Can crabs be counted (on)? Implications of *C. productus* and *C. antennarius* distributions in kelp forests and urchin barrens on kelp forest resilience

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INTRODUCTION

The ecological theory of alternate stable states dates back to literature as early as 1891, with an array of researchers being credited for its founding studies (Lotka 1965, Lewontin 1969, Peterson 1984). The theory of alternative stable states defined simply is the existence of an ecological system in varying community structures under the same environmental conditions (Schroder et al. 2005). Debate over the presence or absence of multiple stable states remains (Petraitis & Dudgeon 2003), with kelp forest ecosystems being noted as a key study system to test this theory. These rocky subtidal ecosystems appear in two stable states- kelp forests or urchin barrens- which have been studied extensively on both the western and eastern coasts of Northern America (Mann 1977, Stewart & Konar 2011, Filbee-Dexter & Scheibling 2014). The shift from forest to barren is accredited to sea urchin populations becoming locally abundant and overgrazing the kelp beds (Carr & Reed 2015). This shift in stable states greatly alters the ecosystem community structure, by decreasing primary and secondary productivity of coastal waters, and threatening the high productivity and biodiversity of kelp forest ecosystems (Mann 1977). Unfortunately, widespread urchin barrens are currently occurring on the western coast of North America and becoming increasingly common, following a series of perturbations to the kelp forest.

Initially, urchin barrens were thought to be a result of the removal of a major urchin predator, the sea otter, *Enhydra lutris* (Stewart & Konar 2011). Sea otters are a keystone species in subtidal systems, and their absence causes increased herbivory, resulting in the destruction of macrophyte associations (Estes & Palmisano 1974). Similarly, it was observed that a reduction in the population of another predator of the purple urchin, the sunflower star (Freeman 2005), *Pycnopodia helianthoides*, led to an increase in urchin density, and thus urchin barrens (Eckert et al. 2000). The widespread death of sunflower stars is attributed to the sea star wasting disease, which led to behavioral changes, lesions, loss of turgor, limb autotomy, and ultimately death characterized by rapid degradation (Hewson et al. 2014).

Without regulation of the urchin population, the increase of urchin density is the leading cause of the shift in stable state, and a reduction in their population size is required to induce a shift back to kelp forest ecosystems. There are several ecological mechanisms that could potentially contribute to a decline in urchin populations, and thus, an increase in kelp forest resilience and the potential of kelp forest recovery. These include: disease, storms, starvation, and predation. Currently, two types of diseases are spreading throughout purple urchin populations, but little is understood of their ability to decrease urchin densities significantly (Lester et al. 2007). Storms have the potential to completely shift stable states from urchin barren to kelp forest, but this is variable and not a long term solution (Ebeling et al. 1985). Urchin barrens have persisted for years because purple urchins have the ability to utilize their gut for nutrient storage during times of limited food supply, suggesting that starvation will not reduce urchin density (Lawrence et al. 1966). Lastly, the significance of predation on urchins is exceedingly important to limit their population density, and could potentially be the main contributor to the decline of urchin populations.

Purple urchins are important prey of many kelp forest inhabitants, including otters, sheephead (*Semicossyphus pulcher*) lobster (*Panulirus interruptus*) sunflower stars, leather stars (*Dermasterias*) and *Cancer* crabs. Although otters have been noted as key predators on urchins, they hold little to no significance in urchin barrens. There have been recent observations of sea otters not preying on urchins in urchin barrens across Central California due to their reduced nutritional value (Smith *et al.* unpublished data). Early studies of otter-urchin dynamics even suggest that otters are unable to control urchin populations when purple urchin recruitment vastly increases, allowing urchins to alter the kelp forest community (Pearse & Hines 1987). The distributions of sheephead and spiny lobster are limited to south of Point Conception, reducing their impact on urchin densities along the entire coast (Tegner & Dayton 1981, Ling et al. 2017). As previously stated, sea star wasting disease catastrophically reduced sunflower star populations, greatly reducing predation stress on urchin populations (Eckert et al. 2000). *Dermasterias* was thought to consume purple urchins, but recent research suggests that they account for little to no predation on purple urchins (Mark Carr personal comm.). In contrast, recent research conducted on *Cancer* species found that they are voracious predators of purple urchins (Mark Carr personal comm.). While similar studies have found that crabs eat urchins in both kelp forest and urchin barren states in Nova Scotia (Drummond-Davis et al. 1982), their prevalence in California kelp forest ecosystems is unknown. Studies in Nova Scotia's kelp forest ecosystems found that of multiple predators on urchins, *Cancer irroratus* was contributing to the majority of decline in urchin density (Scheibling 1996), especially in urchin barrens (Bernstein et al. 1981). Despite accounts of predation by *Cancer* spp. on urchins, a population density estimate is required to determine their ecological significance and ability to contribute to kelp forest resilience and recovery.

