Dugan et al. 2003, Orr et al. 2005).

Alternatively, predator and prey migrations can increase the capacity of predators in their primary habitat through prey subsidies. When salmon migrate to freshwater streams to spawn, bears congregate at the stream to forage on them. The bears then distribute the nutrients received from the salmon throughout the terrestrial ecosystem by dropping the carcass in nearby forests (Reimchen 2000) and through excretion (Hilderbrand et al. 1999). For those salmon die after spawning, their carcasses subsidize the riparian system which leads to an increase in the resident salmonoid growth rates (Wipfli et al. 2003).

Anthropogenic impacts can affect the connectivity between habitat types (McCauley et al. 2012) which in turn can have negative impacts on species populations, and climate change can intensify the effects of anthropogenic habitat loss (Travis 2003). When salmon spawning grounds are limited due to anthropogenic impacts such as mining discharge and addition of diversion dams, and results in a decrease in population abundance and shift to homogeny in the genetic structure (Williams 2006). Even in the more remote areas of the world, species are affected by anthropogenic impacts. Antarctic krill are in danger because the identified hotspot of their activity in the southern Scotia Arc is also used by humans for fishing and, further, the distribution and abundance of this species is changing in response to long-term climatic changes (Perry et al. 2019). In contrast, management practices can help to mitigate these negative impacts. Practices

such as protecting habitat through limiting access and protecting critical terrestrial and marine areas, banning oil drilling, invasive species removal, and fishing regulations can benefit many species.

One management strategy utilized in marine ecosystems to protect critical habitat includes creating marine protected areas (MPAs). MPAs are often designed to help conserve populations of exploited species – species targeted in commercial fisheries – leading to increases in population abundance, size structure, and biomass (Lester et al. 2009). Population recovery, especially of predators inside reserves, can lead to a shift in the trophic dynamics of the ecosystem within the MPA (Shears & Babcock 2003, Behrens & Lafferty 2004, Lafferty 2004, Guidetti 2006, Guest et al. 2009, Babcock et al. 2010). A number of considerations go into the development of MPAs, including factors like the size, placement, and enforcement effort that affects the efficacy (Mills et al. 2010, Arias et al. 2016). Mismatches between MPAs, and the actual habitat use of the species can lead to unsuccessful protected areas (Kelly & MacDiarmid 2003, Mills et al. 2010). Understanding the habitats essential to the target species life history fine-scale traits such as habitat preference or home range can better inform management practices and lead to more efficient MPAs (Palumbi 2004, Parnell et al. 2006, Blamey & Branch 2009, Roberts et al. 2011).

The California spiny lobster, *Panulirus interruptus*, is an example of a species that uses a variety of habitats at different seasonal and spatial scales (Kay et al. 2012a,b). They are often found in the subtidal of kelp forests, and their population abundance and mean size is tightly coupled with fine-scale habitat features, such as the density and diversity of understory kelp (Mai & Hovel 2007). Historically, their diet mostly consists

of mollusks, crustaceans, and echinoderms; with mollusks being the dominant food resource, followed by crabs and sea urchins (Winget 1968). When their abundance is high, spiny lobsters act as keystone predators, helping to maintain high kelp forest diversity by preying on sea urchins (Tegner 2000, Chávez-Hidalgo & Chávez 2016). During their summer reproductive season, in some locations, lobsters make a seasonal foraging shift and occupy intertidal habitats on nights with more extreme nocturnal high tides, and spend daytime hours sheltered in subtidal crevices (Robles 1987). At night, they thus have access to energetically dense prey resources, such as mussel beds (*Mytilus spp.*) (Robles 1987, Robles & Robb 1993, Robles et al. 2001). Other species of lobster, such as the American lobster (*Homarus americanus*) in New England (Jones and Shulman 2008) have also been shown to visit habitats that subsidize their diets during times of high energetic need.

In the intertidal, lobster foraging on mussels decreases spatial competition for hard substrate, allowing for higher algal density (Robles & Robb 1993, Robles 1997). The different spatial scales characterizing prey patches in the intertidal result in differences in lobster habitat use during foraging. For example, mussels are best characterized as habitat on a sub-meter scale, as they occur in small, patchy beds throughout the intertidal, while other prey species such as crabs and limpets may be best characterized at larger spatial scales (>10 meters) as they are found widely through the entire area (Windell 2015). When the mussel beds are present, spiny lobsters will focus foraging efforts on these small but dense mussel beds to fuel their high energetic needs of reproduction (Robles 1987), and they will widen their foraging range to feed on other prey items when the mussels are not present.

California spiny lobster populations are susceptible to population-level changes due to commercial fishing pressure through decreases in mean size, abundance, biomass, and fecundity of lobsters in fished areas (Iacchei et al. 2005). Further, when the size of lobsters decrease, so does their functional role in rocky reef ecosystems (Dayton et al. 1998). The lobster fishery began in 1871, and in 1887 the average carapace length (CL) of the lobster was about 150 mm and 260 traps would yield almost 105 kg of lobster, but by 1975 the mean CL decreased to around 90 mm and 19,000 traps were needed to match the catch of 260 traps in 1887 (Dayton et al. 1998). Due to their ecological importance, as well as being the third highest grossing fishery in California (Frimodig & Buck 2017), there is a need for management action to maintain a sustainable abundance and individual size. MPAs have been shown to be successful for lobster populations in southern California. An MPA that covered 35% of lobster fishing area resulted in a 225% increase in total catch outside of the MPA (Lenihan et al. 2021). In the northern Channel Islands, MPAs have been shown to increase the abundance of lobsters within MPAs and induce spillover, and the increase in abundance is also influenced by fine-scale habitat features (Kay et al. 2012). The MPAs that protect lobsters also affect the larger ecosystem. Lobster fishing has also shown to indirectly increase epidemics in sea urchins through the loss of sea urchin population control by lobster foraging (Lafferty 2004). Outside of an MPA, sea urchin density increased dramatically, and disease was found to be four times greater than within the protected site which had a significantly higher abundance of lobsters (Lafferty 2004). Further, rocky reefs inside reserves have shown to protect predators that feed on sea urchins, and this dynamic helps to support and sustain kelp

forests; and outside of protected areas, urchin populations are relieved of predation pressure which can lead to an urchin barren (Behrens & Lafferty 2004)

In contrast, previous studies at Catalina Island have observed that lobster populations outside of a long standing MPA exhibited higher abundances, larger sizes, and more fecund female lobsters than populations inside of the MPA, due to the presence of a sustained mussel bed at the site outside of the MPA (Windell 2015). Outside the MPA, the lobsters were preferentially feeding on *Mytilus*, but within the MPA, lobsters prey on other intertidal invertebrates due to the lack of a sustained mussel population (McCormick 2016). This study was the first to quantify the spiny lobster energetic dependence on the intertidal during their reproductive season, but it occurred only during a single summer season. Therefore, it is still unknown how seasonal and annual variability affects lobster abundance and reproductive success, as well as the propensity with which subtidal resources are consumed by lobsters at these locations. The goals of this project are to: 1) Assess the scale of lobster habitat use during foraging between sites that differ in intertidal resource availability; 2) Assess the differences in: abundance, size, sex, and reproductive condition, between the lobsters inhabiting subtidal and intertidal habitat; and 3) Compare the annual and seasonal diets, and trophic dynamics between sites with different intertidal resource availability on Catalina Island.

Understanding the diet and resources critical for spiny lobster success will help to inform future MPA designations for lobsters, but also provide another metric for assessing the success of existing MPAs for other species. In this study, I used modern geospatial techniques to assess the intertidal habitat inside and outside of a marine reserve to then compare with the diet of at each site to assess the habitat use in terms of

resource availability. One way to study lobster diet preference is using Stable Isotope Analysis (SIA). SIA is a tool used by ecologists to trace the flow of elements, typically carbon and nitrogen, in a system using natural tracers - isotopes (Fry 2006). The ratio of heavy to light nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$ denoted $\delta^{15}\text{N}$) increases with increasing trophic level and can thus be a powerful indicator of trophic position. Carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$ denoted $\delta^{13}\text{C}$) change little with trophic level, but do vary among primary producers (i.e., kelp vs. phytoplankton) depending on photosynthetic pathways, and can help determine the source of dietary carbon (Peterson & Fry 1987, Post 2002, Fry 2006). The natural variation in these isotope ratios can be measured and traced within a community to help understand the structure of the food web and size of the trophic niche – how organisms or populations utilize resources. This method has been employed previously for other species that inhabit southern California rocky reefs (Hamilton et al. 2011).

SIA can also be used to describe the isotopic niche of a species by quantifying dietary diversity among individuals in a population (Newsome et al. 2007). I compared the niche composition metrics (Layman et al. 2007) for lobster prey to the isotopic niche of lobsters over space and time (Jackson et al. 2011). Further, SIA can be used to estimate the relative prey contribution to the diet of spiny lobsters to determine if there is a preferred prey resource by using isotopic mixing models. Given the isotopic composition of the predator and the prey, mixing models can estimate the relative contribution of each prey to the diet of the predator (Phillips 2012). Through these methods, I sought to understand the importance of the intertidal habitat in the life history of spiny lobsters on Catalina Island.

EXPERIMENTAL DESIGN AND METHODOLOGY

Study site

The study area was located on Santa Catalina Island, located 20 nautical miles offshore of Los Angeles, California, at Big Fisherman Cove ($33^{\circ}26'37''$ N, $118^{\circ}29'05''$ W) and Bird Rock ($33^{\circ}27'03''$ N, $118^{\circ}29'15''$ W; Fig. 1). At each site, this study was conducted on intertidal benches that had previously been used to examine the ecology of lobsters on Catalina Island (Robles 1987, Robles and Robb 1993, Robles et al. 2001). Big Fisherman Cove is located at the USC Wrigley Institute for Environmental Studies (WIES) and has been part of the USC Wrigley marine reserve since 1988. Bird Rock is a rocky islet located several hundred meters offshore, across a deep (> 40 m depth) channel, is more exposed to swell and wave action, and historically has been the location of intense spearfishing and lobster fishing on Catalina Island. The two sites have the distinction of having data from before and after the establishment of the Wrigley marine reserve. The intertidal benches at both sites are characterized by a rocky substrate with a sea grass bed in the lower intertidal zone, red turf algae and coralline algae in the mid-intertidal, and fucoid algae in the upper intertidal. Big Fisherman Cove has lower mussel recruitment than Bird Rock and no permanent mussel cover (Robles et al. 2001). In contrast, Bird Rock historically has had a persistent mussel bed; however, in recent years the number of mussels has been declining at the site (C. Robles pers. comm.).

Study species

The spiny lobster range extends from Point Conception, California to Baja California, Mexico and are found in the intertidal zone to depths as great as 240 feet

(Duffy 1973). They occupy the shallow depths and even use the intertidal habitat during the summer, reproductive season (Robles 1987). During this time, females can carry between 120,000 and 680,000 eggs, with clutch size positively associated with the size of the lobster (CA DFG 2001). The lobsters at this site have been shown to be nocturnal foragers, they utilize the nighttime high tide to access the intertidal zone to forage on mussel beds (Robles & Robb 1993).

Although the channel separating the two sites in this study is within the depth limits of spiny lobsters, the adult lobster populations in each site are considered independent because while genetic analysis indicate they are the same population (Garza, pers. com. 2018) likely due to larval dispersal, once settled, adult spiny lobsters display high site fidelity and small foraging ranges (Withy-Allen & Hovel 2013), thus it is unlikely they migrate across the channel separating the sites.

