Modes of Species Distributions in Central California Kelp Forests: A Study of *Embiotocidae* and *Sebastes*

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Introduction

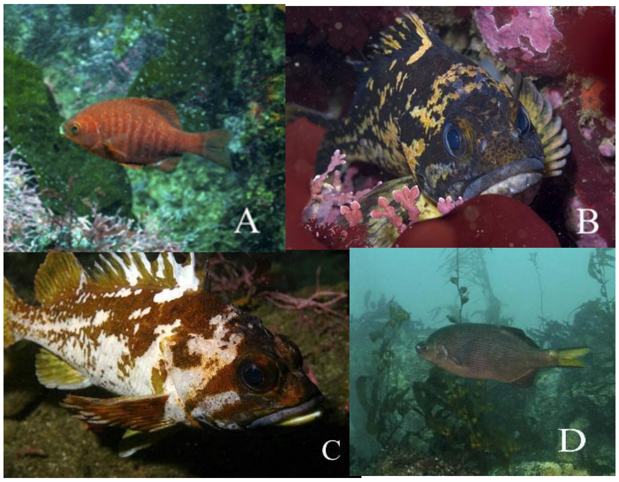


Figure 1. Images of species studied. Images from kelp forests. Photos: (A, B, D) Chad King. (C) Josh Pederson.
A- Black Perch (*Embiotoca jacksoni*)
B- Black and Yellow Rockfish (*Sebastes chrysomelas*)
C- Gopher Rockfish (*Sebastes carnatus*)
D- Striped Perch (*Embiotoca lateralis*)

Over the years, many ecological studies have aimed to address the underlying mechanisms of species coexistence. How can singular ecosystems support such vast species populations? The competitive exclusion principle, as described by Garrett Hardin in 1960, maintains that no two species can occupy the same niche, which in turn drives organisms to evolve, adapt, or die in instances of resource overlap. Niche diversification and resource partitioning are the theorized outcome of interspecific competition, allowing an ecosystem to support a multitude of species without the risk of overexploitation (Walter 1991). Food, habitat, temperature, and regional variations are just some of the many factors that contribute to the formation of local communities (Hines 1982). By approaching niche diversification as the product of a multi-dimensional ecosystem, we become better informed on the roles and interactions of species within a habitat. Habitat association in particular drives niche diversification (Hines 1982). A group of similar species utilizing the same resources can coexist if their habitat associations differ whether it be through stratification in the water column to exploit different food sources, or the partitioning of plants in the Amazon based on preferences in soil type (Hallacher & Roberts 1985, Phillips *et al.* 2003). Niche diversification informs us about the roles that species have in an ecosystem and the importance of their interactions, whether interspecific or intraspecific.

Rockfish, of the family *Sebastes*, and perches, of the family *Embiotocidae*, represent a handful of the species found in the kelp forest off California's central coast. Both families exhibit marked similarities in morphology, experiencing high degrees of dietary overlap that have fostered unique interspecific relationships, motivating ecologists and biologists alike to examine their patterns of association (Larson 1980b, Hallacher & Roberts 1985, and Holbrook & Schmitt 1989). Larson (1980b) maintains that *Sebastes chrysomelas* “aggressively exclude" *Sebastes carnatus* from the preferred food-rich shallow water regions. Additionally, a 1989 study observed that *Embiotoca jacksoni* and *Embiotoca lateralis* are distributed relative to depth and implied this was due to the distribution of abundance of their preferred food source and foraging microhabitat, which they believe contributes to varying degrees of interspecific competition (Holbrook & Schmitt 1989). This inspired our team of researchers to explore these distributions *in situ* by conducting population distribution surveys of *Embiotoca lateralis, Embiotoca jacksoni, Sebastes chrysomelas,* and *Sebastes carnatus.* By recording their observed distributions across a variety of microhabitats, we would be able to address several hypotheses.

Our study aims to explore the patterns of fish assemblages in relation to depth, substrate, and the presence of other fish species as a possible product of niche diversification and resource partitioning. Here, we propose several hypotheses: 1) fish assemblages occur in random patterns relative to depth, 2) fish groups are randomly distributed relative to substrate type and substrate cover type, and 3) fish groups are randomly distributed relative to other fish groups. By uncovering the mechanisms of coexistence and resource partitioning conclusions can be drawn about the spatial structuring of communities. This information is valuable to the integrity of future ecosystem management and conservation, especially in the face of threats such as climate change.