To investigate the distributions of *Cancer* spp. we conducted subtidal surveys on their species-specific densities and distributions in forests and in barrens, recording their depth and size. We hope that our study will produce insight into the ecological significance of rock crabs in the kelp forest and help develop our understanding of the factors that govern alternative stable states of rocky reefs in Central California.

MATERIALS AND METHODS

Study System

Site

Hopkins Marine Station is the marine laboratory of Stanford University, located in Pacific Grove, California on the southern end of the Monterey Bay in central California (36°37'11.5"N 121°54'13.0"W) on the west coast of the United States. The facility is directly adjacent to the Monterey Bay Aquarium. The shoreline at this site is mostly rocky granite outcroppings interspersed with sandy beaches. Underwater, the substrate is similar, made up of high relief granitic reefs and boulder fields with sand channels that break up large patches of reef. Water temperatures in the summer can be as low as 50F due to upwelling, and as high as 60F in the winter in the absence of upwelling. During October and November 2019 when data was being collected for our study, water temps were around 55F. The kelp canopy at Hopkins is almost exclusively giant kelp, but bull kelp (*Nereocystis luetkeana*) dominated forests are also present in central California and on some parts of the Monterey Peninsula. The giant kelp in the study site is anchored to the reef, and since this site is protected from the predominant swell direction (NW), the forest is able to grow relatively undisturbed, with a thick canopy by the end of every summer. Not only is this forest protected from extreme wave action, it is also protected from all recreational and commercial take, and has been since the implementation of the Lover's Point State Marine Reserve in 2007. The lack of take has resulted in a noticeable increase in the size and abundance of many fish and invertebrates relative to non-protected areas. The species assemblage consists of algae, fish, mammals, birds, and invertebrates that are typical for Central California. However, Hopkins also hosts some species usually found further south such as California sheephead and calico bass (*Paralabrax clathratus*). Southern sea otters, *Enhydra lutris,* are very common at Hopkins, as are California sea lions, *Zalophus californianus,* and harbor seals, *Phoca vitulina.* Since the urchin population explosion and subsequent outbreak of urchin barrens in 2013, a large urchin barren has persisted at Hopkins, directly adjacent to the kelp forest and cable. This made Hopkins an ideal site to conduct our study, as we could survey in both forest and barrens with minimal variation in conditions.

Diving is made easy at Hopkins, as there is a permanent cable running along the bottom in the north-south direction in about 10 meters of water, attached to a floating mooring around its midpoint. It is marked in 10-meter increments and is clearly marked from about 0 meters to the 160 mark. It is often used as a reference point by divers, and can easily be reached from shore via swimming or skiff. Although the cable was not used as an underwater reference point in this study, the mooring was used as a landmark representing one of the densest areas of forest.

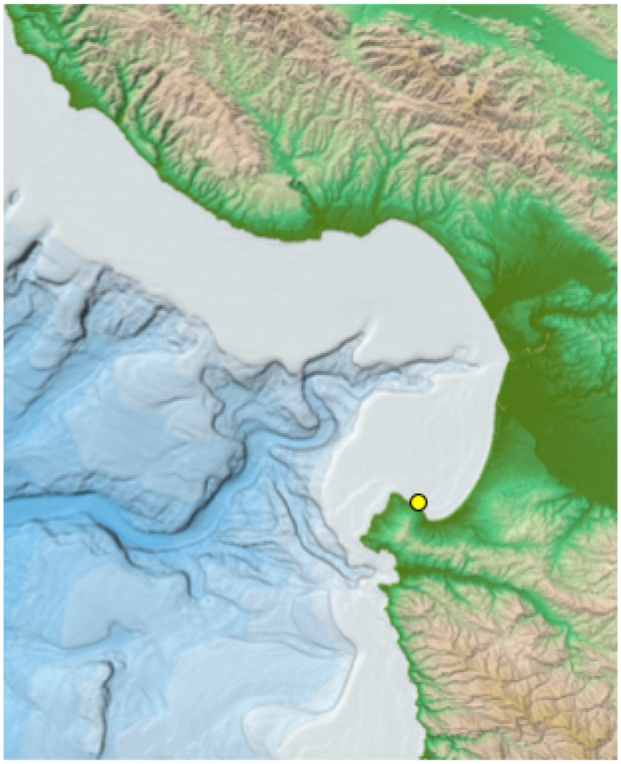


Fig. 1. Map of Monterey Bay (left). Yellow circle designates location of Hopkins Marine Station on the southern end of the Monterey Bay.

Fig. 2. Map of Monterey Peninsula (right). Yellow circle designates location of Hopkins Marine Station on the eastern side of the Monterey Peninsula inside Lover's Point State Marine Reserve.

