Recruitment and habitat association of *Stronglyocentrotus purpuratus* in temperate kelp forest and barren habitats

Annakate Clemons, Lindsay Cullen, Monica Falcon, Mara Salisbury
Department of Ecology and Evolutionary Biology—University of California, Santa Cruz 2017

Abstract
Recruitment is fundamental to the replenishment of populations and the structure and dynamics of marine communities. The recruitment success of the purple sea urchin, *Strongylocentrotus purpuratu*s, is known to impact the state of kelp forest ecosystems. Active grazing by large populations of urchins can shift them to a barrens state (Bernstein et al. 1981). Our study focuses on associations between juvenile urchins and biotic and abiotic features of kelp forest ecosystems. Studies show that these sea urchins settle on or around crustose coralline algae and use it as a food source (Pearce & Scheibling 1990). We hypothesize that there are patterns of association between juvenile urchins and substrate type, different algal assemblages in kelp forests and barrens affecting recruitment, and significant relationships between juvenile urchins and other mobile invertebrates. To test these, we conducted field surveys with uniform point contact methods in the kelp forest and adjacent urchin barren ecosystems at Hopkins Marine Station in Monterey, California. We found different community structures in the kelp forest and barrens sites, and a positive association between juvenile urchins and crustose coralline algae. Additionally, we observed compelling relationships between juveniles and hermit crabs. Urchins drastically affect the resilience of kelp forests. Evaluating patterns of urchin recruitment will provide us with the necessary insight to develop effective kelp forest conservation approaches.

Introduction
Marine species exhibit a bipartite lifecycle that contributes largely to the structure of marine communities. A bipartite lifecycle is one in which adults eject their larvae into the water column to be dispersed by ocean currents (i.e. currents). The settlement of these pelagic individuals to new environments and their subsequent occurrence there is an event described as recruitment. Recruitment is instrumental to the replenishment of populations (Rogers et. al. 1984, Hamilton et. al. 2006, Pusack et. al. 2014). Population dynamics, in turn, play a fundamental role in the structure and productivity of ecosystems. For instance, populations of purple sea urchins, *Strongylocentrotus purpuratus*, can dramatically alter the form and function of kelp forest systems. In high densities and when food becomes a limited resource, purple sea urchins actively graze on kelp and convert forests into collapsed, or barrens states (Ebeling et. al. 1985, Leinaas & Christie 1996, Steneck et. al. 2002). Barrens diminish many of the ecological and commercial services that forests provide, thus it is critically important to understand how the recruitment of sea urchins contributes to the persistence of these habitats.

Studies show that juvenile urchins preferentially recruit to crustose coralline algae (Andrew & Choat 1985, Rowley 1989, Harrold 1991). Juveniles utilize the microbial film layer these algae produce as a food source to support their early growth (Pearce & Scheibling 1990). Adult purple urchins graze their immediate surrounding area leaving only crustose coralline algae. Thus the area around adults has a higher proportion of encrusting algae than other locations (Cameron 1980). Coralline algae induces the settlement of other invertebrates such as chitons, abalone and sea star larvae (Barnes and Gonor, 1973; Shepherd & Turner 1985; Barker, 1977). Other studies show that juvenile urchins recruit to adult spines (Andrew & Choat 1982). This cycle is thought to create a positive feedback loop where adults graze and therefore clear competing substrate for juveniles which leads to the formation of urchin barrens (Fowler-Walker

& Connell 2002). In intertidal habitats, juvenile urchins are more densely distributed with adults (Ebert, 1968; Schroeter, 1978). However, in the subtidal, juveniles thrive in a variety of different habitats that are not always associated with adults (Tegner and Dayton, 1977). We aim to build on these studies by examining how recruitment contributes to observed distributions of juveniles.

In order to assess this relationship, we observed and compared two different communities: a kelp forest and an urchin barren. Barrens are alternative stable states of kelp forests. A reduction in predation pressure can increase urchin populations. Large aggregations graze heavily on kelp forests, eventually converting them to barrens (Bernstein et al 1981). Crustose coralline algae is resistant to grazing and outcompetes other algae for space. This prevents kelp forests from returning to a healthy state (Breitburg 1984). We also examined habitats on a finer scale by comparing areas within cracks and out of cracks at both sites. This was motivated by the observation that urchins in kelp forests are almost exclusively in cracks while they are found out in the open in barrens (Bernstein et al. 1981). We asked the following questions: (1) are habitats in cracks different from surrounding habitats, (2) is the substrate juveniles are most often found on disproportionate to what is available in cracks, (3) is there an apparent association between juveniles and adults and/or other species present in cracks, and (4) what factors might be influencing the number of juveniles in a habitat. We addressed the following hypotheses:

Hypothesis 1: There are patterns of association between juvenile urchins and substrate type. We predict that juvenile urchins will most commonly be associated with encrusting algal species and diatoms because they are the preferred habitat for recruitment.