Methods

General Approach

We conducted an observational field study using SCUBA at Hopkins Marine Station in Pacific Grove, California (36.6202° N, 121.9041° W). To test our hypotheses, we conducted fish swaths and uniform point contact (UPC) surveys at various depth profiles on both the deep and shallow sides of the underwater cable present at Hopkins. By comparing UPC data and fish population data from subsequent surveys, we are able to form confident conclusions about fish assemblages as they relate to habitat. Multiple regression methodology of data analysis was used to understand the data as this method allowed us to consider various factors influencing the fish at once. Understanding various factors that influence the abundance and distribution of the test species will help us understand if the patterns we observed were random or not. Determining if these patterns are random or not will inform us about the various fish species and the relationship between them.

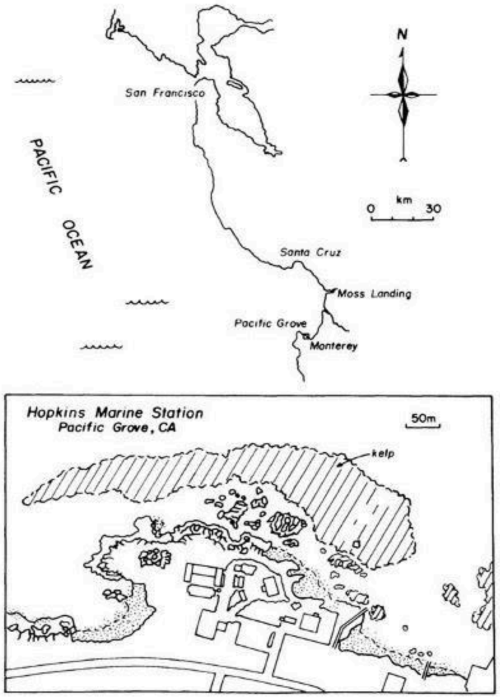


Figure 2. Map of Hopkins location along the California coast. The study site was limited to the shaded area in the lower portion of the figure.

System Description

This research was conducted in the kelp forest offshore of Hopkins Marine Station (Figure 2). Hopkins lies within the Lovers Point-Julia Platt State Marine Reserve and has been protected by the State of California since 1931 (Jones 1985). This means that Hopkins is only accessible to those conducting scientific research making the system free from overfishing, unauthorized resource extraction, and other instances of anthropogenic interference. The reef at Hopkins Marine Station is characterized by a dense *Macrocystis pyrifera* forest, an abundance of sessile invertebrates, various species of fish native to California's waters, and varying substrates over a variable depth profile. Monterey Bay is composed of "complex patterns of rock outcrops on the shelf, and coarse-sand bodies" making it a habitat that is ideal for both rock and sand dwelling species of fish and invertebrates (Eittreim *et al.* 2002). *M. pyrifera*, the dominant algae in this location, acts as a habitat and nutrient source for many species in the system, making it an important element to consider when studying the system and how various species interact and disperse. It is the combination of these biotic and abiotic factors that make this a good study system for our research (Paddock & Estes 2000). Understanding how the four species we looked at are distributed within this kelp forest environment will tell us more about their interactions with one another, their preferences for habitat, and their species-specific requirements for growth which in turn can help us as researchers understand how to best protect them and the resources they require.

Our study looked at four species of fish: black surfperch (*Embiotoca jacksoni*), striped surfperch (*Embiotoca lateralis*), gopher rockfish (*Sebastes carnatus*), and the black and yellow rockfish (*Sebastes chrysomelas).* These species are demersal nearshore fish that are endemic to central California's waters which gives us an increased chance at seeing them in our study (Sivasundar & Palumbi 2010). Although each of these fish have distinct morphologies they are better characterized by their limited benthic dispersal, their importance to commercial fishing, and their year-round presence in kelp forests (Stephens *et al.* 1984, Paddack & Estes 2000, and Ebeling *et al.* 1980a). These four species were chosen due to past research outlining how their interspecific relationships may have motivated the distinct assemblage patterns they display (Hixon 1980, Larson 1980b, Hallacher & Roberts 1985). Our goal was to see if we would find similar relationships to those previously presented as well as to make a case for understanding the possible underlying mechanisms behind their distributions as it related to depth, substrate type and cover, and the presence of other species.

