Two voracious herbivores and their species associations in shared microhabitat

Introduction

The concept of interspecific competition controlling an ecosystem's biological structure has been historically well represented in ecological research (Darwin 1859, Tansley 1917, Diamond 1975, Goldberg and Barton 1992). Much of this research focus was prompted from the development of the Competitive Exclusion Principle which states that species that overlap in niches, defined as the accumulation of a species' abiotic and biotic requirements, cannot coexist in a shared ecosystem with limited resources (Hardin 1960). When occurrences of closely related species in the same system are found, studies often aim to explain the evolutionary mechanisms at play that allow for this sustained species diversity, given the contradiction of overlapping niches (Hardin 1960). In order to assess these processes of natural selection that maintain systems of sympatric coexistence, patterns of individual species interactions must be observed.

More specifically, the interaction between related species for limited microhabitat resources is of interest when considering the role of intersecting habitat niches and the consequences this has on spatial segregation within an ecosystem. Experimental studies have identified habitat that serves as refuge from predators as an important competitive resource for a wide variety of both terrestrial and aquatic prey species (Kneib 1987, Steger 1987, Persson and Eklöv 1995, Wieters et al. 2009, Williams et al., 2016). Additionally, these investigations of interspecific competition for refuge microhabitat have indicated an effect of structural characteristics of habitat on the competitive behavior between species (Persson 1991, Orrock et al., 2013). Understanding how these species interactions change with the structure of their limited microhabitat can be essential in maximizing the efficiency of conservation efforts to protect species and communities when habitat quality is threatened or needs to be artificially reestablished with habitat restoration.

One such ecosystem that is important when considering habitat restoration is the temperate kelp forest. This system exhibits high species richness with a multitude of species interactions that are not fully understood but support an ecosystem that is highly important to many human communities (Carr and Reed 2016). Kelp forests contribute complex spatial structures to nearshore biological communities and are dominated by macroalgae that provide three-dimensional habitat within the water column as well as substantial biomass from key primary production (Schiel and Foster 2015).

A global threat to these highly diverse and productive marine systems is the bioengineering effect of uncontrolled sea urchin herbivory on foundational macroalgae that can quickly shift ecosystems to alternately stable barren states (Mann and Breen 1972, Paine and Vadas 1969, Pearse et al. 1970, Shepherd 1973, Dayton et al. 1973, Ebeling et al. 1985).

In the Northeastern Pacific Ocean, *Strongylocentrotus purpuratus,* the purple urchin, and *Mesocentrotus franciscanus*, the red urchin, are the main species of sea urchins. *S. purpuratus* is usually found in higher abundances and is also largely responsible for overgrazing events (Carr and Reed, 2016). Crevice habitat is an important aspect of the fundamental niche of these urchin species because it provides refuge from predators like sea otters (*Enhydra lutris*)**,** shelter from high water turbulence, and accumulates a reliable food supply of drift algae, mostly *Macrocystis pyrifera* **(**Limbaugh 1961, Lowry and Pearse 1973, Tamaki et al. 2018, Basch and Tegner 2007).

Urchin ecology is an important research focus because of the consequences urchin behavior has on entire kelp forest ecosystems. However, the literature has mostly followed individual species' feeding behaviors, specifically *S. purpuratus*, to explain drastic regime shifts (Ebeling et al. 1985, Harrold and Reed 1985, Harrold and Pearse 1987). The sympatric association, and particularly overlap in habitat niche, between *S. purpuratus* and *M. franciscanus* populations raises questions of coexistence. Partly due to the difficulty of conducting experimental studies that test for competition, we found only one competitive interaction study between these two urchin species (Schroeter 2016).

Our study aims to contribute to this knowledge gap by examining patterns of interspecific association between *S. purpuratus* and *M. franciscanus* in their shared refuge microhabitat. Additionally, determining what defines urchin refuge habitat helps to inform requirements for habitat structure in restoration efforts such as artificial reef development.