Hypothesis 2: There are different algal assemblages between kelp forests and barrens that affect the recruitment of juvenile urchins to these sites. We predict that urchin barrens provide a more suitable habitat for urchin recruitment than kelp forests due to their associated algal assemblages. We predict there will be a larger assemblage of preferred habitat in the cracks of kelp forests than on the reef in kelp forests.

Hypothesis 3: There are patterns of association between juvenile urchins and other mobile species commonly found in cracks. We predict that adult urchins have a positive effect on juvenile urchins because they create a more preferred habitat for juvenile recruitment via active grazing.

Kelp forests are dynamic ecosystems that can be greatly affected by a number of abiotic and biotic factors. Changes to these systems may have long lasting effects on their health and productivity. Over the past few decades, urchins have been a popular subject of study due to their potentially detrimental effect on kelp forest communities. By understanding urchin recruitment patterns and their relationship with the surrounding habitat we can better understand the factors that set off catastrophic grazing events. Kelp forests are some of the most productive ecosystems on the planet. Our study aims to provide valuable insight into the behavior and recruitment of urchins which is crucial for preserving these habitats and the services they provide.

Methods

General Approach

We conducted an observational field study to better understand patterns of recruitment pertaining to juvenile urchins. All measurements were performed on SCUBA in November, 2017. All surveys in the kelp forest were performed on thirty meter by four meter transects running east and west of the permanent cable, perpendicular to shore. The barrens surveys were also performed using a transect running east and west in a previously observed reef habitat. Our objectives were to determine: (1) if there are associations between substrate and juvenile urchin populations, (2) the different algal compositions between kelp forests and barrens, and (3) patterns of association between juvenile urchins and mobile invertebrates. We used a number of different techniques to

do this. In the kelp forest community, we used uniform point contact (UPC) methods to determine the substrate composition of cracks and reef. We also measured the dimensions of cracks, which included width, length, and depth in order to standardize the cracks that we surveyed. In addition, we opportunistically surveyed cracks where juvenile urchins were present. This allowed us to determine patterns of association between substrate and other common invertebrates. In the urchin barrens, we used quadrats to perform UPC methods because urchins were found exposed on the reef. This allowed us to compare substrates present among the reef to what juvenile urchins were settled on.

System Description

This study was conducted at Hopkins Marine Station. In this location we were given the opportunity to observe recruitment of urchins in both a healthy kelp forest community and an urchin barren. Hopkins is a protected area near Monterey Bay, California. The Hopkins subtidal ecosystem possesses large granite benches that lead to high-relief outcrops. These are surrounded by varying bottom types including sand, shell fragments, and bedrock (Gerard 1976). Areas of high relief provide crack habitats for many benthic species to graze and settle. We conducted our surveys at varying depths and along the 70, 120, 130, and 140 meter marks on the permanent cable. Our other study site was an urchin barren located around the point from the kelp forest (Figure 1). This is an area dominated by red turf algae and crustose species with no *Macrocystis* present. Adult purple urchins litter the reef. In the absence of *Macrocystis*, we expected to see a higher proportion of crustose coralline in the barrens.



Figure 1: The kelp forest and barrens surveyed adjacent to the Hopkins Marine Station.

Juvenile Associations with Substrate Data Collection

To determine whether juveniles were disproportionately associated with certain substrates, we only surveyed cracks in the kelp forest where juvenile urchins were present. In these cracks, we recorded FSW, the number of juveniles, and number of adults. We then placed a seamstress tape directly above each juvenile and recorded the substrate beneath the 5, 10, 20, 40, and 80 centimeter marks. We also noted which of these points were marked inside of cracks and which were outside (i.e. on the reef) (Figure 2).