Study Design

Fish Relation to Depth

We hypothesized that fish assemblages will occur randomly with no relation to depth. To test this, we conducted fish swaths at varying depths in three different regions along the cable at Hopkins. Conducting swaths at different depths and at various regions of the cable allowed us to increase our field of study and gave us more insight into the distributions of the test species. We define deep as being greater than 30 feet and shallow as being less than or equal to 30 feet. To analyze our data, we ran a multiple regression analysis comparing spatial distribution to depth, mean substrate, mean relief, and species. Our significance was set at a p-value of 0.1 or less. This method allowed us to compare the importance of various independent factors which was integral to determining their individual significance on the fish distribution.

Fish Relation to Substrate Type and Substrate Holder

Next, we tested whether or not species relation to substrate type and primary substrate holder was random. Our null hypothesis was that fish assemblages are randomly distributed across substrate type and substrate holder. Data was collected for this analysis via fish swath and UPC surveys. Our analysis included a multiple regression analysis allowing for us to accept or reject the null hypothesis for substrate type and a chi squared test for primary substrate holder. Finding a p-value of 0.1 or less in the multiple regression analysis will allow for the rejection of the null in relation to the substrate type (bedrock, boulder, cobble and sand). Finding a significant chi squared value will show if there is a relationship between fish assemblage distribution and substrate holder (red algae (RA), brown algae (BA), live holdfast (LH), dead holdfast (DH), bare sand (BS), shell debris (SD), bare rock (BR), or sediment/mud).

Species to Species Relation

Our null hypothesis states that fish species are randomly distributed relative to other observed species. If there is a p-value of less than 0.1 for the relation between any two species, we will have found a non-random pattern of species distribution between them which would allow us to reject the null hypothesis. Previous data has characterized the relationships between *E. lateralis* and *E. jacksoni* as well as between *S. carnatus* and *S. chrysomelas* (Hixon 1980, Larson 1980a, and Hallacher & Roberts 1985). Therefore, we will be able to compare our data with these relationships and determine whether they are the same or not.

<u>Data Collection</u>

Data collection occurred on the mornings of November 16th, 18th, and 23rd under the supervision of Professors Carr and Raimondi of the University of California, Santa Cruz. We descended to the 100-meter mark on the underwater cable at Hopkins that runs parallel to the shore. We then swam down the cable to either the 140-, 110-, or 80-meter mark on the cable depending on the day. These meter marks represented the starting point of the three regions we sampled: 140-110 meters, 110-80 meters, and 80-50 meters (Figure 3). Once at our meter mark we swam perpendicular to the cable in either the offshore (“deep” side) or onshore direction (“shallow” side). We kept swimming this direction until reaching our target depth of 37 or 35 feet on the deep side and 24, 27, or 30 feet on the shallow side. Once our target depth was reached, we turned 90 degrees to conduct a fish swath parallel to the cable. We recorded our depth every 5 meters to stay within the same depth profile as we reeled out the tape, and to keep the data from being biased due to fish attraction to divers. Fish surveys were done by first looking at a “snapshot” of what fish were seen every 5 meters in an area extending 2 meters out from each side of the tape and 2 meters up into the water column then moving to count any fish present on sand or in crevices. Each five meters this process began again thereby creating some method of replication in each of the surveys. After completing the fish surveys buddy pairs worked together to perform a UPC survey on the way back. Our UPC consisted of recording relief, substrate, and substrate cover every 0.5 meters along the 30 meter transect. The relief categories were 0-10 cm, 10 cm-1 m, 1 m-2 m and >2 m and substrate categories were bedrock, boulder, cobble, and sand. Primary substrate cover was characterized as either red algae (RA), brown algae (BA), live holdfast (LH), dead holdfast (DH), bare sand (BS), shell debris (SD), bare rock (BR), or sediment/mud (not observed). We conducted the fish swath and UPC at four depths for each of the three regions resulting in a total of 859 data points for analysis.