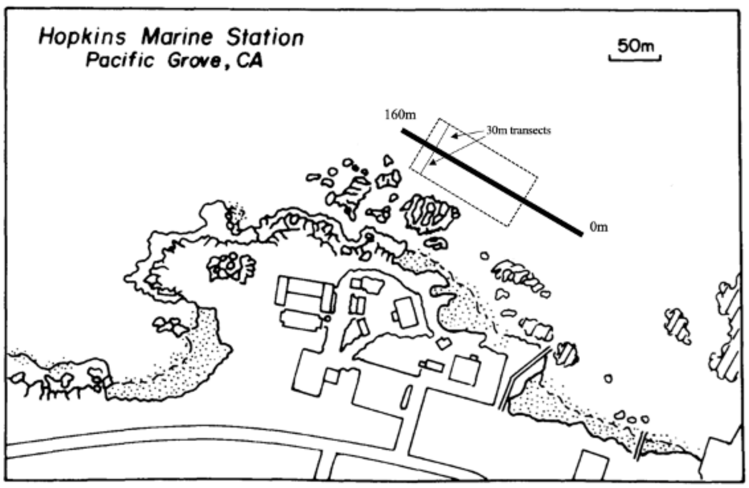


Figure 1: Diagram of Hopkins Marine Station, modified from Watanabe 1984. Black line indicates approximate location of the permanent cable. Dashed rectangle shows approximate study site.

In this study we will be assessing species associations between *S. purpuratus* and *M. franciscanus* within their shared refuge microhabitat in a Central California kelp forest at Hopkins Marine Station. With subtidal observational data, we will describe their habitat associations, consider patterns of non-random association, and analyze how species associations are affected by the quality of refuge habitat. We predict that these urchin species' abundances will be dependent on one another within a shared crevice and that this pattern of association will change as habitat quality changes. This observational study will provide insight into the interspecific associations between these closely related kelp forest herbivores as well as contribute to our understanding of the influence of limiting refuge habitat has on these species associations.

Methods

General Approach – To assess habitat association, species associations in shared habitat, and association by habitat quality, we conducted three days of observational field study in a kelp forest.

System – This study was conducted in the kelp forest directly offshore of Hopkins Marine Station in Monterey, California (36°62'N, 121°90'W) on November 16th, 18th and 23rd, 2021. There are two main urchin species, *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus,* that inhabit Monterey Bay. Both *S. purpuratus* and *M. franciscanus* consume drift algae (mostly *M. pyrifera*) as their main food source. Under a diverse kelp canopy, granitic bedrock provides a diverse base of sandy, open rock, and crack substrates that urchins inhabit. It provides varied terrain and rugosity. Hopkins has a history of research for its diversity of species and its long-standing status as a Marine Life Refuge since the 1930's which limits extractive activities and other anthropogenic effects on the kelp forest. This site provided sufficient sample sizes of our study subjects as well as adequate rugosity to assess species interactions in crevice habitat. Hopkins Marine Station also provides accessible data collection with a reef system that can be accessed from shore and a permanent underwater cable that helps orient sampling within the kelp forest to ensure accurate spatial distribution of sampling at this site. Figure 1 shows the spatial design of our site at Hopkins Marine Station.

Preliminary Study –

*Figure SEQ Figure * ARABIC 2*: Photo of how we conducted our study for H_{A1} and H_{A2}, showcasing the modified meter bar sampling tool to measure crevice width, length, and depth. Divers: Rosie Campbell and Nathan Hunter, Photo: Rae Mancuso.

H_{01}: *Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus* are randomly associated with sand, rock, and crevice substrate types.

H_{A1}: If *Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus* are overrepresented on a specific substrate type compared to expected random distributions on available substrate, then substrate associations exist.

To characterize the shared habitat of *S. purpuratus* and *M. franciscanus*, we conducted a habitat association study at Hopkins Marine Station, Monterey, CA on November 16th, 2021. We performed five uniform point contact (UPC) transects via subtidal SCUBA survey methods to test our hypothesis. Each transect was 30 m x 2 m and was sampled in five-meter increments. Both urchin species were tallied up within each substrate category (sand, open rock, crevice). If urchin abundance in a five-meter section was over 20 individuals, the distance along the transect was recorded where the count reached 20 and total density was calibrated later in data analysis to save air underwater and improve counting accuracy. Finally, we performed a Chi-square analysis to determine significance of habitat associations. The results from this preliminary study informed our data collection for the following study by indicating specific microhabitats of coexistence for the two species of interest.