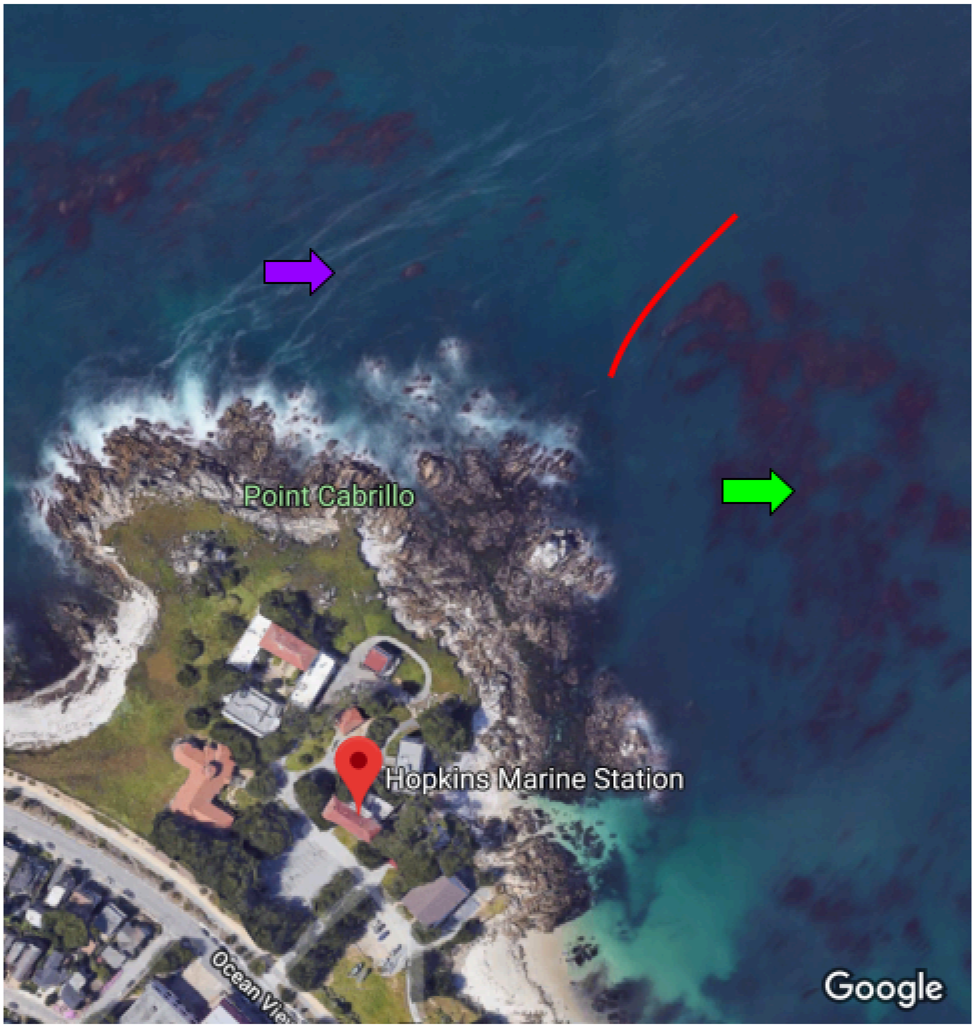
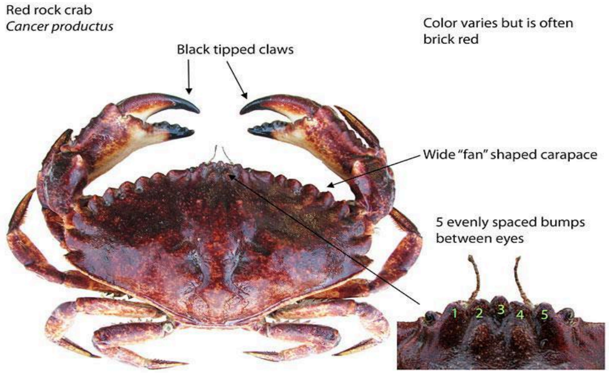


Fig. 3. Aerial view of Hopkins. Red line roughly demarcates ecotone between kelp forest and urchin barren. Barrens surveys were performed in the area of the purple arrow, while forest surveys were conducted in the kelp forest at the green arrow.

Species

The red rock crab, *Cancer productus,* and the pacific rock crab, *Cancer antennarius,* are sympatric species commonly found in Central California. Red rock crabs can be found from Kodiak Island, Alaska, USA to Bahia Magdalena, Baja California, Mexico, from the intertidal to depths of around 100m on gravel, reef, sand, and mud substrates (Schmidt 1921, Carroll & Winn 1989). Pacific rock crabs range from Sequim, Washington, USA to Baja California, Mexico, from the intertidal to depths exceeding 100m on rocky shore, reef, and sand substrates (Winn 1985, Carroll & Winn, 1989). Both are common in the coastal waters of Central California where our study was conducted. As juveniles, these crabs are important prey for many species of benthic fish and invertebrates (Van Blaricom 1982). Adults make up a substantial portion of the diet of southern sea otters, (Tinker *et al*. 2019). Nonetheless, *Cancer* spp. are voracious predators and scavengers, preying on various molluscs, crustaceans, and echinoderms and scavenging almost any available carcass, which they locate using their incredibly acute sense of smell (Carroll & Winn 1989).