Sampling Design

Sample collections and intertidal characterizations were conducted during the summers of 2017 – 2019 and the winter of 2019. At each site I used six 20 x 1 meter (20m²) band transects: three located on the intertidal bench at approximately 1.2 m above mean lower-low water (MLLW) paired with three located in the subtidal at a depth of approximately 6m (Fig. 1). The intertidal transect was used for intertidal habitat characterization, and both the intertidal and subtidal transects were used for lobster survey and collection dives. I used previously collected data from 2013 to understand the annual variability in foraging, and to compare dates before and after a warming event (“The Blob” and El Niño 2014).

HABITAT CHARACTERIZATION

To describe the species and habitat composition of the rocky intertidal and the abundance of prey resources, I used digital images captured by handheld digital cameras and drones. In the summers of 2017 and 2018, the photographic habitat surveys were conducted using methods outlined in Robles et al. (2009, 2010) at low tide along each 20m² intertidal transect. Photos were taken along the transect at a height of approximately 2 meters above the ground using a Nikon Coolpix B500 16-megapixel camera. Each photo covers a 1 m² quadrat, defined by cones in the four corners which serve as control points. Coordinates of each cone (X, Y, and Z) were measured using a Total Station laser surveyor (TOPCON©), referencing each photograph to a tidal and global (WGS84 10S) datum that allows for the recreation of each photomosaic in ArcGIS.

Beginning in 2019, drones were used to collect photo quadrat data. A DJI Mavic 2 Pro with a 20-megapixel camera was used for habitat surveys. The drone was equipped with an internal GPS unit. I conducted low altitude flights (2.5 m above the ground) – the improved camera resolution allowed for a moderate increase in camera height. The increase in camera height, compared to hand-held imagery described above, captures a larger area per image, thereby reducing the time needed to sample each transect to an average of 8 minutes per transect.

Before flying, I laid out a transect to mark the center of my study area. I used an on-screen grid overlay in the mobile app, DJI Go to aid in drone flying. The transect was visible on screen and the grid acted as a guide to maintain a proper course. Additionally, the grid was used to capture images with 50% overlap between them to ensure high quality photomosaics. The pilot manually flew the drone over the study area in three

parallel lines maintaining a consistent altitude of three meters and keeping in line with the transect. The first line was highest in the intertidal zone, and each subsequent line was approximately 0.5 m lower in the intertidal to maintain proper image overlap (Fig. 2). A picture was taken approximately every 0.5 m, or when no less than 50% of the image overlapped with the previous image. This resulted in approximately 85 images/transect captured at each of my sites (Fig. 3). With this survey approach, I achieved a Ground Sampling Distance (GSD) of 0.07 cm resulting in a pixel size of 0.0049 cm².

Survey images from the 2017-2018 transects were mosaiced using the georeferencing tool in ArcGIS 10.1. Drone images from the 2019 surveys were mosaiced in Pix4D software using Structure from Motion (SFM) approaches. Structure from Motion (SFM) is a photogrammetry approach that uses multiple images collected from a moving camera to track the motion of stationary objects through the images. The amount the object moves from image to image depends on their depth. From this information, the software can determine the object's location in space and the depth of the object. Using many of these objects within the survey area, the software creates an orthomosaic (Fig. 3) and 3D point cloud of the area. The final products can be analyzed in both 2 and 3 dimensions in geospatial software such as ArcGIS to extract data on spatial variation in habitat distribution and prey resource abundance from the final images.

LOBSTER POPULATION METRICS

To determine lobster abundance inside and outside the MPA as well as seasonal habitat preference, lobsters were surveyed in the summers of 2017 to 2019, and the winter of 2019. Lobsters are primarily nocturnal foragers (Robles et al. 2001), therefore, nighttime survey were conducted to obtain the best estimate of habitat foraging

preferences. Dives were conducted to sample intertidal and subtidal transects during the nighttime high tide ($>1.5\text{m}$) using SCUBA. During observational dives, I recorded the density of lobsters observed along each 20 m^2 ($20\text{m} \times 1\text{ m}$) transect. Lobsters were then collected within the same transects to measure a suite of population metrics. From each captured lobster I recorded the carapace length (cm), sex (male, female, immature) and reproductive stage. The reproductive stage of females was recorded as plastered (having spermatophores fixed to their sternum), eggs (having visible egg masses), or non-reproductive (neither spermatophores nor egg masses visible). These population metrics were compared to data collected previously in the summer of 2013, utilizing the same methods, to further assess annual variability within the lobster population.

ISOTOPIC SAMPLING

I sampled the intertidal sites for invertebrate prey species (mussels, crabs, barnacles, and limpets) and primary producers (turf and coralline algae) and water samples at a depth of three meters. In the subtidal, I also collected invertebrate prey items (e.g., sea urchin *Centrostephanus coronatus*, wavy top turban snail *Megastrea undosa*). I collected a minimum of ten samples of each invertebrate prey species and algae for isotope studies when possible. For the lobster isotopic samples, a second walking leg was collected from each lobster captured during the SCUBA surveys. Muscle from urchins around the Aristotle's lantern, from the claws of crabs, the muscular foot from the limpet, and the depressor muscle from barnacles were dissected and rinsed with deionized water.

STABLE ISOTOPE ANALYSIS

Lobster and prey tissue samples were dried at 60°C for 60 hours, and finely ground using a SPEX Sampleprep mixer mill. Prior to stable isotope analysis, coralline algae samples were acidified with HCl to remove inorganic carbon. Samples from Big Fisherman Cove in January 2019 were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer at University of California, Davis stable isotope facility. All other samples were analyzed using an ECS 4010 elemental combustion system (Costech Analytical Technologies, Valencia, CA, USA) interfaced to a Delta V Advantage isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) through a ConFlo IV system (Thermo Scientific) at the Idaho State University stable isotope facility. Samples that were lipid rich (>3.5 C:N) were corrected to account for the negative $\delta^{13}\text{C}$ bias introduced by lipids (DeNiro and Epstein 1977) by applying a linear lipid normalization (Post et al. 2007).

Data analysis

HABITAT CHARACTERIZATION

To analyze the percent cover of organisms on the orthomosaics created from my images, I used the Image Classification toolset in ArcGIS 10.6.1. This is an automated classification approach in ArcMap that uses the spectral reflectance of objects in an image to classify them into categories. Categories of habitat classification were selected based on benthic species that are important within the California spiny lobster life history (Robles & Robb 1993). I focused on mussels (*Mytilus spp.*), barnacles (*Tetraclita rubescens*, *Chthamalus spp.*), red turf algae, the fucoid *Silvetia spp.*, and foliose red

algae. I did not classify mussel and algal groups further as it would require genetic testing for species level identification. Multiple training samples were taken for each classification by selecting samples of pixels to create a spectral signature of the species or group. The training samples were tested using the Supervised Image Classification which uses the spectral signatures from the training samples to classify each pixel in the image. Once a high confidence in the classification was reached, the training samples were then used to classify the transect images collected at each site. I was then able to extract percent cover data from the classified image based on the number of pixels corresponding to each habitat classification relative to the total pixels in the image.

A non-metric multidimensional scaling (nMDS) analysis was used to summarize differences between the transects and sites in species composition of the intertidal habitat, and a PERMANOVA was used to test whether the sites differed in composition, and if there is year to year variability within the sites. A total of $n = 3$ intertidal benches at Bird Rock, and $n=3$ intertidal benches at Big Fisherman Cove were sampled in 2017, 2018, and 2019. The data were square-root transformed to account for the right skew common in habitat cover data.

LOBSTER POPULATION METRICS

I used two-way ANOVA to determine if there are significant differences in the density or mean size of lobsters between sites (Fisherman's Cove/Bird Rock) and zones (intertidal/subtidal) (models: density = site + zone + (site * zone) + error, and mean size = site + zone + (site * zone) + error). Additionally, Chi-Squared tests were used to test for differences in the sex ratio (male vs female) and reproductive condition (presence vs absence of eggs on females) of lobsters.

STABLE ISOTOPE ANALYSIS

I assessed the annual and seasonal variation in dietary niches space of prey communities and lobsters at both Bird Rock and Big Fisherman Cove (Layman et al 2007) using SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011). The metrics of analysis include: 1) Nitrogen range (NR): the range of $\delta^{15}\text{N}$ - an indicator of trophic variability; 2) Carbon range (CR): the range of $\delta^{13}\text{C}$ - an indicator of diversity at the base of the food web; 3) Total area (TA): the measure of the trophic extent of the food web; 4) Nearest neighbor distance (NND): the mean distance of each species to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ centroid as a measure of diversity in the food web; and 5) Standard deviation of nearest neighbor distance (SDNND): the standard deviation of the NND - a measure of the distribution of trophic niches within the community. In this study I used these metrics to compare the prey communities at Bird Rock and Big Fisherman Cove. To assess the lobster niche as a species, I used the same package to create $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots and measure the standard ellipse area (SEA) which gives an estimate of isotopic niche area. This estimation is used for individual species within a community because it is less sensitive to sample size, and is an ideal tool for comparing isotopic niche between groups with dissimilar sample sizes (Jackson et al. 2011). In this study, I used SEA to estimate the niche space of lobsters within the community and assessed the annual and seasonal variation in SEA between Big Fisherman Cove and Bird Rock.

Diet preferences and the proportion of the diet composed by different prey sources were assessed using MixSIAR (Stock et al. 2018), a Bayesian mixing model for biological tracers (i.e., stable isotopes). Mixing models assume that the isotopic composition of the predator reflects that of the prey. By combining the lobster isotope

data with potential prey isotope data and estimates of trophic fractionation rates, I estimated the diet composition of lobsters at each site (Phillips 2012). I applied Bayesian mixing models with uninformed priors to analyze the stable isotopes from the muscle samples of the lobster and potential prey to estimate the diet composition of the lobster in each location. I analyzed the lobsters and prey from each location, Bird Rock and Big Fisherman Cove, independently. For each location, I performed a diet analysis of the summer and winter lobster and prey. For the summer analysis, I included subtidal and intertidal prey: mussels, crabs, limpets, snails, and urchins. For winter, I only included subtidal prey, snails and urchins, as the intertidal is inaccessible during the winter months (Robles et al. 1990, Windell 2015). To account for trophic fractionation, I assumed a carbon trophic discrimination factor of $0.8\text{‰} \pm 0.1$ and a nitrogen trophic discrimination factor of $3.3\text{‰} \pm 0.15$ based on values derived from rock lobster leg muscle (Suring & Wing 2009).

While MixSIAR is a powerful tool for diet assessment, there are many limitations in using mixing models. MixSIAR assumes that all prey species are included in the model. While I am confident that the major contributors to adult spiny lobster diet were captured (Barkai et al. 1996, Alka et al. 2016), more in-depth diet studies would be needed to determine if all potential resources were captured. Additionally, the closer the prey isotope values are to one another, the less power the model has in determining the proportional contributions of the prey to the consumer (Layman et al. 2012). In my study, there is high overlap in prey species, particularly the mussel and barnacle species. To address this concern, I omitted barnacle species from the analysis because a gut

content analysis of the lobsters at my site showed little evidence of barnacle foraging among the spiny lobsters (Garza, personal comm. 2017).