Study Design –

> *Hypothesis*$_{02}$: In crevice habitat, the relative abundances of purple and red urchins are independent of one another.
>
> *Hypothesis*$_{A2}$: If red urchin abundance can be used to predict purple urchin abundance in shared crevices, then they are non-randomly associated.

A team of three divers conducted counts of *M. franciscanus* and *S. purpuratus* within crevices along seven 30 m x 2 m (60 m^2) swaths over two days (November 18th and 23rd, 2021). Assigning crevices as replicates, total counts of both species found in each crevice were recorded. Differing from the habitat association methods, no count limits were put in place and only urchins in crevices were counted. Flashlights were used to illuminate the less visible urchins (Figure 2).

Hypothesis$_{03}$: If non-random associations between purple and red urchins are found, there will be no change in association pattern when crevice quality varies.

Hypothesis$_{A3}$: If non-random associations between purple and red urchins are found, then these non-random associations will vary with crevice quality.

Crevice quality was estimated by taking field dimensions of each crevice observed along the 30 m transect that contained urchins. Width, length, and depth of each crack was measured with a meter stick in tandem with our urchin abundance data collection (Figure 3). *Analysis* – We used JMP statistical software to analyze our observed data. To test our hypotheses we used a generalized linear model (GLM) to determine the effect of species abundances on one another as well as the influence of crevice quality on these species patterns. We used a poisson distribution to capture the logarithmic trend in species associations. Results were assessed at the $p < 0.05$ significance level.

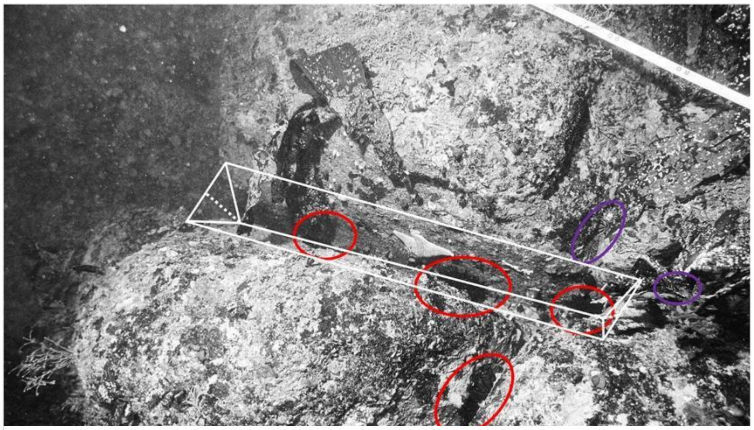


*Figure SEQ Figure * ARABIC 3*: Visual description of how we calculated each crevices' surface area using field measurements, assuming cracks exhibited a V-shaped cross section. Purple circles indicate *S. purpuratus* and red circles indicate *M. franciscanus* individuals. Photo: Rae Mancuso.

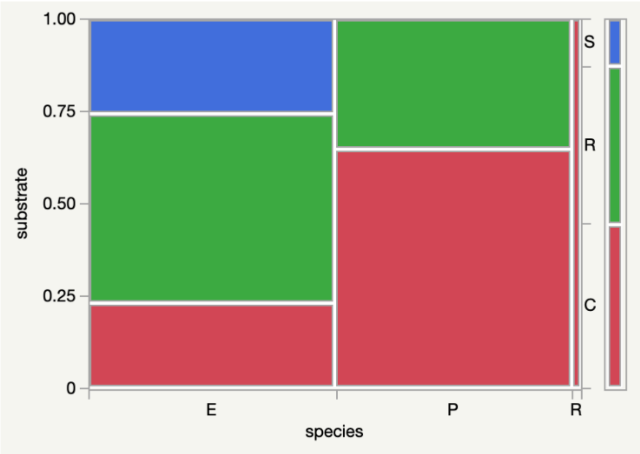


*Figure SEQ Figure * ARABIC 4:* This mosaic diagram is comparing the expected distribution of individuals of each species assuming random distributions across available substrates (H_{01}) with the observed counts of *S. purpuratus* (P) and *M. franciscanus* (R). Both species show nonrandom distributions between observed and expected distributions across substrates (X^2, p<0.001) where S. purpuratus is observed only on rock and crevice and *M. franciscanus* is only observed within crevice.