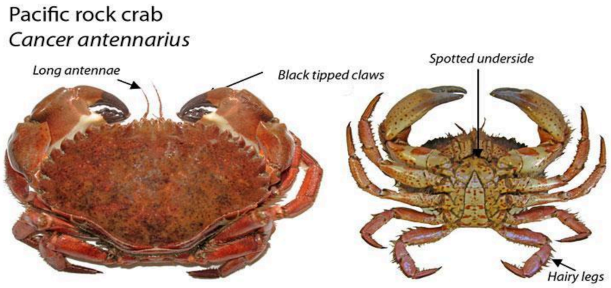


Fig. 4. Red rock crab identification (left). Key ID references during our surveys were the length of antennae and presence of speckled underside.

Fig. 5. Pacific rock crab identification (right).

The purple urchin, *Strongylocentrotus purpuratus*, is a commonly encountered grazer in the kelp forest, primarily consuming brown algae. In a healthy forest, these urchins are found tucked into cracks and crevices, hiding from predators, consuming drift kelp and performing the important role of detritivore (Graham *et al.* 2008). However, if trophic balance is altered, by either the loss of a predator or reduction in primary productivity/food availability, urchins will leave their refuge and actively seek food, and can deforest entire reefs if unchecked (Graham *et al.* 2008, Carr & Reed 2015).

Design and Sampling Methods

Design

In order to assess possible patterns and differences in crab distribution in forest and barren, we performed surveys of rocky reef in either the kelp forest or urchin barren stable state, counting crabs of the genus *Cancer*. When a crab was encountered, we recorded its species and size as well as the depth, substrate, and relief where it was found in order to gain an understanding of crab density in kelp forests and urchin barrens and analyze possible relationships between crab morphometrics and their distribution. We looked for evidence of a difference in population density of crabs between forest and barrens on a species and genus level, a relationship between depth and crab size, and a difference in size distribution of crabs between forest and barrens.

If there is a difference in crab density between forest and barrens, we predict that an analysis of variance test will yield a significant (P<.05) difference. If there is a relationship between crab size and depth, we predict that a regression analysis will yield a significant (P<.05) relationship. If there is a difference in size distribution between forest and barrens, we predict that a KS test will yield a significant (P<.05) difference in distribution.

Hypotheses

Q1) *Does the density of* C. antennarius *and* C. productus *differ in kelp forest or urchin barren habitat?*

1) We predict that we will find *C. antennarius* density in forest to be different from *C. antennarius* density in barrens using an analysis of variance test. We will reject the null hypothesis if the ANOVA test yields a significant (P<.05) difference in *C. antennarius* density between forest and barren habitat.

2) We predict that we will find *C. productus* density in forest to be different from *C. productus* density in barrens using an analysis of variance test. We will reject the null hypothesis if the ANOVA test yields a significant (P<.05) difference in *C. productus* density between forest and barren habitat.

Q2) *Does the density of all crabs differ between kelp forest and urchin barren habitats?*

We predict that we will find aggregated crab density (both *C. antennarius* and *C. productus*) in forest to be different from aggregated crab density in barrens using an analysis of variance test. We will reject the null hypothesis if the ANOVA test yields a significant (P<.05) difference in crab density between forest and barren habitat.

Q3) *Is there a relationship between depth and crab size?*

We predict that we will find a relationship between depth and crab size using a regression analysis. We will reject the null hypothesis if the regression yields a significant (P<.05) relationship between depth and crab size.

Q4) *Does the size distribution of crabs differ between kelp forest and urchin barren habitats?*

We predict that we will find the size distribution of crabs in forest to be different from the size distribution of crabs in barrens using a Kolmogorov-Smirnov test. We will reject the null hypothesis if the KS test yields a significant (P<.05) difference in size distribution of crabs between forest and barren habitat.

Sampling Methods

We assessed crab density by conducting underwater transects using SCUBA on rocky reef that was characterized as either kelp forest or urchin barren at Hopkins. Our survey team was two divers, the authors, and both of us were very familiar with both the barren and forest areas from diving in both prior to the study. We used a swath survey method to count red and pacific rock crabs on an isobathic 30x4m transect.

The only required sampling gear was one 30m tape and a light for each diver. We launched an inflatable skiff with an outboard motor from shore for many of our dives to facilitate faster transport to the barrens and faster tank changes between dives. Lights were important for finding crabs in cracks and crevices, and almost all crabs we found were deep within cracks in the reef or under rocks. Because depth was considered as a possible influence on crab abundance, we chose to lay our transect tape on an isobath with as little variation in depth along the transect as possible. We prioritized consistent depth over consistent heading and therefore the transects often meandered along the reef, following a depth contour. Maximum and minimum depth of each transect were recorded. Each survey was done entirely in forest or barren and there was never an instance where both biomes were surveyed within one 30m transect. All transects were laid preferentially on rocky reef or boulder field if possible, avoiding sand. When a suitable survey site was located, one diver attached the tape to the substrate and unreeled it while maintaining constant depth. Once the entire 30m of tape was unreeled, the reel was attached to the substrate and each diver assumed a 2m wide swath on either side of the tape, working side by side towards the "0" end of the tape.