To determine the substrate composition of the barrens, we sampled with quadrats using UPC methods. Whenever we came across a juvenile urchin on top of the reef, we placed the center of the quadrat over the juvenile. Sixteen evenly spaced points evenly spaced were then sampled to record the substrate surrounding the juvenile (Figure 3). Any juvenile that was found in a crack in the barrens was sampled using the same crack sampling method performed in the kelp forest. In order to test for association between juveniles and substrate,

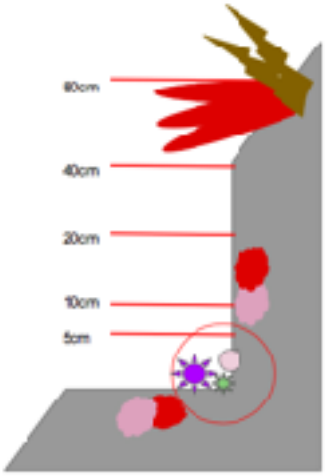

Figure 2: Opportunistic UPC sampling method when juveniles were present.

we used a Chi-Squared analysis.



Figure 3: Urchin Barren UPC method with quadrat.

Available Substrates Data Collection

To characterize the available substrates in both sites inside and outside of cracks, we used UPC methods. Our standard crack width was anywhere between 20 and 40 centimeters. Our standard length for cracks was one meter. To establish the depth of the crack, we inserted a meter bar at the widest part until we hit bottom. In addition, we noted the depth the crack was found at in feet of seawater (FSW). If there were juveniles, we noted how many there were and the substrate they were on. We also recorded the number of adult purple urchins. To conduct a UPC of the crack, we inserted a meter bar into the crack at three different locations (evenly spaced apart). At each location the bar was inserted, we took five UPC points of the top and bottom of the crack. This gave us thirty points per crack (Figure 4). Measurements were taken regardless of whether there was a juvenile was present or not. We ran a Chi-Squared analysis to determine if there were significant differences in the proportions of available substrates.

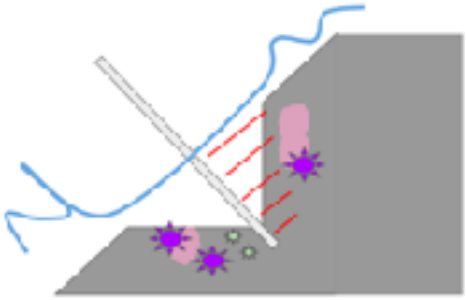

Figure 4: UPC method with meter bar to test for the available substrates within a crack.

Juvenile Associations with Other Species

In order to determine whether juveniles have associations with other invertebrates found in cracks, we noted the number of adult urchins and any other mobile invertebrate within a 10 cm diameter of the juvenile during our opportunistic surveys. We then used a linear regression analysis to see whether the number of other invertebrate species had any correlation to the number and size of juveniles.

Results

Juvenile Associations with Substrate

Juvenile urchins were found disproportionately on crustose coralline algae compared to other substrates in associated habitats (Figure 7). Juvenile urchins were also frequently found on red encrusting algae, rock, and diatom substrates (Figure 5). These substrates are very similar to the ones found inside of cracks and very different from those outside of cracks (Figure 6).

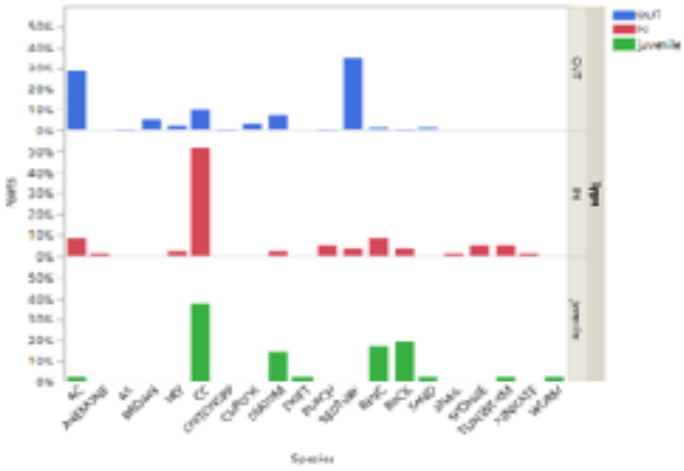

Figure 5: Bar graph of the proportion of substrates inside and outside of cracks compared with the proportion of juvenile urchins associated with each substrate. OUT describes out of crack habitats (i.e. on top of reef) in kelp forest and barrens environments and IN describes inside of crack habitats. AC=articulated coralline algae, BROWN=brown algae, BRY=bryozoan, CC=crustose coralline algae, CUPCOR=cup coral, RENC=red encrusting algae.