Results

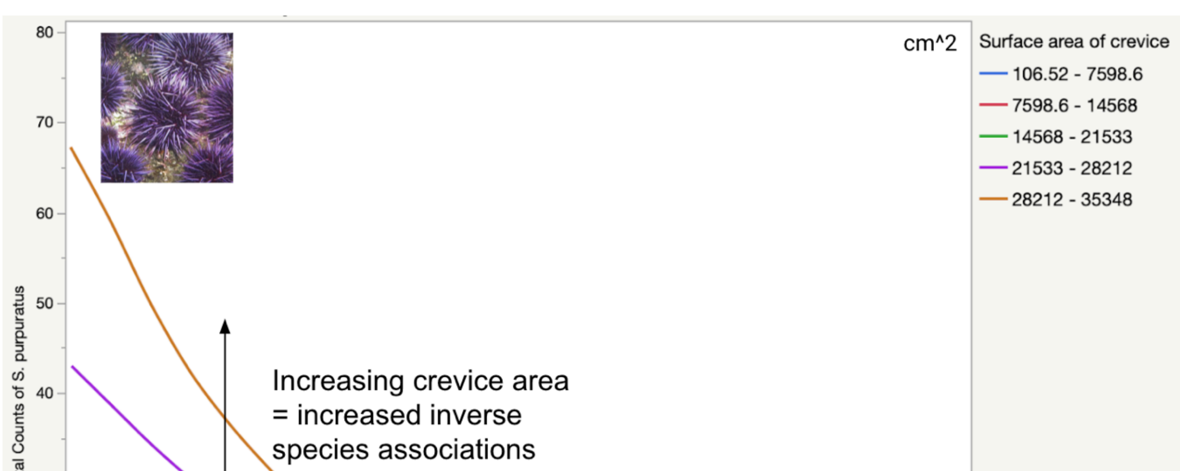
Preliminary Habitat Association Study – With the results from the Chi square analysis of our habitat data, we rejected the null hypothesis. We found both purple and M. franciscanus to be non-randomly associated with specific substrate types (Figure 4). *S. purpuratus* were found on rock in 35.39% of total counts, 64.71% in crevices, and 0% on sand. These findings deviated from the expected values of available substrate by -16.25% for rock, +41.76% for crevice, and -25.51% for sand. *M. franciscanus* were only found in crevices. This finding deviated from the expected values for rock by -51.54%, +77.05 for crevices, and -s25.51% for sand based on the availability of these substrate types at our study site. Both purple and *M. franciscanus* occurred in crevices for the majority of observations, with no observations of *M. franciscanus* elsewhere. With these findings, we determined the most relevant location for studying associations between purple and M. franciscanus was where both species co-occurred, in crevice habitat.

General Results -- We counted a total of 260 *M. franciscanus* and 1,312 *S. purpuratus* through 139 sampled crevices. On average, there were ~ten *S. purpuratus* and ~two *M. franciscanus* per crevice. Based on our data and our computed generalized linear model, we rejected our first null hypothesis and accepted our alternate hypothesis. Assuming a poisson distribution, we found the abundances of *S. purpuratus* and *M. franciscanus* can be used to predict one another. We rejected our second null hypothesis and accepted our alternate hypothesis as the relationship between species varied with changes in crevice quality, represented by crevice surface area (cm^2). We found an inverse relationship between *S. purpuratus* and *M. franciscanus*. For crevices with low calculated surface area, we generally found the abundance of *S. purpuratus* to be greater than *M. franciscanus*. When the crevice area increases, the inverse relationship between *S. purpuratus* and *M. franciscanus* becomes more severe (Figure 5, GLM, $p < 0.001$).

Alternate Hypothesis #1 – As predicted, we found *S. purpuratus* abundance to depend on *M. franciscanus* abundance, and thus rejected our null hypothesis. We found a significant, non-linear relationship between *S. purpuratus* and *M. franciscanus* abundances where the count of *M. franciscanus* can be used to predict the abundance of *S. purpuratus* in a shared crevice (GLM, $p< 0.05$).