Crab sampling: We used lights to look for crabs both on top of the substrate but also inside every crack and crevice. Every time a crab was encountered, we recorded the species of crab, the meter mark where it was found, the depth at which it was found, the substrate it was found on, the relief of its surroundings, and the estimated width of its carapace. Substrate was characterized as S=sand, C=cobble (0-10cm), B=boulder (10cm-1m), and BR=bedrock (>1m). The relief value was generated by drawing an imaginary horizontal 1m square with the crab at the center and estimating the greatest vertical distance between two points in the square. Relief was characterized as categories, where 0=0-10cm, 1=10cm-1m, 2=1-2m, and 3=>2m. Carapace width was the estimated widest point of the carapace to the nearest centimeter.

RESULTS

We tested our hypotheses by running statistical analyses on our data, and the most significant (P=.035) result we found was the difference in size distribution of crabs between kelp forest and urchin barrens using a KS test, supporting our hypothesis that there is a difference in crab size distribution between forest and barrens (Fig. 9). We did not find significant (P<.05) results for our other hypotheses, indicating no support for our predictions of a species or genus wide density difference between forest and barrens or a relationship between crab size and depth.

Q1) *Does the density of* C. antennarius *and* C. productus *differ in kelp forest or urchin barren habitat?*

1) We predict that we will find *C. antennarius* density in forest to be different from *C. antennarius* density in barrens using an analysis of variance test. We will reject the null hypothesis if the ANOVA test yields a significant (P<.05) difference in *C. antennarius* density between forest and barren habitat.

> The ANOVA test that we ran did not find a significant difference between *C. antennarius* density in forest and *C. antennarius* density in barrens (Fig. 6). We accept the null hypothesis that there is no difference in *C. antennarius* density between forest and barren habitat.

2) We predict that we will find *C. productus* density in forest to be different from *C. productus* density in barrens using an analysis of variance test. We will reject the null hypothesis if the ANOVA test yields a significant (P<.05) difference in *C. productus* density between forest and barren habitat.

> The ANOVA test that we ran did not find a significant difference between *C. productus* density in forest and *C. productus* density in barrens (Fig. 6). We accept the null hypothesis that there is no difference in *C. productus* density between forest and barren habitat.

Q2) *Does the density of all crabs differ between kelp forest and urchin barren habitats?*

We predict that we will find aggregated crab density (both *C. antennarius* and *C. productus*) in forest to be different from aggregated crab density in barrens using an analysis of variance test. We will reject the null hypothesis if the ANOVA test yields a significant (P<.05) difference in crab density between forest and barren habitat.

The ANOVA test that we ran did not find a significant difference between crab density in forest and crab density in barrens (Fig. 6). We accept the null hypothesis that there is no difference in crab density between forest and barren habitat.

Q3) *Is there a relationship between depth and crab size?*

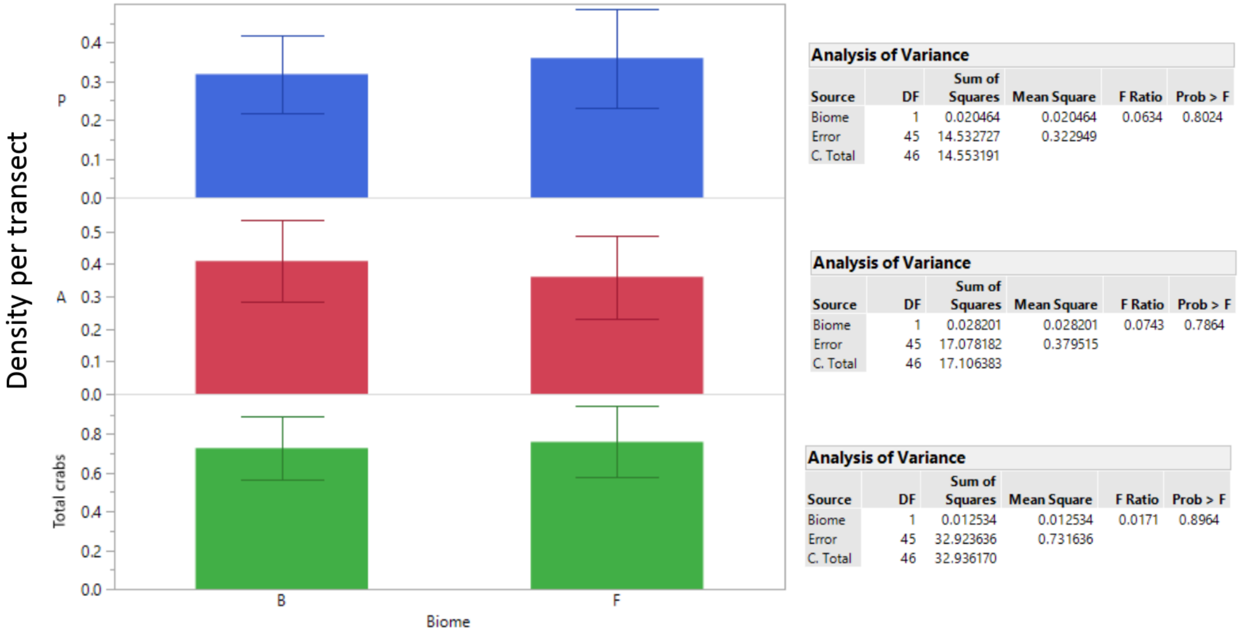
We predict that we will find a relationship between depth and crab size using a regression analysis. We will reject the null hypothesis if the regression yields a significant (P<.05) relationship between depth and crab size.