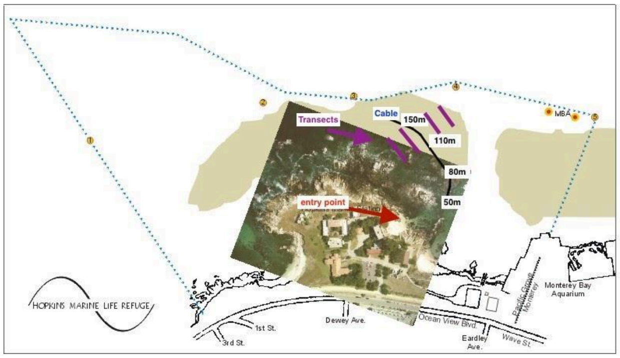
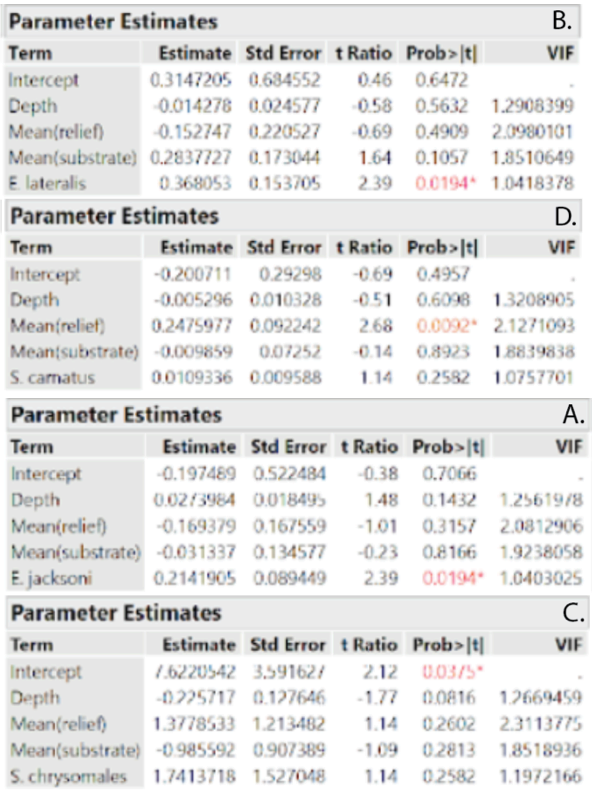


Figure 3. Map of Hopkins Marine Station. Cable shown with regions sampled depicted. Transects shown by purple lines, parallel to cable.

Results

General Results

Our data indicates that fish are assembling in non-random patterns with respect to depth, substrate cover and type, and the distribution of other fish species. As a result, we are able to reject our three previously stated null hypotheses.



Parameter Estimates B.

Term	Estimate	Std Error	t Ratio	Prob>|t|	VIF
Intercept	0.3147205	0.684552	0.46	0.6472	.
Depth	-0.014278	0.024577	-0.58	0.5632	1.2908399
Mean(relief)	-0.152747	0.220527	-0.69	0.4909	2.0980101
Mean(substrate)	0.2837727	0.173044	1.64	0.1057	1.8510649
E. lateralis	0.368053	0.153705	2.39	0.0194*	1.0418378

Parameter Estimates D.

Term	Estimate	Std Error	t Ratio	Prob>|t|	VIF
Intercept	-0.200711	0.29298	-0.69	0.4957	.
Depth	-0.005296	0.010328	-0.51	0.6098	1.3208905
Mean(relief)	0.2475977	0.092242	2.68	0.0092*	2.1271093
Mean(substrate)	-0.009859	0.07252	-0.14	0.8923	1.8839838
S. carnatus	0.0109336	0.009588	1.14	0.2582	1.0757701

Parameter Estimates A.

Term	Estimate	Std Error	t Ratio	Prob>|t|	VIF
Intercept	-0.197489	0.522484	-0.38	0.7066	.
Depth	0.0273984	0.018495	1.48	0.1432	1.2561978
Mean(relief)	-0.169379	0.167559	-1.01	0.3157	2.0812906
Mean(substrate)	-0.031337	0.134577	-0.23	0.8166	1.9238058
E. jacksoni	0.2141905	0.089449	2.39	0.0194*	1.0403025

Parameter Estimates C.

Term	Estimate	Std Error	t Ratio	Prob>|t|	VIF
Intercept	7.6220542	3.5916277	2.12	0.0375*	.
Depth	-0.225717	0.127646	-1.77	0.0816	1.2669459
Mean(relief)	1.3778533	1.213482	1.14	0.2602	2.3113775
Mean(substrate)	-0.985592	0.907389	-1.09	0.2813	1.8518936
S. chrysomales	1.7413718	1.527048	1.14	0.2582	1.1972166

Figure 4. Summary of Multiple Regression Analysis. Each fish against depth, relief, substrate type and cover, and other species. A.) *E. lateralis*, B.) *E. jacksoni*, C.) *S. carnatus,* D.) *S. chrysomelas.*