RESULTS

HABITAT CHARACTERIZATION

The comparison of intertidal habitat composition between Big Fisherman Cove and Bird Rock shows distinctly different benthic assemblages (PERMANOVA, $F_{1,13}=12.28$, Table 1, Fig. 4a) and no significant difference at each site between the years (PERMANOVA, $F_{2,13}=1.86$, Table 1). The primary benthic habitat cover at Big Fisherman Cove was distributed among *Silvetia compressa*, red foliose algae, turf, and barnacles (Fig. 4b). At Bird Rock, the primary benthic habitat had 30% more turf algae than at Big Fisherman Cove. There was negligible mussel cover at Big Fisherman Cove ($>0.5\%$) while mussels comprised 2% of the total habitat at Bird Rock. The mussel bed is only found on the western most transect, BRA, which had an average cover of 5% between 2017 and 2019.

LOBSTER POPULATION METRICS

In 2013 survey dives, 172 lobsters were observed – 131 at Bird Rock and 41 at Big Fisherman Cove. In 2013, there was a higher density of lobsters found in the intertidal compared to the subtidal during the nocturnal high tides ($F_{1,32} = 8.07$, $p = 0.008$, Fig. 7a, Table 2) and of the lobsters surveyed, there was a higher density at Bird Rock than Big Fisherman Cove ($F_{1,32} = 21.79$, $p < 0.001$, Fig. 5a, Table 2). In the 2018 and 2019 summer surveys, I observed 199 lobsters – 137 at Bird Rock, and 62 at Big Fisherman Cove. The same patterns were observed in 2017: There was higher lobster

density in the intertidal than subtidal during the nocturnal high tides ($F_{1,20} = 11.81$, $p = 0.003$, Fig. 5b, Table 3) and a higher density at Bird Rock than Big Fisherman Cove ($F_{1,20} = 13.958$, $p = 0.001$, Fig. 8b, Table 3). In both the 2013 and 2018-19 surveys, the interaction between zone and location is non-significant, indicating that the differences in density between zones was consistent between locations, such that lobsters have higher densities in the intertidal compared to subtidal at both locations during the nocturnal high tide.

A total of 113 lobsters were collected in the 2013 collection dives – 62 at Bird Rock and 51 at Big Fisherman Cove and 58% of the total were female. In the 2017-2019 surveys, a total of 148 lobsters were collected – 84 at Bird Rock and 34 at Big Fisherman Cove in the summer, and 56% were female. In the winter, 23 lobsters were sampled at Bird Rock and 7 at Big Fisherman Cove, and 55% of the total were female. In the 2013 lobster surveys, the sex-ratio was more skewed towards females at Bird Rock compared to Big Fisherman Cove (Chi-squared test, $\chi^2 = 17.36$, $p < 0.001$; Fig 6a). Of the lobsters collected at Bird Rock during the nocturnal high tide, 77% were female, while at Big Fisherman Cove, 44% of lobsters collected were female. Lobster reproductive condition was almost 20% greater at Bird Rock compared to Big Fisherman Cove (Fisher's exact test, $\chi^2 = 9.93$, $p = 0.002$; Fig 6b). Of the collected female lobsters at Bird Rock 97% were carrying eggs, while at Big Fisherman Cove 78% of female lobsters were carrying eggs in 2013.

In the 2017-2019 lobster surveys, I observed the same pattern with sex ratios skewed more towards females and higher reproductive condition in the intertidal at Bird Rock compared to Big Fisherman Cove. The proportion of female to male lobsters was

25% greater at Bird Rock relative to Big Fisherman Cove during the nocturnal high tides ($X^2=6.069$, $p < 0.001$, Fig. 7a). At Bird Rock, 63% of the lobsters collected were female, compared to 38% at Big Fisherman Cove. Lobster reproductive condition was 38% greater at Bird Rock compared to Big Fisherman Cove ($X^2 = 23.94$, $p < 0.0001$, Fig. 7b). At Bird Rock, 92% of the female lobsters were reproductive, compared to 54% at Big Fisherman Cove during 2017-2019.

STABLE ISOTOPE ANALYSIS

I found the community range of $\delta^{13}\text{C}$ at Bird rock to be similar to that of Big Fisherman Cove (Bird Rock $\delta^{13}\text{C} = -20.84\text{‰}$ to -7.96‰ , Fisherman Cove $\delta^{13}\text{C} = -22.81\text{‰}$ to -9.78‰ , Fig. 8a). The community at Bird Rock was more nitrogen enriched than those collected from Big Fisherman Cove (Bird Rock $\delta^{15}\text{N} = 8.67\text{‰} - 24.50\text{‰}$, Fisherman Cove $\delta^{15}\text{N} = 3.94\text{‰} - 16.74\text{‰}$, Fig. 8b). At both sites, the lobsters feed at the same trophic level, with some slight variation between sites due to the nitrogen enrichment at Bird Rock (Fig. 9). The individual lobsters are more uniformly distributed through the niche space in the summer at Bird Rock than Big Fisherman Cove (Fig. 9). In the winter, fewer lobsters were sampled, but it appears there is more uniformity in the diet among individuals in the winter at both sites (Fig. 9).

I calculated the Layman metrics of the communities at Bird Rock and Big Fisherman Cove without the lobster to understand the differences of the underlying prey communities at each site (Table 4). All prey (Big Fisherman Cove $n=215$, Bird Rock $n=164$) species collected were included in this calculation. The nitrogen range of the prey community is greater at Bird rock than at Big Fisherman Cove, but there is no difference in the carbon range. Thus, the total prey niche area (TA) is larger at Bird Rock (27.53‰^2)

than Big Fisherman Cove (22.01‰^2 , Fig. 10). This prey niche area represents the potential maximum niche size of the lobsters at each site, so the lobsters at Bird Rock have the potential for a large niche area than the lobsters at Big Fisherman Cove, based on the prey niche distribution. The mean distance to the centroid, another measure of niche diversity of the sites, is higher at Bird Rock (3.63‰) than Big Fisherman Cove (3.1‰), but this is likely due to the enriched nitrogen values of crabs at Bird Rock. At Bird Rock, MNND and SDNND are higher than at Big Fisherman Cove, suggesting that the prey are more divergent in their trophic niche at Bird Rock, than Big Fisherman Cove, but the prey niche spaces at Big Fisherman Cove are more evenly distributed.

I found seasonal differences in the isotopic niche space of lobsters at Bird Rock and Big Fisherman Cove. The isotopic niche space of lobsters is larger in the summer at both Bird Rock and Big Fisherman Cove (Fig. 11a, Table 5a), while the niche space is similar between the sites in the winter. There is overlap of the summer and winter confidence interval at Big Fisherman Cove suggesting they are not significantly different, but this is likely due to the limited sample size of lobsters collected at Big Fisherman Cove in the winter. Much of the variability in niche space is in the range of $\delta^{15}\text{N}$ for individuals at Bird Rock, but in the $\delta^{13}\text{C}$ range for individuals at Big Fisherman Cove. In both cases, the vector of isotopic niche expansion is the same, and in the direction of decreasing in $\delta^{13}\text{C}$ and increasing in $\delta^{15}\text{N}$ (Fig. 12) from summer to winter. There is little annual variation in the summer isotopic niche space at both sites in the summer. In contrast to the broader isotopic niche of the prey community, the niche space of lobsters is smaller at Bird Rock across all years compared to that of lobsters at Big Fisherman Cove (Fig. 11b, Table 5b).

Results of the mixing model suggest there are site differences in the diets of lobsters during the summer (Fig. 13). At both sites, subtidal resources dominated the diet, but at Bird Rock, lobster diets are subsidized with intertidal resources. Urchins make up 42% of the diet of male lobster and 45% of the diet of female lobster, while snails comprised 48% of the diet of males, and 42% of the diet of females at Bird Rock (Table 6). Mussels comprised more of the diet of female lobsters than male lobsters at Bird Rock, 7% and 4% respectively. Crabs and limpets contributed the least to both male and female diets, with less than 4% attributed to each. At Big Fisherman Cove, urchins were the largest contribution of both male and female lobster diets, comprising 96% of the diet. There is no difference in the male and female lobster diets at this site (Fig. 13c, d) and intertidal resources comprised less than 2% of the diet (Table 6).

Variability in the winter foraging patterns at Bird rock and Big Fisherman Cove is lower between sites than in the summer (Fig. 14). At Bird Rock, snails represented most of the diet of males and females, comprising 77% and 86% of the diets respectively. At Big Fisherman Cove, snails and urchins evenly contributed to female diets, and urchins comprised 63% of the diet of males (Table 7).

DISCUSSION

The results of this study show that the intertidal habitat are important for California spiny lobsters during their breeding season (May through August) on Santa Catalina Island, California. During this time, spiny lobsters widened their foraging range from the subtidal into the adjacent intertidal zone at night. This movement to the intertidal, and their associated foraging during these forays, subsidizes their subtidal diets during reproduction, a time of high energetic cost. This cross-system foraging subsidy is

not unique to the California spiny lobster and has been exhibited in other lobster species such as the American lobster (*Homarus americanus*) in New England (Jones & Shulman 2008), and western rock lobster (*Panulirus cygnus*) in Australia (MacArthur et al. 2008). The American lobster is generally found in deep offshore waters, but migrates to shallower water in the early spring to late fall and they utilize the intertidal resources such as mussels and crabs to subsidize their diets (Jones & Shulman 2008). Similarly, the western rock lobster shelters in reefs during the day, but forages along the shallow reefs at night (MacArthur et al. 2008).

The community niche of the prey is similar between Bird Rock and Big Fisherman Cove, as estimated by all Layman statistics, suggesting that the difference in the lobster SEA is not due to site differences in prey isotopic signatures, but rather relative availability and utilization of the prey across habitats at both sites. At Bird Rock, the mussels are larger, more abundant, and easier to access than the mussels at Fisherman's cove, where there is no true bed of mussels. Mussels are a high value prey item, with the caloric value of 0.55 ± 0.04 kcal/g wet weight, compared to sea urchins with a caloric value of 0.39 ± 0.04 kcal/g wet weight (Stewart & Konar 2012). This high energetic value is likely a significant factor driving the feeding preference for mussels across a range of lobster species (Robles 1987, Barkai et al. 1996, Haley et al. 2011, Alka et al. 2016). Diet switching to increase reproductive output or success is a common phenomenon exhibited across marine and terrestrial species. For some, prey availability and nutritional quality have direct effects on factors of reproduction like egg size and number of offspring, or the ability of the species to maintain physiological condition conducive to breeding (Reynolds et al. 2003, Hall et al. 2018, Xavier et al. 2018). The

success of reproduction can even be negatively influenced by the absence of a single amino acid (Koch et al. 2011). Therefore, the increased reproductive success of female lobster at Bird Rock, coupled with the increase in energetically rich mussels in their diet, suggests that the small bed of mussels on a 20 m² stretch of intertidal habitat is likely an integral part in their reproductive success.