The regression analysis test we ran did not find a significant relationship between depth and crab size (Fig. 7). We accept the null hypothesis that there is no relationship between depth and crab size.

Q4) *Does the size distribution of crabs differ between kelp forest and urchin barren habitats?*

We predict that we will find the size distribution of crabs in forest to be different from the size distribution of crabs in barrens using a Kolmogorov-Smirnov test. We will reject the null hypothesis if the KS test yields a significant (P<.05) difference in size distribution of crabs between forest and barren habitat.

While there was not a significant difference in average crab size between forest and barrens (Fig. 8), the KS test we ran found a significant (P=.035) difference in size distribution of crabs between forest and barrens (Fig. 9). We reject the null hypothesis that there is no difference in size distribution of crabs between forest and barren habitat.



Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Biome	1	0.020464	0.020464	0.0634	0.8024
Error	45	14.532727	0.322949		
C. Total	46	14.553191			

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Biome	1	0.028201	0.028201	0.0743	0.7864
Error	45	17.078182	0.379515		
C. Total	46	17.106383			

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Biome	1	0.012534	0.012534	0.0171	0.8964
Error	45	32.923636	0.731636		
C. Total	46	32.936170			

Fig. 6. Density of *C. productus* (P) (P=.8024), *C. antennarius* (A) (P=.7864), and both *C. productus* and *C. antennarius* (Total Crabs) (P=.8964) in both barrens (B) and forest (F) habitat. The ANOVA test found no significant (P<.05) difference in forest and barrens density in either species nor in all crabs.

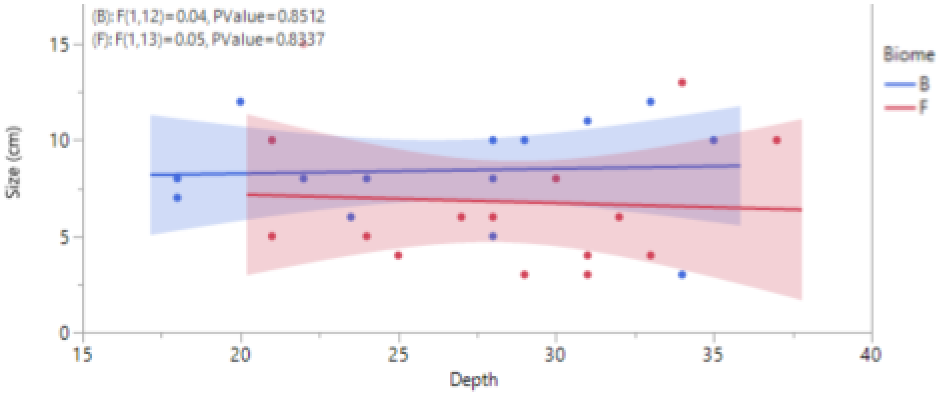
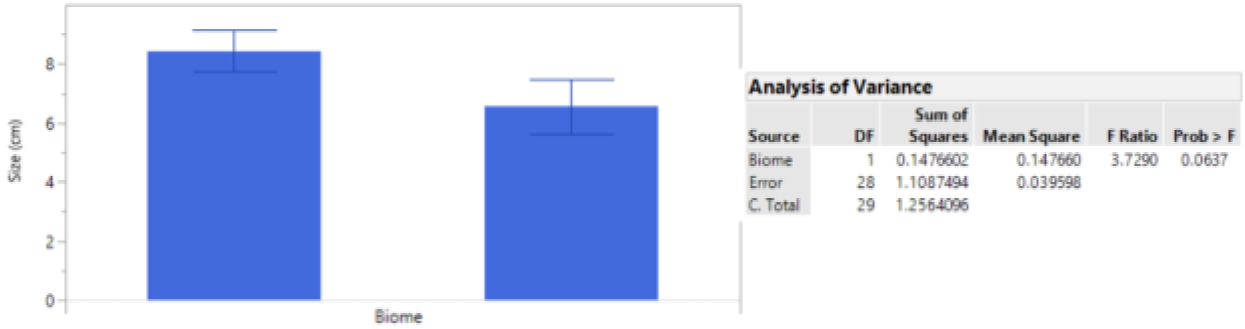