Fish Relation to Depth

We hypothesized that the fish we sampled would show a random pattern of association with respect to depth. Our data allows us to reject the null hypothesis as it shows that the fish sampled have non-random patterns of distributions with depth. Two of the sampled fish species, *E. lateralis* and *S. carnatus,* had a non-random pattern of association with depth (Figure 4). Although not statistically significant, we note that *E. lateralis* has a p-value of 0.1432 in the depth category which is the smallest value observed and therefore we chose to factor it into our conclusions. We also see that *S. carnatus* has a non-random association with depth, with a p-value of 0.0816. Therefore, our null hypothesis was rejected because two of the four fish species showed a non-random association with depth.

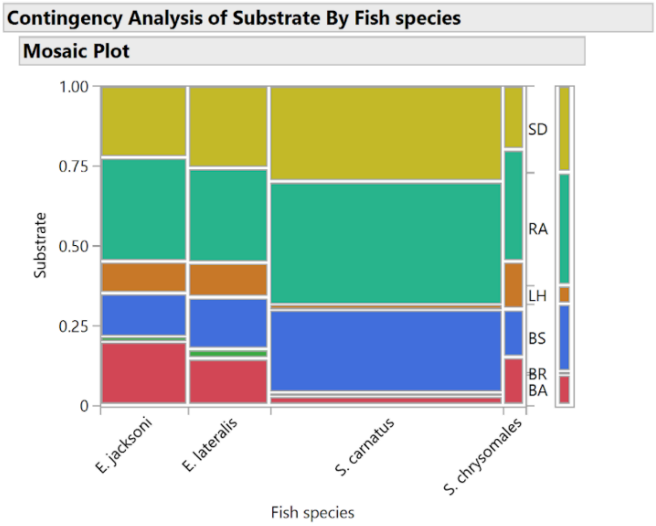


Figure 5. Contingency analysis of substrate by fish species is depicted in the mosaic plot. The mosaic plot helps identify patterns of association by providing a direct comparison between the observed distributions and a theoretical random distribution.

Fish Relation to Substrate Type and Substrate Holder

We hypothesized that our fish surveys would reveal a random distribution with substrate type and cover. The data allows us to reject this null hypothesis, as it reveals that the fish have a non-random distribution across the different substrate types and covers (Figure 5). *E. jacksoni*, displayed a strong association with brown algae (BA) substrate cover, while *E. lateralis*, is highly associated with red algae (RA) substrate cover. *S. carnatus*, has a strong association with bare sand (BS) substrate, and *S. chrysomelas*, has a strong association with live *M. pyrifera* holdfast (LH) substrate cover.

Species to Species Relation

We predicted that fish groups would be randomly distributed relative to other species, however our data indicates otherwise and allows us to reject our null hypothesis. After sampling, we found that fish did not have random group distributions, but instead had non-random patterns of association relative to other fish species. Our results show that *E. lateralis* and *E. jacksoni* are positively associated with one another ($p = 0.0194$, Figure 4). This finding disproves our hypothesis in that the fish species sampled actually have a non-random distribution relative to the other fish species. Notably, *S. chrysomelas* has no association with *S. carnatus*, and *E. lateralis* has no association with *S. carnatus*.

Discussion

In this study we found that our observed species display non-random patterns of distribution with respect to depth, substrate type and cover, and the presence of other species of fish. Our results indicate that there are a multitude of factors that influence the distribution of fish within species rich environments.

Fish Relation to Depth

S. carnatus has a strong positive association with shallow-depth regions (<30 feet), contradicting the findings of previous studies which identify *S. chrysomelas* as the dominant, shallow-occupying species. Our surveys yielded 82 counts of *S. carnatus* and 7 counts of *S. chrysomelas* across the three regions sampled; such a significant contrast in population size allows us to confidently exclude competitive dominance as a factor in their distributions. We, therefore, challenge the previous findings of Larson (1972) and Hallacher & Roberts (1985), who observed *S. chrysomelas* to be socially dominant over *S. carnatus*. With limited competition from *S. chrysomelas* (only 7 individuals), *S. carnatus* can inhabit the prey rich shallow reef. Work done with salamanders showed density dependent competition effects lead to lower counts of the competitively dominant species thereby allowing more of the other species (Anderson 2021). Additionally, Chen (1971) proposed that differences in the colorations of the two species of rockfish are indicative of their bathymetric distributions. If so, this implies that the interspecific relationships of these two species have been at play for centuries, and have driven advantageous morphological adaptations, so much so that the species are diverging. In our surveys, we observed fluctuations in the population sizes of *E. lateralis* with relation to depth, with more individuals occurring in deep water regions (> 30 ft). In total we observed 26 *E. jacksoni* and 24 *E. lateralis*, these population sizes enable us to draw more accurate conclusions about their relationships. *E. lateralis* tend to favor preying on foliate algae in shallower depths, and at deeper depths consume a varied diet in comparison to *E. jacksoni* (Holbrook & Schmitt 1989). Holbrook and Schmitt also found that *E. lateralis* prefer shallower depths containing foliate algae as their diet, but possible loss of foliate algae in the future could transfer their range to a deeper one.