In this study, at both Bird Rock and Big Fisherman Cove, lobster populations were generalist predators that exhibited similar trophic niches. However, together the mixing model (Fig. 13, 14) and lobster niche metrics (Table 5) together suggest the range and distribution of individual diet specialization varied across sites and seasons. At Bird Rock in the summer, lobsters, particularly females, forage on mussels. However, their diet predominantly consisted of a mix of snails and urchins with relatively few individuals specializing on either prey. At Big Fisherman Cove, individuals have a gradient of foraging preference, with most individuals foraging predominately on sea urchins, with the remaining lobsters specialized on snails or consumed a mix of these two prey items (Fig. 9). In the winter, at both sites the reduction in niche size was driven by the lack of intertidal resources and the apparent reduction individual resource specialization, with most lobsters consuming a mix of urchins and snails, though those at Bird Rock exhibited a higher proportion of urchins in their diet (Fig. 14). Seasonal diet switching based on resource availability is seen in many other systems. From lake fish (Pool et al 2017) and carp (Coulter et al. 2019), to Neotropical frugivorous bats (Shipley and Twining 2020), species exhibit niche width expansion coinciding with seasonal changes in prey or habitat availability. Historically it is thought that an increase in prey diversity should lead to a dietary niche expansion of the consumer (Yoder et al. 2010),

but this isn't the case for all predators. The effect on niche size is dependent on the per capita effect the predator has on the prey population (Jones & Post 2016). When predator foraging has a strong ecological effect on the prey population, resource depletion limits the dietary breadth of the species (Jones & Post 2016). In the present study, we see a larger niche space at Big Fisherman Cove than at Bird Rock in the summer, but the mixing model suggest more diverse prey utilization at Bird Rock. The findings in Jones & Post (2016) suggest that this may be due to the difference in the per capita effect due to the preference of mussels at Bird Rock.

As opportunistic predators, spiny lobsters will switch to foraging on lower value prey when high value prey items are not present (Barkai et al. 1996, Briones-Fourzán et al. 2019). For the Rock lobster, *Jasus lalandi*, after a preferred food resource has been depleted, the population diet shifts to smaller, low-energy food resources to maintain their population densities (Haley et al. 2011). I saw effects of the consumption of lower value prey at Big Fisherman Cove in the decreased density, size, and proportion of reproductive females of when compared to Bird Rock. Since the quality of prey available is lower in the intertidal at Big Fisherman Cove, the value of prey subsidy and therefore the effect of increasing the capacity for a larger abundance of lobsters is decreased, with effects on lobster reproductive success (Polis et al. 1997). The western rock lobster, *Panulirus cygnus*, experiences a higher survival rate when more mussels are incorporated in their diet, and individuals fed a diet containing mussels either solely or as a supplement, had a faster growth rate than those without mussels in their diet (Johnston et al. 2007).

The mussel cover throughout southern California has been declining for decades (Smith et al. 2006), and recruitment is significantly lower than throughout the rest of the California and Oregon communities (Connolly et al. 2001, Broitman et al. 2008). In a 2013 habitat study using the same methods as this paper, the mussel bed at Bird Rock was calculated to cover 4.2% of the habitat (Windell 2015), compared to the 2% cover measured 5 years later in this study. In 2014, a warming event, nicknamed “The Blob” affected the entire North Pacific Ocean, causing large scale temperature increases in surface water through the region (Zaba & Rudnick 2016). The mussel beds were already in a state of decline throughout southern California, before the marine heat wave (Smith et al. 2006), and these temperature anomalies are not likely the sole cause of the decline in mussel cover as they have been shown to be resilient to climate change (Liu et al. 2014, Miller & Dowd 2019). Indirect effects of the increased surface temperature, like increase in predation rate (Contolini et al. 2020, Hull 2020), or limitations at the base of the food web (Delgadillo-Hinojosa et al. 2020) may have contributed to the decline of the mussel bed. Compared to the 2013 survey, I observed a lower reproductive condition of the females collected in Big Fisherman Cove and a decrease in the proportion of females at this site but increase in the proportion of females and reproductive condition at Bird Rock. Further monitoring is necessary to understand the relationship between mussel bed cover and the proportion of mussels in the diet of lobsters at Bird Rock. Some species have shown that the energy content and nutrients of mollusk species are important for reproductive success (Selman & Lindeman 2018). As the mussel beds on Santa Catalina Island decrease, and therefore the prey value of the subsidizing habitat declines, it is

likely that the capacity for a larger population abundance will also decline at Bird Rock, becoming more similar to the population at Big Fisherman Cove.

FUTURE RESEARCH

While the SIA data revealed important differences in the trophic ecology of lobsters between sites and seasons, it could not provide insight to the actual nutritional value of the different prey species consumed. To better understand the mechanisms behind why I observed differences in the population metrics between the sites, it would be crucial to incorporate nutritional content of the lobster and prey in future studies (Machovsky-Capuska et al. 2016, 2018). This study assessed the temporal variability in the effects of lobster resource use but focused on one study site. Future studies should assess how this translates to the rest of the Channel Islands and through the range of the spiny lobsters.

CONCLUSIONS

While the lobsters were less abundant and with lower reproductive output inside the MPA on Catalina compared to the site open to fishing, this marine reserve has been shown to be effective for increasing the size and density of a number of fish species that reside within the boundaries of the MPA (Froeschke et al. 2006, Selden et al. 2017). The methods presented in this study offer an approach for researchers and managers to use to help assess the effects of reserves on specific target species, and to understand why MPAs work for some species, but not others.

The methods employed in this work represent a novel approach in marine ecology as they integrated modern diet assessment techniques and use of geospatial technology to increase the efficiency of data collection. The use of stable isotope analysis with open-

source software analysis allows for a non-lethal way of assessing the long-term diets of protected species that other researchers can replicate and expand on the data available. Using photographic transects and ArcGIS software allows us to collect more data in less time with comparable results compared to traditional field sampling methods. The application of drones represents the next step in the use of digital survey methods as they are cost effective and require few people to conduct survey an area. They are also able to capture large survey large areas in a short amount of time relative to traditional quadrat-based survey methods (Garza 2019). Many different projects – especially long-term monitoring projects of intertidal and subtidal habitat features – would benefit from incorporating drone and other photographic based geospatial techniques in future collections to reduce the cost and time of sampling. As demonstrated in this study, incorporating fine scale habitat analysis into the design of MPAs will likely increase the protection effect on the target species.

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43:1241–1248

APPENDIX I. TABLES

Table 1. PERMANOVA of 2017-2019 benthic habitat comparison of Bird Rock and Big Fisherman Cove

Source	df	SS	R2	F	P
Site	1	0.476	0.420	12.086	0.001*
Site:Year	2	0.146	0.129	1.860	0.124
Error	<u>13</u>	<u>0.512</u>	0.451		
Total	16	1.134	1.000		

Table 2. Two-way ANOVA of 2013 lobster density. 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*
Location x Zone	1	0.042	0.042	2.00	0.167
Error	<u>32</u>	<u>0.681</u>	0.021		
Total	35	1.36			

Table 3. Two-way ANOVA of 2019 lobster density. 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	0.496	0.496	11.81	0.003*
Location	1	0.586	0.586	13.96	0.001*
Location x Zone	1	0.046	0.046	1.09	0.308
Error	<u>20</u>	<u>0.840</u>	0.420		
Total	23	1.97			

Table 4. Community metrics described in Layman et al 2007 to compare the isotopic community at Bird Rock and Big Fisherman Cove. The ranges in the parentheses represent the 95% confidence interval calculated in SIBER. Nitrogen range (NR), carbon range (CR), total area (TA) and mean distance to centroid (CD) give an idea of the community structure, and mean nearest neighbor distance (MNND) and standard deviation of nearest neighbor distance (SDNND) reflect the relative position of species to each other within the niche space.

Layman Metrics	Bird Rock	Big Fisherman Cove
NR	7.73 (7.61 - 8.64)	5.72 (5.55 - 6.55)
CR	8.06 (7.75 - 8.67)	8.49 (7.76 - 9.43)
TA	27.53 (26.20 - 32.20)	22.01 (20.81 - 27.98)
CD	3.63 (3.60 - 4.00)	3.1 (2.94 - 3.35)
MNND	3.43 (3.19 - 3.78)	2.52 (2.16 - 2.95)
SDNND	1.58 (1.46 - 2.23)	1.32 (1.38 - 2.03)

Table 5. Lobster isotopic niche space results from SIBER analysis assessing: A. seasonal differences in lobster niche size at Bird Rock and Big Fisherman Cove, and B. the annual variation in lobster isotopic niche size at Bird Rock and Big Fisherman Cove.

A.

Site	Year	<i>n</i>	Lobster niche (‰²)	
			Mode	95% Confidence Interval
Bird Rock	Summer	88	0.922	0.746 - 1.211
	Winter	23	0.502	0.329 - 0.761
Big Fisherman Cove	Summer	50	1.005	0.748 - 1.342
	Winter	10	0.587	0.290 - 1.197

B.

Site	Year	<i>n</i>	Lobster niche (‰²)	
			Mode	95% Confidence Interval
Bird Rock	2017	34	0.765	0.543 - 1.103
	2018	11	0.421	0.223 - 0.841
	2019	43	0.545	0.395 - 0.738
Big Fisherman Cove	2017	22	1.092	0.722 - 1.730
	2018	16	1.144	0.695 - 1.962
	2019	12	0.974	0.512 - 1.792

Table 6. Percent of prey contribution to the lobster diet as determined by MixSiar model for lobsters collected in the summer at A. Bird Rock and B. Big Fisherman Cove.

A.

Bird Rock

Lobster Sex	Prey	Mean	SD	95% Confidence Interval	
				Lower	Upper
Male	Crab	3%	3%	0%	8%
	Limpet	3%	3%	0%	10%
	Mussel	4%	3%	1%	11%
	Snail	48%	6%	39%	59%
	Urchin	42%	9%	25%	54%
Female	Crab	4%	2%	1%	8%
	Limpet	3%	3%	0%	8%
	Mussel	7%	4%	2%	13%
	Snail	42%	5%	34%	51%
	Urchin	45%	8%	31%	57%

B.

Big Fisherman Cove

Lobster Sex	Prey	Mean	SD	95% Confidence Interval	
				Lower	Upper
Male	Crab	1%	1%	0%	2%
	Limpet	0%	0%	0%	1%
	Mussel	1%	1%	0%	2%
	Snail	3%	2%	1%	6%
	Urchin	96%	2%	92%	99%
Female	Crab	1%	1%	0%	2%
	Limpet	0%	0%	0%	1%
	Mussel	1%	1%	0%	2%
	Snail	2%	1%	1%	5%
	Urchin	96%	2%	92%	99%

Table 7. Percent of prey contribution to the lobster diet as determined by MixSiar model for lobsters collected in the winter at A. Bird Rock and B. Big Fisherman Cove.

A.

<i>Bird Rock</i>					
Lobster Sex	Prey	Mean	SD	95% Confidence Interval	
				Lower	Upper
Female	Snail	86%	4%	78%	92%
	Urchin	14%	4%	8%	22%
Male	Snail	77%	5%	69%	86%
	Urchin	23%	5%	15%	31%

B.