Alternate Hypothesis #2 – As we predicted, as crevice quality varies, the non-random association between purple to M. franciscanus changes, thus we reject the null hypothesis. We determined that crevice surface area (cm^2) is the best representation of crevice quality due to its significant measured effect size in our generalized linear model compared to other crevice metrics (GLM, $p < 0.001$). Our other tested habitat quality measurements included depth, width, length, triangular volume, and area and volume assuming a rectangular shape, all of which proved to be less significant than triangular surface area when predicting the inverse relationship between urchin abundances.

We found that when the crevice surface area increases there is an increased inverse relationship between *S. purpuratus* and *M. franciscanus* abundances within the same crevice (Figure 5, GLM, $p < 0.001$). Within the smallest crevice surface area size class there is little to no



change in the *S. purpuratus* to *M. franciscanus* ratio (Figure 5). However, with increasing surface area, this ratio becomes increasingly variable, with a contrast of strongly favoring *S. purpuratus* (~65:1) and a dramatic reversal to favoring *M. franciscanus* (~1:9) (Figure 5).

Discussion

General Results – We accepted our alternate hypotheses based on observed non-random patterns of abundance between *S. purpuratus* and *M. franciscanus*; and changes in these association patterns as crevice quality varied. When crevice quality (surface area) increased there was an increased inverse relationship between *S. purpuratus* and *M. franciscanus* abundances.

Crevice Habitat – Crevices between rocks create habitat for many benthic species in the giant kelp forest and studies have shown that this habitat is used, both naturally and experimentally, for refuge by multiple species (Lowry and Pearse 1973, Tamaki et al 2018). Adult *S. purpuratus, M. franciscanus*, and *Haliotis* spp. individuals were found to occupy crevice habitat in clusters, likely in avoidance of predation from sea otters (Lowry and Pearse 1973). Observations have specifically noted a selection for *M. franciscanus* and *Haliotis spp.* by sea otters over the more abundant *S. purpuratus* (Limbaugh 1961). Additionally, sea star predation has been observed to cause the use of crevices as refuge by *S. purpuratus* (Rosenthal and Chess 1972). The hydrodynamics of crevices may attract and collect more drift algae, the main food source for *S. purpuratus, M. franciscanus*, and *Haliotis* spp.; who, with sufficient quantities, rarely forage outside of crevices (Lowry and Pearse 1973, Basch and Tegner 2007). It has also been shown that feeding rates of other *Strongylocentrotus* species decrease when exposed to greater water flow and this is likely why they were experimentally found to occupy crevice habitats (Tamaki et al 2018).

Competition for Crevice Habitat – We predicted that there exists a crevice of optimized quality. This ideal crevice would be wide enough to collect the most drift algae, deep enough to allow many individuals, yet also remain inaccessible to sea otters. We only sampled crevices within the width range of 5 - 50 cm. We predicted that the lower and upper limits of this range were non-ideal, due to lack of livable space, lack of drift algae, and greater exposure to sea otters. We hypothesized, but could not test experimentally, that there is competition for this ideal crevice.

Other studies have shown multiple species to compete for crevice habitat (Lowry and Pearse 1973, Aguilera and Navarrete 2012). In the same subtidal study system, Hopkins Marine Station, Lowry and Pearse (1973) measured crevice dimensions and found it likely that *H. rufescens* and *H. walallensis* outcompete *S. purpuratus* and *M. franciscanus* for larger crevices; either because the abalone forced the urchins out, or because the urchins were made more susceptible to sea otters and were extracted. They recorded crevice widths between ~3 and ~20 cm. This is inside our sampling range, and following our prediction, the larger of these widths were likely preferred by the two abalone species; however, our observational data did not capture this.