Fish Relation to Substrate Type and Substrate Holder

We hypothesized that substrate type would have a significant influence over the observed assemblages of fish species, however we found this was only true for *E. jacksoni* populations. Previous studies indicate that the *Embiotocidae* congenerics are occupying a depth-related resource gradient, and although we did not observe this trend, we maintain that there is a non-random association with substrate type, furthermore we argue that this is indicative of niche resource exploitation. We were also interested in comparing associations with substrate cover to characterize possible prey or to further characterize habitat qualities.

Previous studies align *E. jacksoni* with understory brown algae, as it is home to their preferred prey type of crustaceans (Holbrook & Schmitt 1989). However, this is more commonly observed in non-upwelling seasons, whereby the dominant *E. lateralis* pushes *E. jacksoni* out of shallow regions and into deeper water regions. The more versatile *E. jacksoni* is able to forage in novel substrates due to the "winnowing" strategy (where food is separated from non-nutritive debris in the oropharyngeal cavity) (Holbrook & Schmitt 1989). *E. lateralis* associated with red algae especially in shallow water where red algae was their main prey (Holbrook & Schmitt 1989). *S. chrysomelas* were found associating with live holdfasts (Figure 5). Evidence supported by their association with high relief, as they tend to find refuge in cracks, crevices, caves, or kelp plants (Hallacher & Roberts 1985). Lastly, *S. carnatus* was found predominantly around bare sand, possibly due to their more frequent aggregation in the shallower areas in our system.

Species to Species Relation

One unexpected result differing from preceding research, and our predictions, was the association of *E. jacksoni* and *E. lateralis* we observed *in situ* (Holbrook & Schmitt 1989). Their study maintains that these two congeneric competitors diversify their niches to occupy separate depth distributions. Our results challenge their findings, and although our sample size is smaller, we theorize that the observed lower levels of resource overlap are due to an abundance of resources present in marine protected areas (Morrison 2021). One likely issue comparing our similar studies and their significance on surfperch distribution in kelp forests is depth ranges studied. Holbrook and Schmitt (1989) characterized shallow as 0-5 meters and deep as 9-12 meters while we characterized deep as more than 10 meters and shallow as equal to or less than 10 meters. Additionally, their study was much broader, spanning multiple years and six study sites at Santa Cruz Island, whereas ours was over the course of three days at one site.

Overall

We found the distributions of rockfish and surfperch at Hopkins Marine Station to be unique relative to the findings of previous studies examining their interspecific relationships (Hallacher & Roberts 1985, Holbrook & Schmitt 1989, and Larson 1980). Due to observed decreases in the expected fish assemblages and habitat diversity, we suggest that there is an absence of interspecific competitive exclusion overall.

Some challenges that we faced over the course of conducting our study included difficulty getting to certain depths, limited by the upper depth limit of the reef. In addition, we had minimal fish count across most surveys. To combat these issues future studies could expand the range of transects or go for an opportunistic method of species counts. Although we were able to replicate our study across different regions, we were unable to repeat our study throughout different seasons and across different reefs due to time constraints. Further exploration of regional variations and seasonal influences would not only expand the population size from which to draw conclusions but would also allow direct comparison of protected and non-protected marine areas in terms of overall success.

Given the current understanding of competition and niche diversification in the context of kelp forest and the species examined here, we believe a more thorough study with experimental manipulation of species present would tell us more about the current state of the kelp bed and to what extent species are competing. Also, studying this would inform conservation efforts, by highlighting changes in strength of competition when populations are smaller and less susceptible to anthropogenic impacts. This study could also provide insight into fish behaviors that would be useful in regulating fisheries.

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