<i>Big Fisherman Cove</i>					
Lobster Sex	Prey	Mean	SD	95% Confidence Interval	
				Lower	Upper
Female	Snail	50%	18%	15%	74%
	Urchin	50%	18%	26%	86%
Male	Snail	37%	17%	9%	62%
	Urchin	63%	17%	39%	91%

APPENDIX II. FIGURES

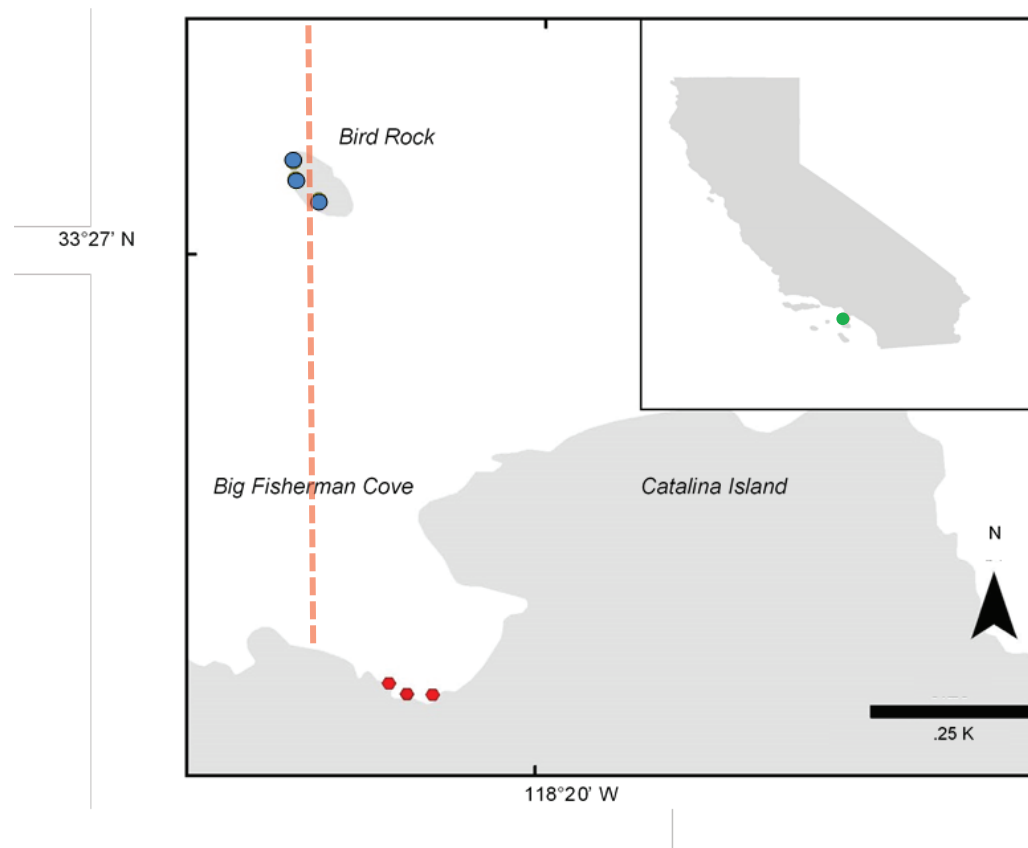


Figure 1. Study sites on Catalina Island, indicated in green on the inlayed map. The three transect locations are indicated in red (Big Fisherman's Cove) and blue (Bird Rock). The dotted red line represents the boundary of the Blue Cavern State Marine Conservation Area, where west of the line is protected, and east is unprotected.

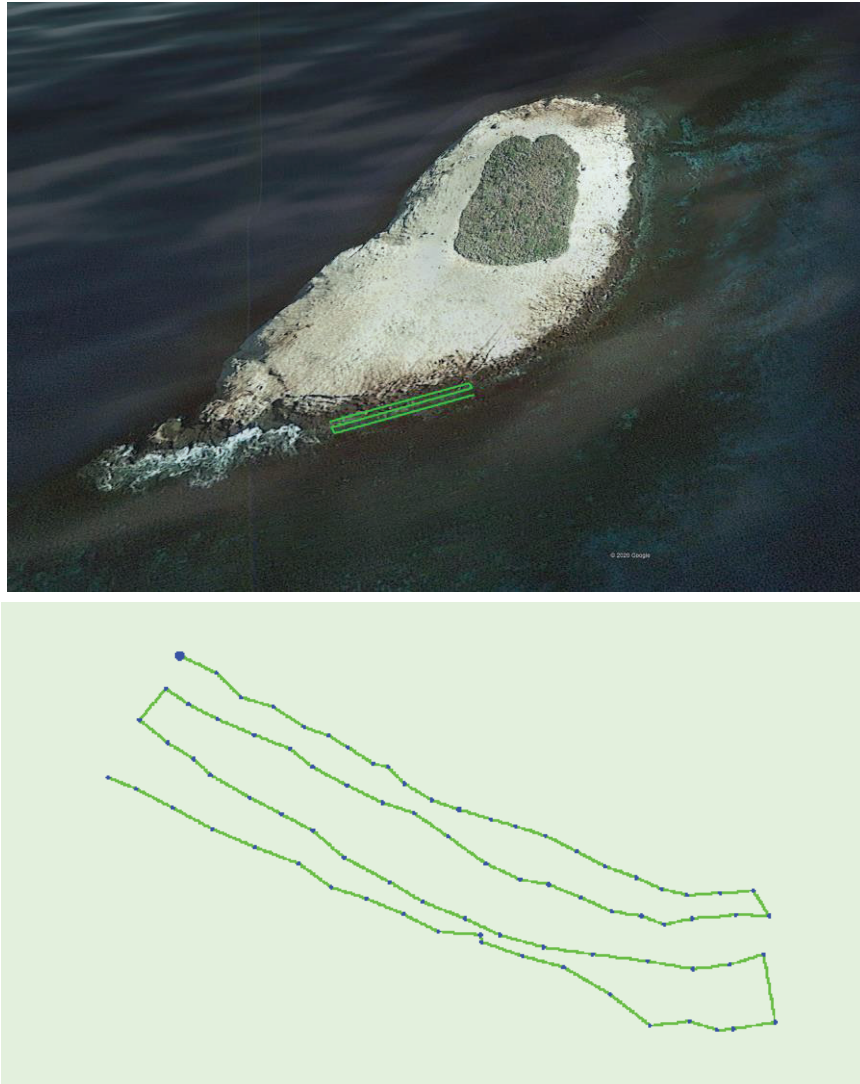


Figure 2. A. Example flight path (in green) for one 20m² transect on Bird Rock. Each pass extends the length of the transect, and each pass is approximately 0.5m lower in the intertidal than the previous pass. B. Drone flight path from the habitat anal

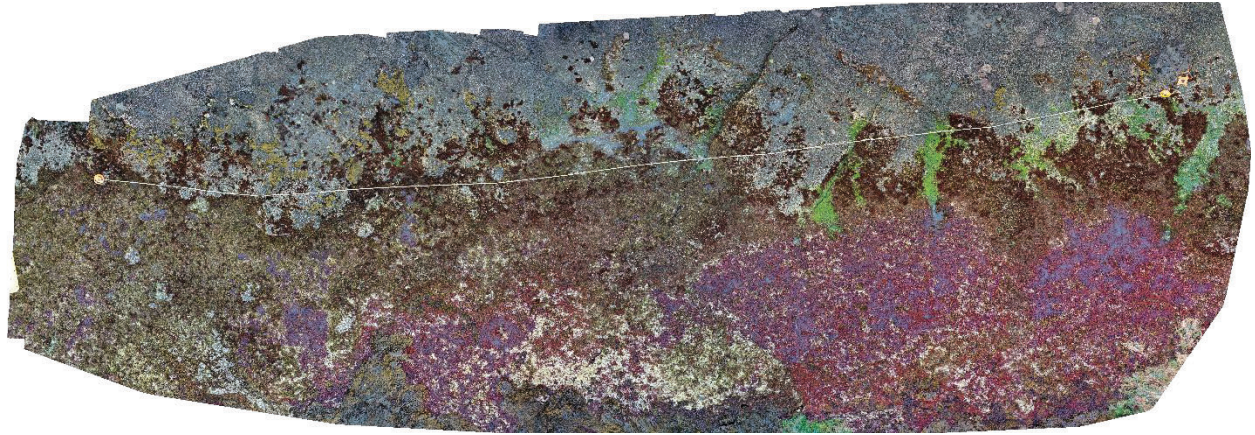


Figure 3. Bird rock photomosaic from 85 drone images after structure from motion (SFM) rendering in Pix4d.

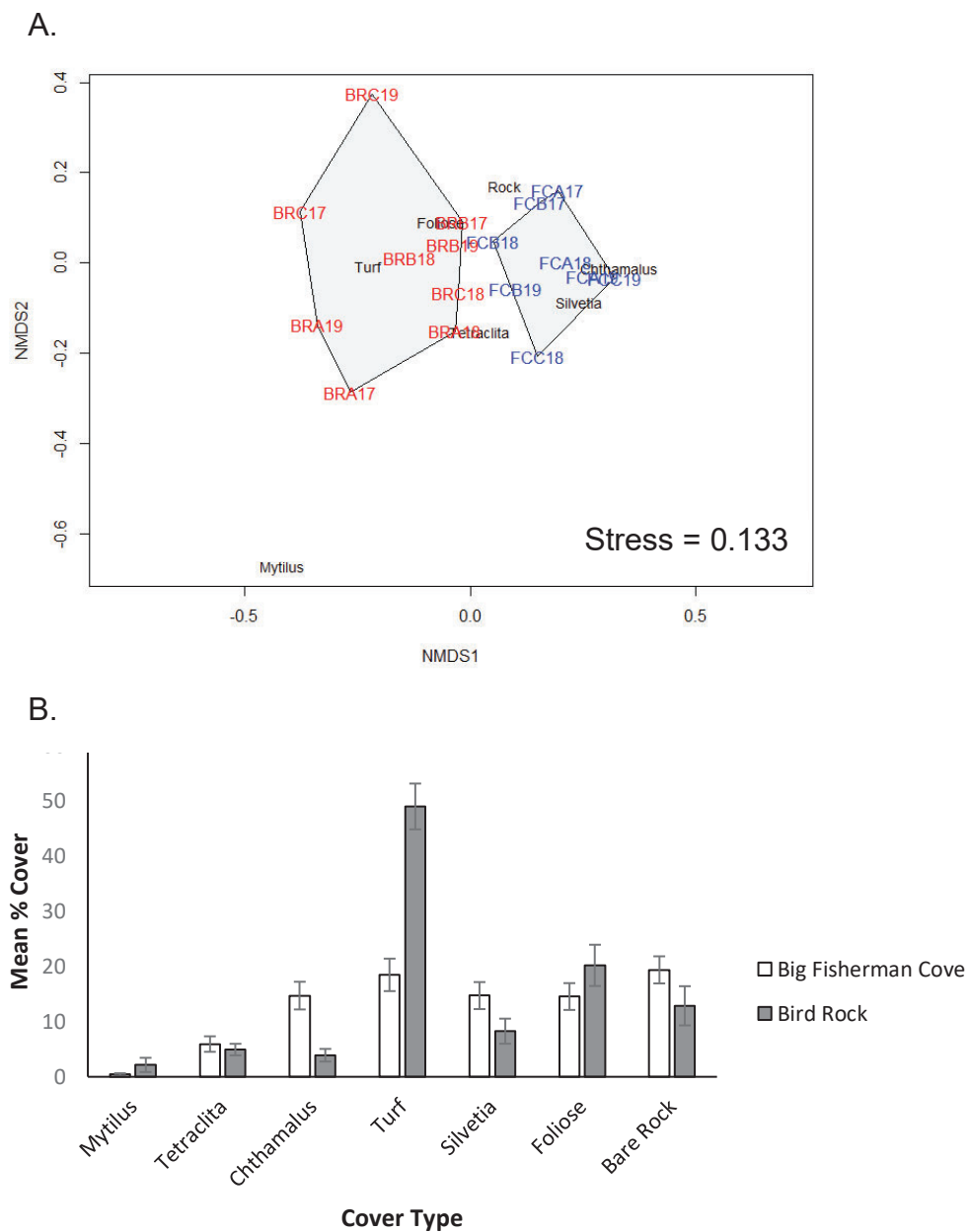


Figure 4. Non-metric multidimensional scaling analysis of intertidal habitat cover at Bird Rock (Red) Big Fisherman Cove (Blue). B. Average intertidal benthic cover from 2017-2019 of Big Fisherman Cove (White) and Bird Rock (Gray). Error bars are ± 1 standard error.