In intertidal systems, crevice habitats are used by many species to avoid wave action, desiccation, heat, and other environmental stressors (Aguilera and Navarrete 2012). The keyhole limpet, *Fissurella crassa*, and the pulmonate limpet, *Siphonaria lessoni*, have significant diet overlap and share crevice habitats when resting (Aguilera and Navarrete 2012). *F. crassa* was found to be competitively dominant and alter the spatial distribution, crevice use, and growth rate of *S. lessoni* (Aguilera and Navarrete 2012). Both *H. rufescens* and *F. crassa*, dominant in their respective systems, asymmetrically compete for crevices of high quality (Lowry and Pearse 1973, Aguilera and Navarrete 2012). In our study system, we suspect that *M. franciscanus* fills this role and can outcompete *S. purpuratus* in high quality crevices that optimize refuge from predators as well as collection of drift kelp food supply.

Implications – This potential for competition between *S. purpuratus* and *M. franciscanus* has implications for future urchin barren creation. Urchin barrens are created by a positive feedback loop in which the effects of many events result in an alternately stable barren state (Ling et al 2009, Filbee-Dexter and Scheibling 2014). The negative association we found between *S. purpuratus* and *M. franciscanus* in crevice microhabitat may be a part of this loop. It could be possible for *M. franciscanus* to competitively exclude *S. purpuratus* from this limited habitat resource as indicated by an increase in their inverse relationship with increases in crevice surface area. If *S. purpuratus* populations are excluded from high quality crevice habitat and forced onto less ideal exposed rock, they would likely lose access to the benefits of the crevice habitat, including drift algae accumulation. This may push *S. purpuratus* into a state of starvation and trigger indiscriminate grazing behavior which can catalyze regime shifts to barren states (Ebeling et al., 1985).

Additionally, these results can inform restoration efforts by providing data that support the importance of physical habitat structures in maintaining species diversity. Artificial reef installations attempting to replicate wild kelp forest community interactions in degraded nearshore environments are an example of an application restoration strategy. With our quantification of the significance of crevice quality on species interactions between these two species of urchins, these types of projects could include a consideration for providing crevice habitat that meets the refuge needs to facilitate species coexistence in a restored kelp forest system.

Changes and Further Study – In our study design we assumed crevices had a V-shaped cross section which may not have been representative of all crevice shapes. If we were to replicate this observational study, we would note the overall shape of each crevice observed. Noting this, would allow us to use the most accurate volume or surface area equation, instead of generalizing. We would also want to note the depth of each crevice. We would use this to investigate a relationship between depth, *S. purpuratus* and *M. franciscanus* inverse relationship, and variations in crevice size.

From the information gained in this study, we see an opportunity to conduct an exclusion experiment that would test for competition between *S. purpuratus* and *M. franciscanus*. Additionally, as a possible mechanism of habitat partitioning, we would like to further investigate the relationship of spatial segregation between clusters of *S. purpuratus* and *M. franciscanus* in crevices. Intraspecific aggregation may further partition the crevice habitat and allow for coexistence (Lowry and Pearse 1973).

From investigations of spatial distributions in and also directly surrounding crevices, we would hope to describe a relationship between and compare individuals of both species that reside inside and outside of crevices. Another possible area to inform this species interaction could include quantifying fitness of both *S. purpuratus* and *M. franciscanus* in terms of mortality rates and reproductive success and comparing these metrics. Lastly, we would like to observe the quantity of drift algae accumulated and consumed within varying crevice qualities to better understand what processes determine the observed change in association pattern with crevice quality.

Conclusion – We observed non-random patterns of association between *S. purpuratus* and *M. franciscanus* in their shared crevice microhabitat and changes in these association patterns as crevice quality varied. Crevice habitats can be considered a limiting resource because they act as protection from sea otter predation and water turbulence, as well as provide ample access to drift algae (Lowry and Pearse 1973, Tamaki et al 2018). Because of these species' shared association with this limited microhabitat resource, there is potential for competitive exclusion (Hardin 1960). Since selective pressure from predation is observed to impact *M. franciscanus* more strongly than *S. purpuratus*, it is possible that *M. franciscanus* populations are competitively dominant over *S. purpuratus* for high quality refuge habitat (Limbaugh 1961, Lowry and Pearse 1973). Although we cannot conclude a competitive species interaction without experimental manipulation, our results support this potential interaction. This evidence includes observations of *M. franciscanus* solely in crevices and our finding that negative species associations increase with larger crevice surface area, a potential measure of high microhabitat quality.

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