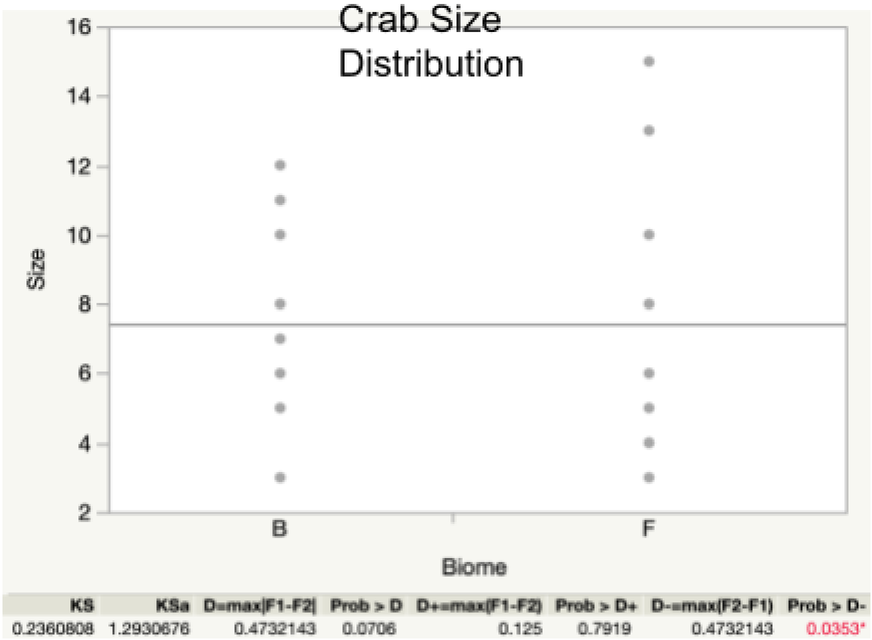
Fig. 7. Regression analysis of a relationship between depth and crab size. The regression found no significant (P<.05) relationship between depth and crab size in barrens (B) (P=.8512) or forest (F) (P=.8337).



Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Biome	1	0.1476602	0.147660	3.7290	0.0637
Error	28	1.1087494	0.039598		
C. Total	29	1.2564096			

Fig. 8. ANOVA test revealed no significant (P<.05) difference in average size of crab between barrens (B) and forest (F) (P=.0637).



KS	KSa	D=max|F1-F2|	Prob > D	D+=max(F1-F2)	Prob > D+	D-=max(F2-F1)	Prob > D-
0.2360808	1.2930676	0.4732143	0.0706	0.125	0.7919	0.4732143	0.0353*

Fig. 9. Kolmogorov-Smirnov test on size distribution in urchin barren (B) and forest (F) reveals significant (P<.05) difference in crab size distribution (KSD=.4732, P=.0353).

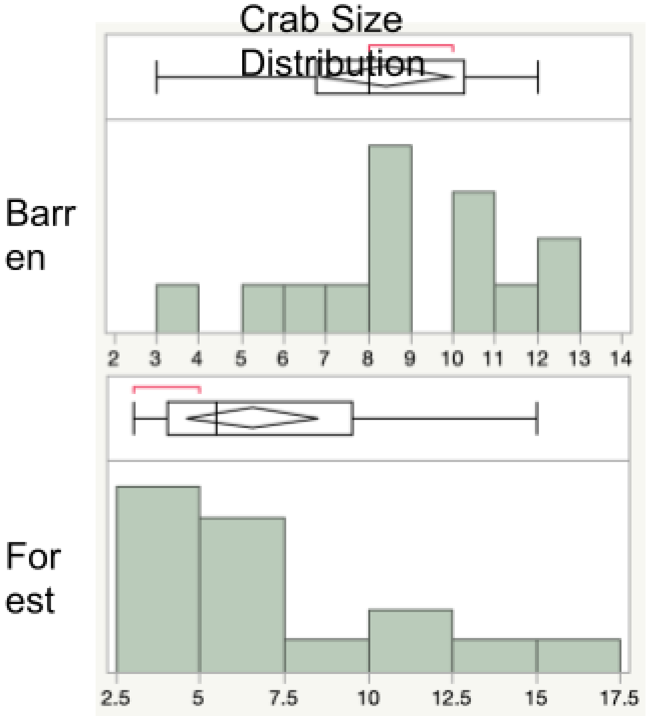


Fig. 10. Crab size distribution in forest and barren. Many more small individuals were counted in the forest than in the barren, but the largest crab was also found in the forest.

DISCUSSION

We believe that the ecological role of rock crabs in kelp forest resilience has been understudied. Shifts between kelp forest and urchin barren stable states require major perturbations to the system such as loss of a keystone predator, a disease epidemic, or widespread physical disturbance (Ebeling et al. 1985, Eckert et al. 2000, Lester et al. 2007, Stewart & Konar 2011). However, it is generally much simpler to determine these drivers of stable state shift than to identify the multitude of smaller factors that contribute to resilience of a state, notably the kelp forest (Petraitis & Dudgeon 2003). We hope to demonstrate that the presence of rock crabs in the kelp forest increases its resilience to state shift. We argue that rock crabs help to limit overgrazing by urchins in kelp forests both by preying on urchins directly and by driving urchins into refuge where they function as a detritivore rather than an active grazer (Campbell *et al.* 2001, Graham *et al.* 2008, Watson & Estes 2011, Spyksma *et al.* 2017, Mark Carr personal comm.). When urchins retreat to a refuge, their negative impact on giant kelp plant densities is reduced, resulting in further resilience of the kelp forest (Graham *et al.* 2008).