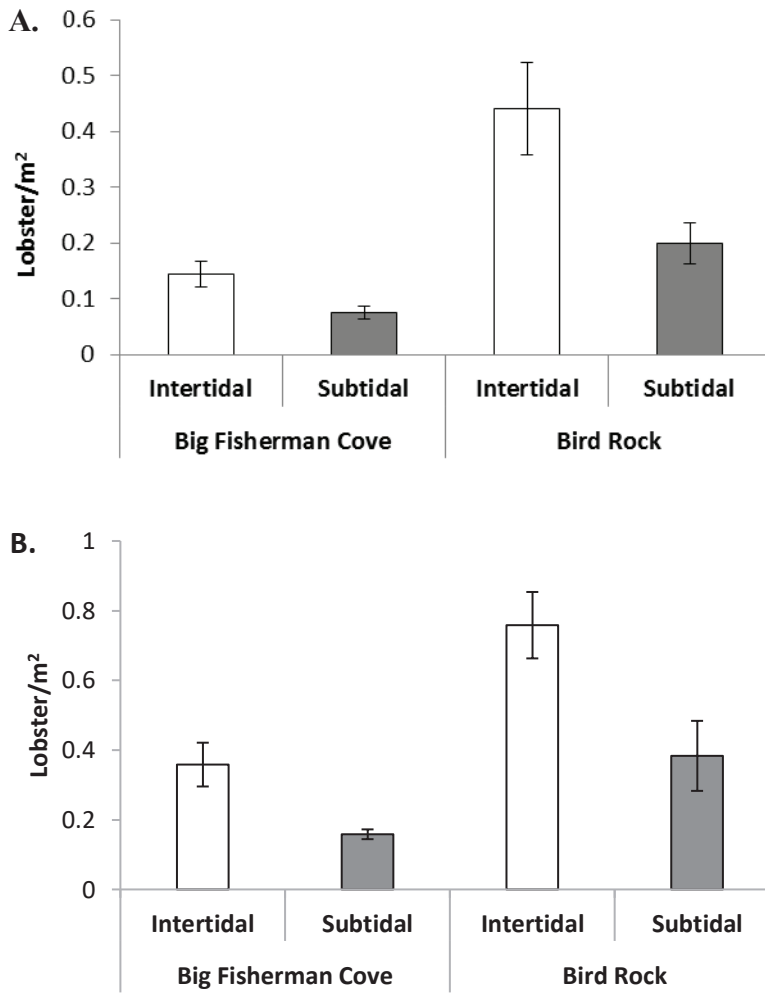


Figure 5. Mean lobster density by Zone (Intertidal and Subtidal) and Location (Big Fisherman Cove) in A) 2013 and B) 2019. Error bars are ± 1 standard error.

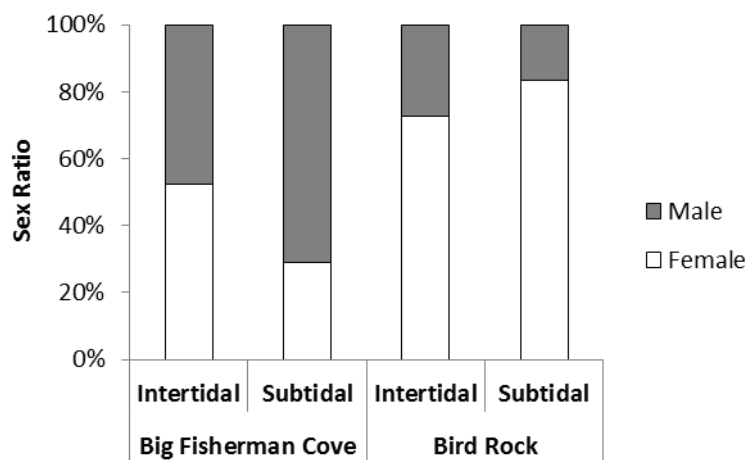
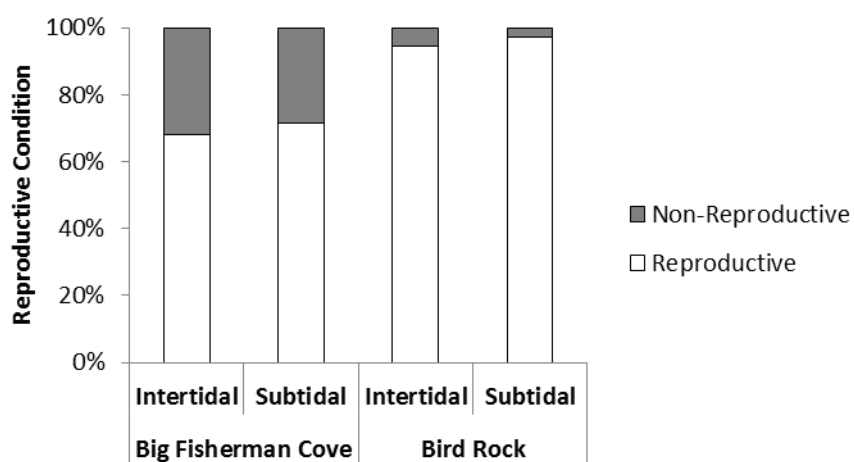
A.**B.**

Figure 6. Lobster demographic surveys 2013. 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.

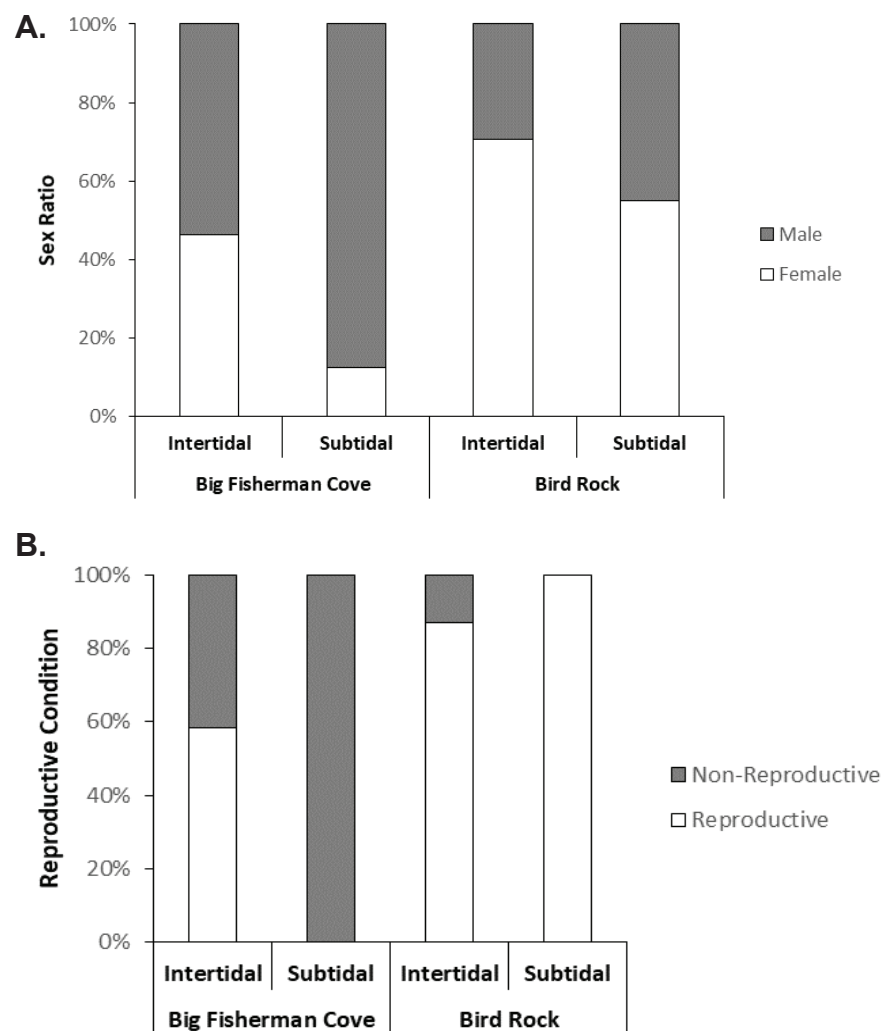
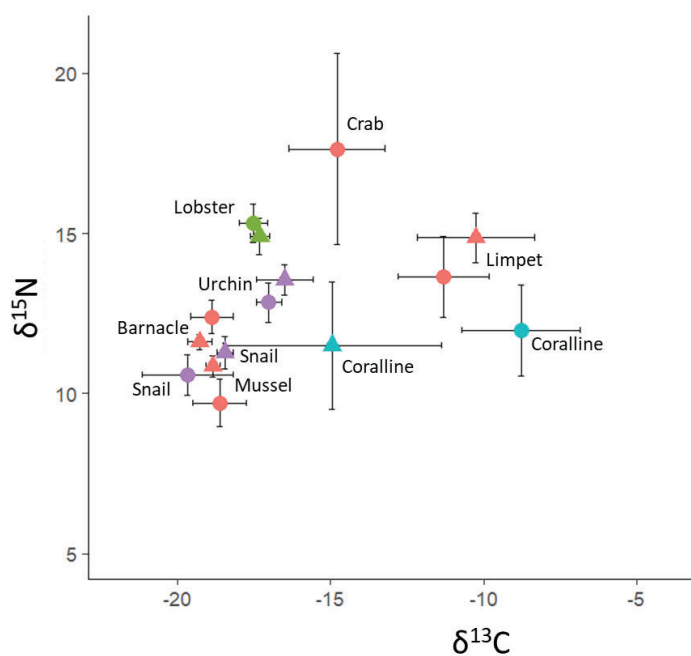


Figure 7. Lobster demographic surveys 2019. A) Proportional comparison of sex between Big Fisherman Cove and Bird Rock. B) Proportional comparison of reproductive condition (presence or absence of eggs on females) between Big Fisherman Cove and Bird Rock.