Our results also indicate that the density of rock crabs in urchin barrens is similar to the density in forest (Fig. 6), which could have an effect on state shift from barren to forest because rock crabs have been shown to prey on starved urchins from barrens (Mark Carr personal comm.). Sea otters are often cited as a possible driver of state shift from barrens to forest, but otters preferentially target gravid urchins in forests and mostly ignore starved urchins in barrens (Smith *et al*. unpublished data). Not only do crabs readily prey on starved urchins, they crush and consume them on the spot, causing a flight response in surrounding urchins, which flee to cover when chemical cues indicating a crushed conspecific are detected (Watson & Estes 2011, Spyksma *et al.* 2017, Mark Carr personal comm.). Otters may not have as much of an effect on urchin behavior inside barren patches because instead of immediately crushing the urchins, they take them to the surface where they are opened and consumed, and the remains fall wherever the otter happened to consume them (Watson & Estes 2011). Therefore, we believe that crabs may have more of an effect on urchin density and behavior in urchin barrens than sea otters.

The significant result we obtained when we compared the size distributions of crabs in barrens and forest raises interesting questions regarding why the distributions are so different (Fig. 9, 10). Why did we find more small crabs in the forest? Prior to conducting the surveys, we worried that increased algal and sessile invertebrate cover would cause an underestimate in forest crab density. However, the results indicate that this cover may not have had this effect, as smaller specimens that are more difficult to spot, and are usually more cryptic, were found in higher numbers in the forest (Fig. 10). We believe that the density estimates were reasonably unbiased by increased cover and that there are truly more juvenile and small crabs in the forest. Why were there fewer large crabs found in the forest? One possible reason for this could be that otters preferentially take large crabs, and since they forage in the forest more often for higher quality urchins, the large crabs were taken by otters (Tinker *et al.* 2019, Smith *et al.* unpublished data). *Cancer* spp. have been shown to make up about 25% of otter diets in Monterey, where the study was conducted (Tinker *et al* 2019). Additionally, crabs are mobile and the larger adults could be moving to and from barrens and forest to feed or shelter, and this could be occurring on a temporal scale of hours, days, weeks, or months. Our surveys were conducted in October and November, and every survey was conducted between 0800 and 1200, limiting our knowledge of crab distributions on seasonal and diurnal temporal scales.

Originally, we set out to analyze crab densities among three biomes: kelp forest, urchin barrens, and the ecotone between forest and barrens, often referred to as an “urchin front” (Rose et al. 1999). However, while this ecotone is dramatically defined at some sites, the forest and barrens at Hopkins transition more gradually, and in most places there is simply a sand channel between a patch of reef representing the kelp forest and a patch of urchin barrens. This aspect of the site, combined with the limited time we had to collect data, forced us to disregard this aspect of the study and only compare forest to barrens. If this study is continued, we are interested in studying the ecotone as it presents an interesting set of questions regarding crabs as a mechanism of resilience. Obviously, this would require us to conduct surveys at different sites where there is a more obvious ecotone, preferably existing on rocky reef, not sand.

The decision to only survey rocky reef was made because kelp forests and urchin barrens are alternative stable states of rocky reef. While *Cancer* spp. are commonly found on other substrates such as mud and sand, we are interested in their effects on the rocky reef stable state, and therefore we did not survey in sand. We believe that we would have encountered more species of crab in the sand, such as *C. magister,* but again, the focus of the study was rocky reef. However, preferentially targeting reef undoubtedly imparted some bias, especially combined with the prioritization of consistent depth over consistent heading. As transects were laid, it was up to the diver to reduce bias by choosing random reef to survey, not purposely running the tape over habitat that looked suitable for crabs.

Another potential source of bias was our estimation of carapace width. There were very few instances where a crab could be measured, and therefore few opportunities for both a true size measurement and calibration of size estimation. Additionally, sometimes crabs were tucked into a hole in a way that concealed most of their carapace, and in these cases where a reasonably accurate size estimate could not be made, size was not recorded. We hope that in future studies we can more accurately record sizes to strengthen our knowledge of rock crab distribution.

A potential further study could incorporate temporal scales, larger geographic ranges, wider depth distributions, and more variance in sampled habitat type to further our understanding of the roles rock crabs play in kelp forest ecosystems. As our research has suggested, the impact of rock crabs on urchins must be further understood to enhance our knowledge not only of kelp forest ecosystem resilience, but also the mechanisms that contribute to a shift in stable state.

ACKNOWLEDGEMENTS

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LITERATURE

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