A. Bird Rock



B. Fisherman Cove

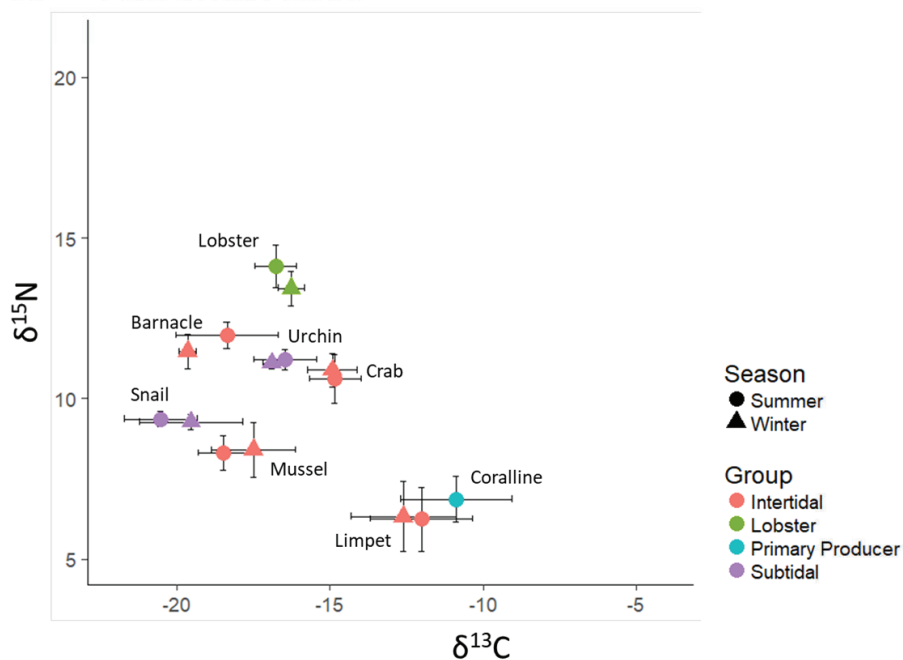


Figure 8. Community $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot of A. Bird Rock and B. Big Fisherman Cove. Each point represents the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, with error bars that represent the standard deviation.

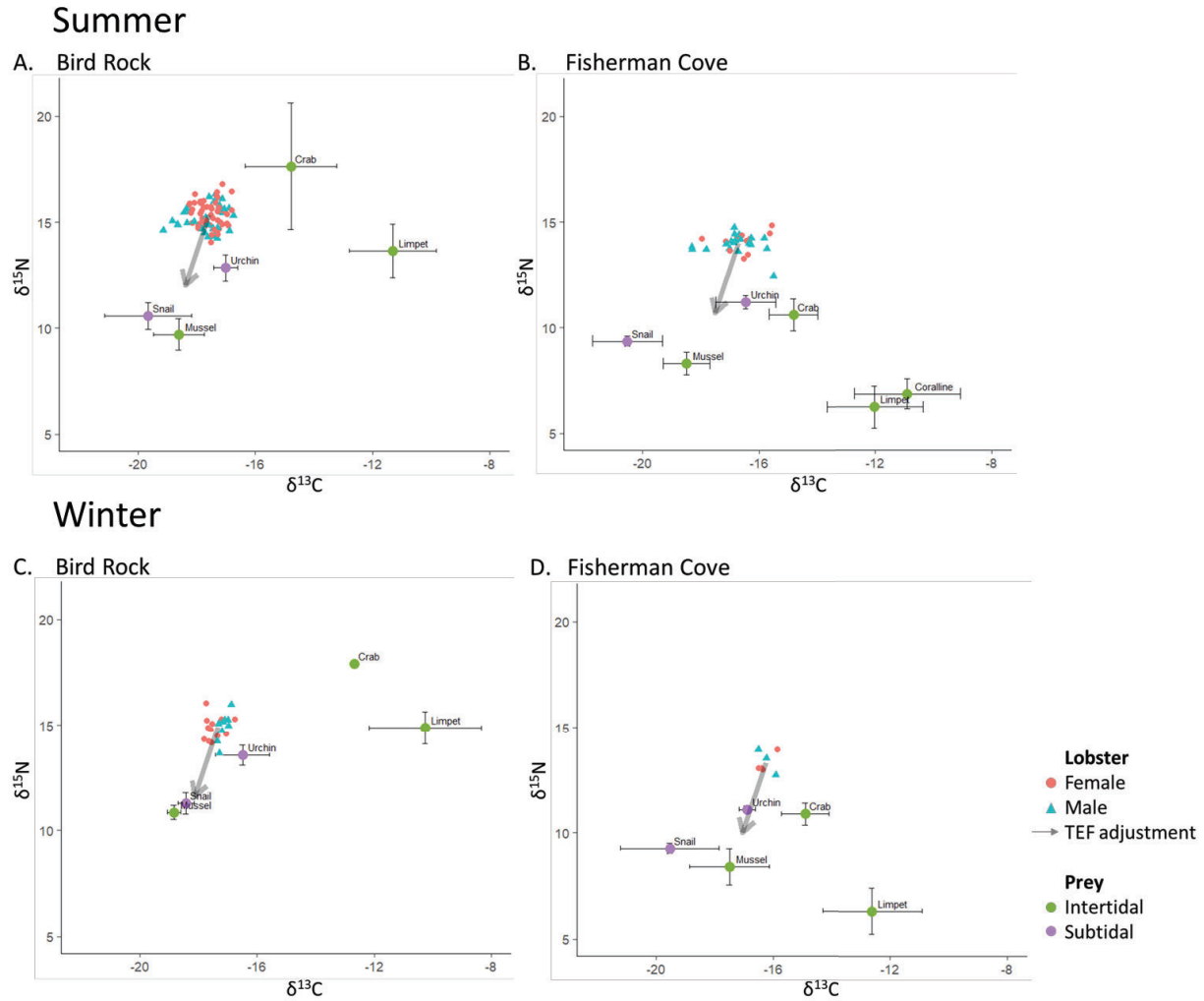


Figure 9. Community $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ with the individual lobsters bi-plot by season for Bird Rock: A. summer and C. winter, and Big Fisherman Cove: B. summer and D. winter. The red circles represent female lobsters, the blue triangles represent male lobsters, and the gray arrow represents the trophic discrimination factor adjustment of -0.8‰ for carbon and -3.3‰ for Nitrogen). The prey are represented by green circles for intertidal species, and purple circles for subtidal species. Error bars represent the standard deviation.

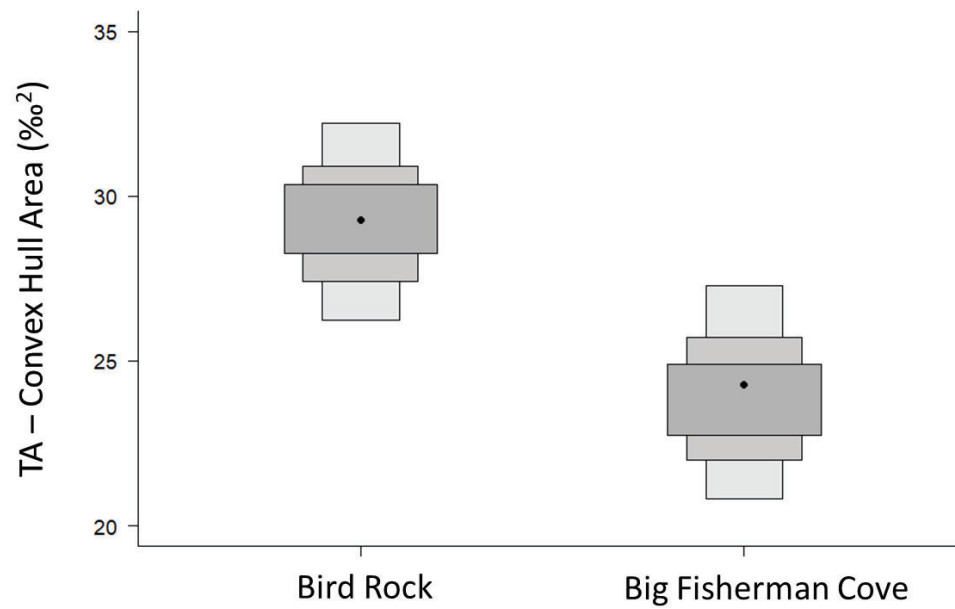


Figure 10. Total area (TA) of the convex hull – a measure of community niche space of the putative prey species for lobsters at Bird Rock and Big Fisherman Cove where the point represents their mode, and shaded boxes represent the 50%, 75%, and 95% credible intervals from dark to light grey.

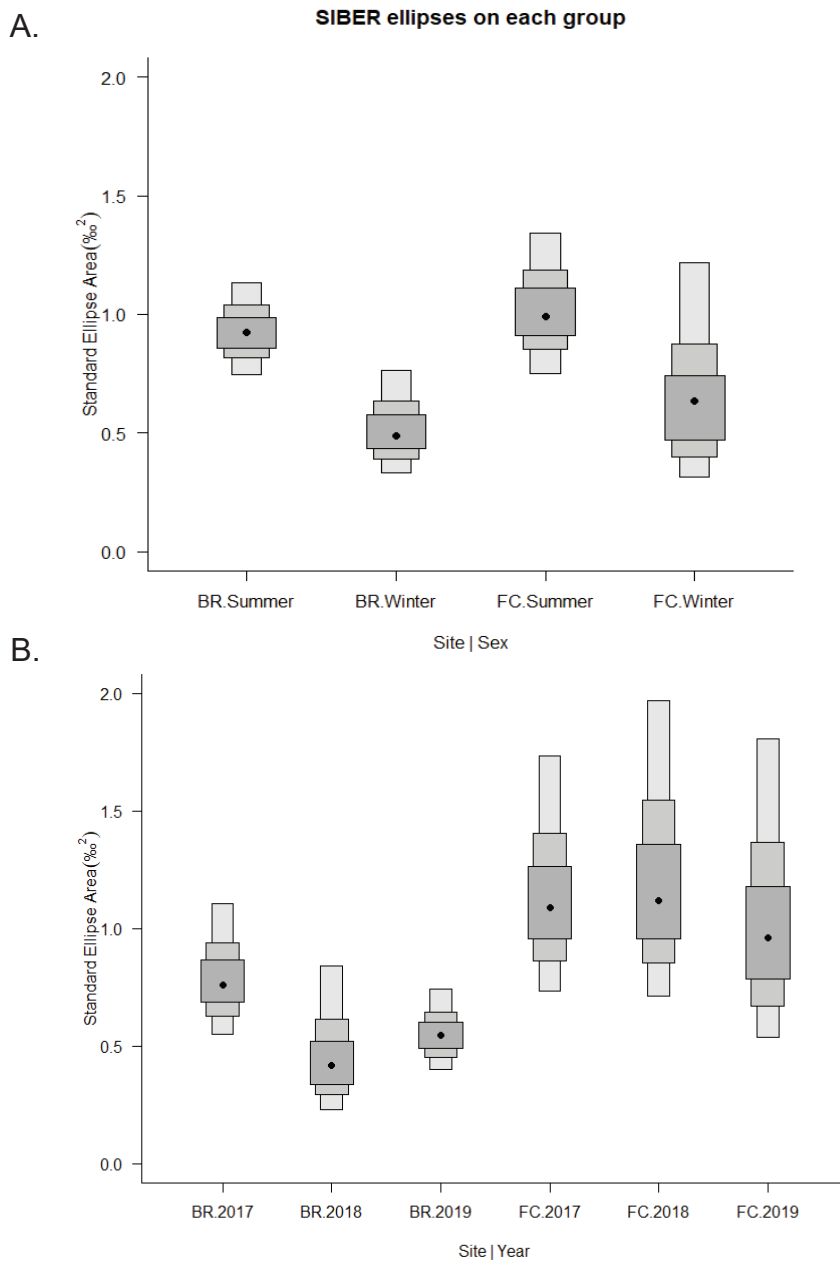


Figure 11. Standard ellipse area – an estimation of dietary niche – of lobsters at Bird Rock (BR) and Big Fisherman Cove (FC) by A) season and B) year where the point represents their mode, and shaded boxes represent the 50%, 75%, and 95% credible intervals from dark to light grey.

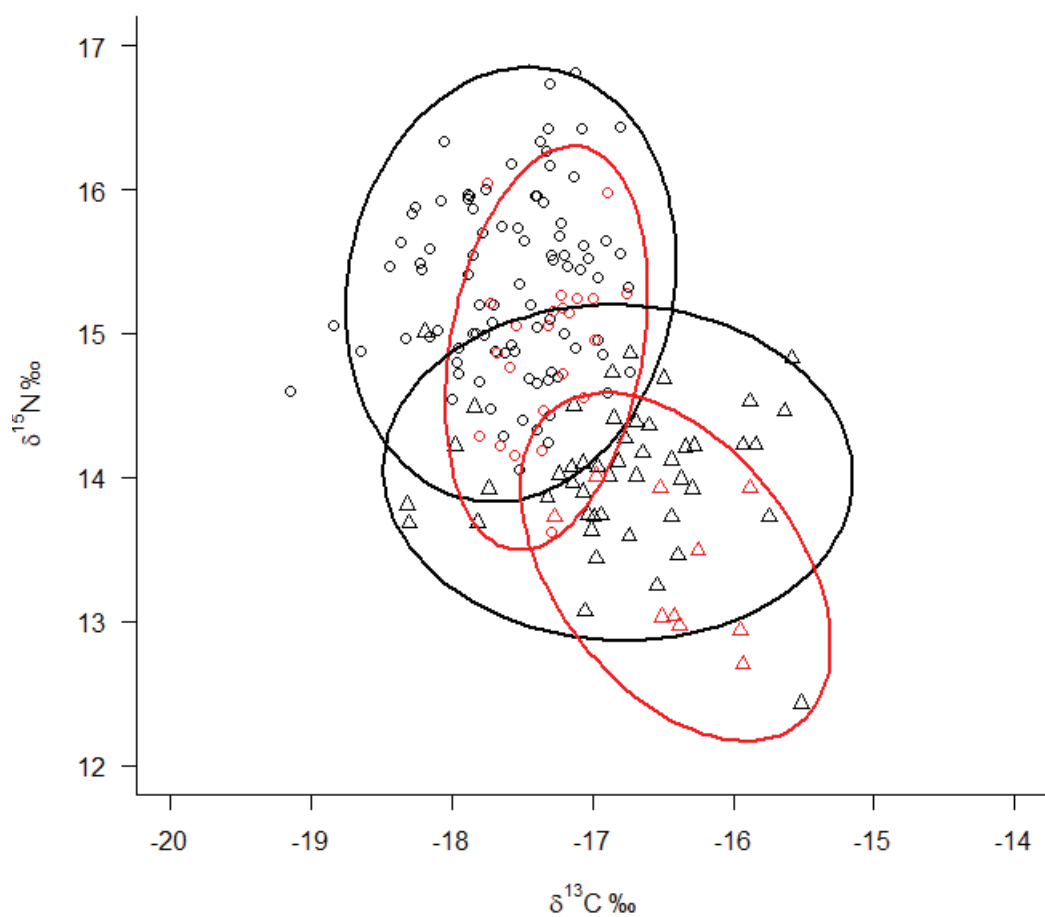


Figure 12. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot of lobsters at Bird Rock (circles) and Big Fisherman Cove (triangles) during summer (black) and winter (red).

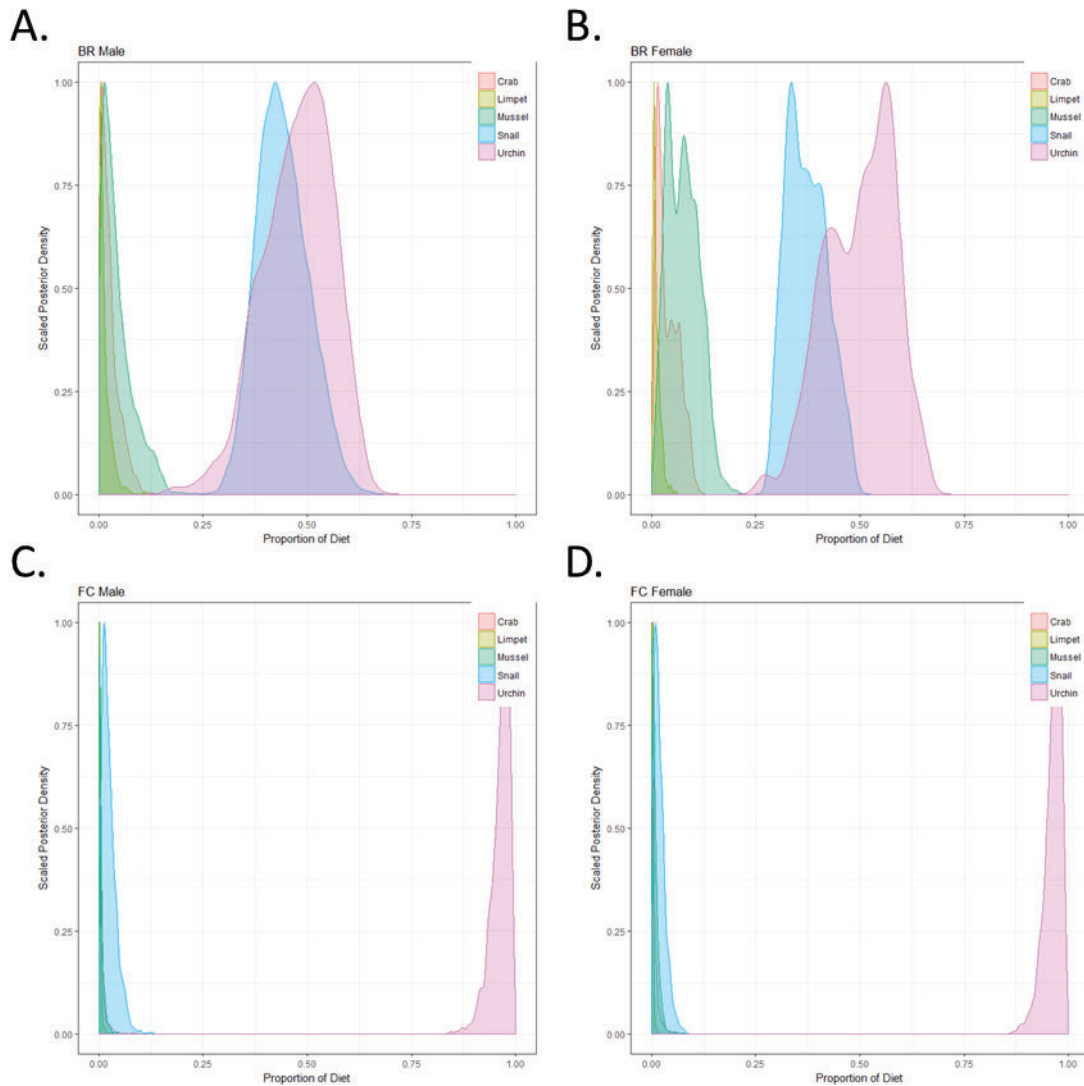


Figure 13. Diet estimates for the lobsters collected in the summer using MixSIAR Bayesian mixing models for Bird Rock A. Males and B. Females and Big Fisherman Cove C. Males and D. Females. The intertidal prey are: crabs - *P. crassipes* (red), mussels - *Mytilus sp.* (green), limpets - *Lottia sp.* (yellow); and subtidal prey are: snails – *M. undosa* (blue), and urchins – *C. coronatus* (purple).

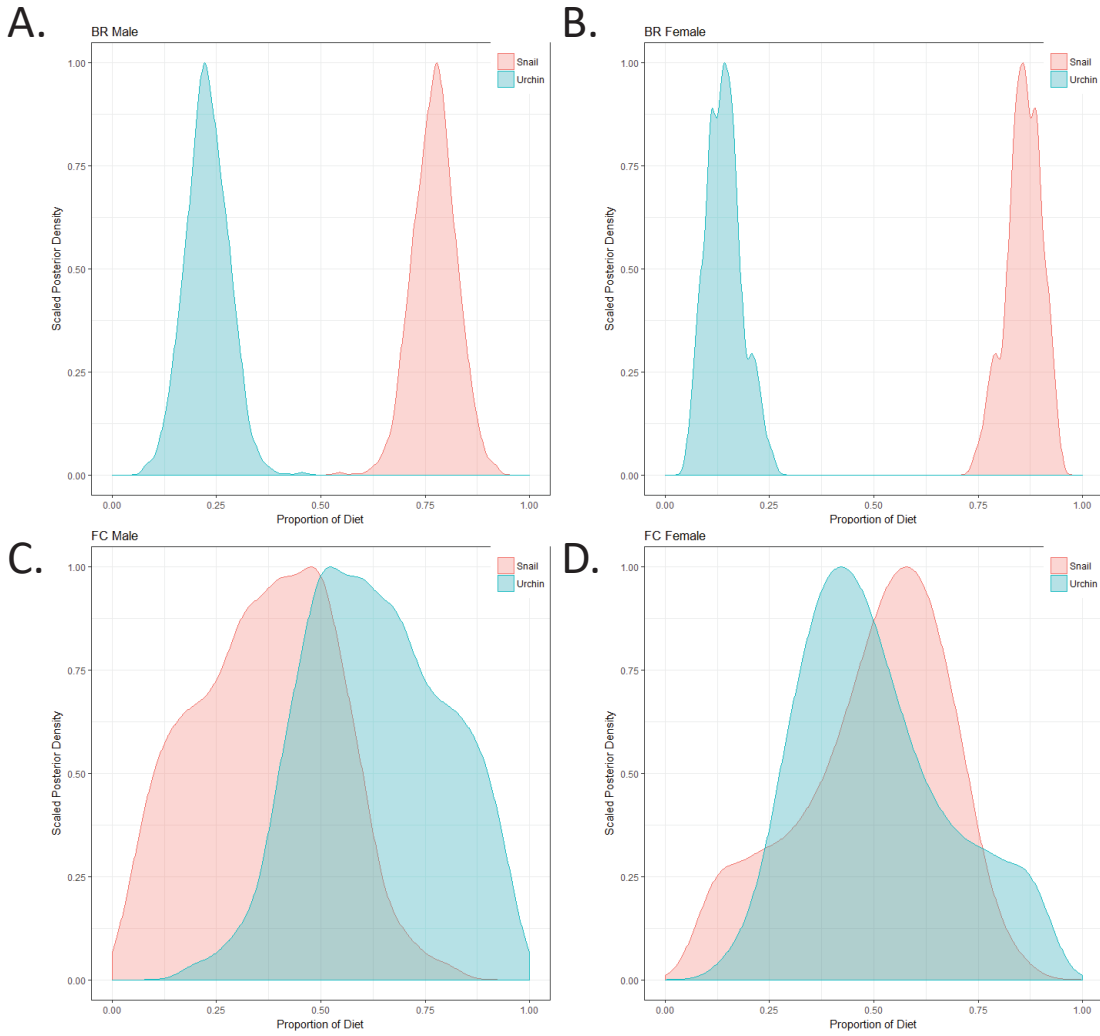


Figure 14. Diet estimates for the lobsters collected in the winter using MixSIAR Bayesian mixing models for Bird Rock: A. Males and B. Females, and Big Fisherman Cove: C. Males and D. Females. The subtidal prey are represented as: snails – *M. undosa* (red), and urchins – *C. coronatus* (blue).