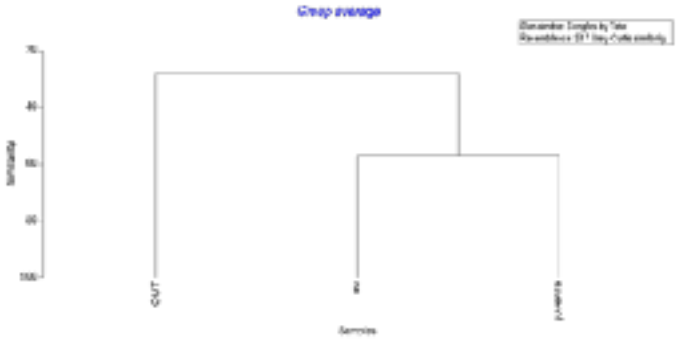

Figure 6: The relationship between juvenile urchins and the presence of their associated substrates inside and outside of cracks.

Test	ChiSquare	Prob>ChiSq
Likelihood	189.975	<.0001
Pearson	174.688	<.0001

Figure 7: Chi-square analysis for whether the substrate juveniles are most often found on is disproportionate to what is available in cracks and out of cracks. P-value<.0001 so there are significant differences in juvenile-substrate associations.

Available Substrates

There are distinct differences in community patterns between kelp forest and barrens habitats, inside and outside of the cracks present in each (Figure 9). Both barrens habitats exhibit similar community structures composed of high proportions of articulated coralline, crustose coralline, red turf algae, and sea urchins. Outside of crack habitats in the kelp forest also portray high proportions of articulated coralline and red turf algae, but exhibit a low proportion of crustose coralline algae. In comparison, inside of crack habitats in the kelp forest are described by high proportions of red encrusting algae, rock, and sand, and low proportions of red turf algae. Cracks in kelp forests exhibit a markedly different community structure from the other habitats, but share a high proportion of crustose coralline algae in common with both barrens habitats (Figure 8).

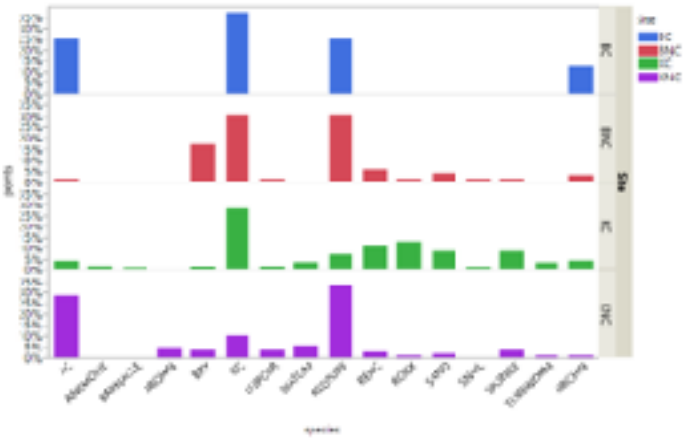

Figure 8: Bar graph of the proportion of substrates observed within each kelp forest and barren habitat. BC describes crack habitats in the barrens, while BNC describes not in crack habitats (i.e. on top of the reef) in the barrens. Similarly, KC represents the crack habitats observed in the kelp forest while KNC represents the not in crack habitats (i.e. on top of reef) in the kelp forest. AC=articulated coralline algae, BROWN=brown algae, BRY=bryozoan, CC=crustose coralline algae, CUPCOR=cup coral, RENC=red encrusting algae.

Test	ChiSquare	Prob>ChiSq
Likelihood Ratio	309.853	<.0001
Pearson	316.06	<.0001

Figure 9: Chi-square analysis for whether there are significant differences between community structures of kelp forest crack, kelp forest not in crack, barrens in crack, and barrens not in crack

habitats. P-value<.0001 so there are significant differences.

Juvenile Associations with Other Species

There are no significant associations between the number of juvenile urchins and the number of adult urchins, the number of snails, or the number of brittle stars (Figure 10). In comparison, there is a strong negative association between the number of hermit crabs (Figures 10, 11) and the size of juvenile urchins as well as a strong positive association between the number of hermit crabs and the number of juvenile urchins (Figures 10, 12).

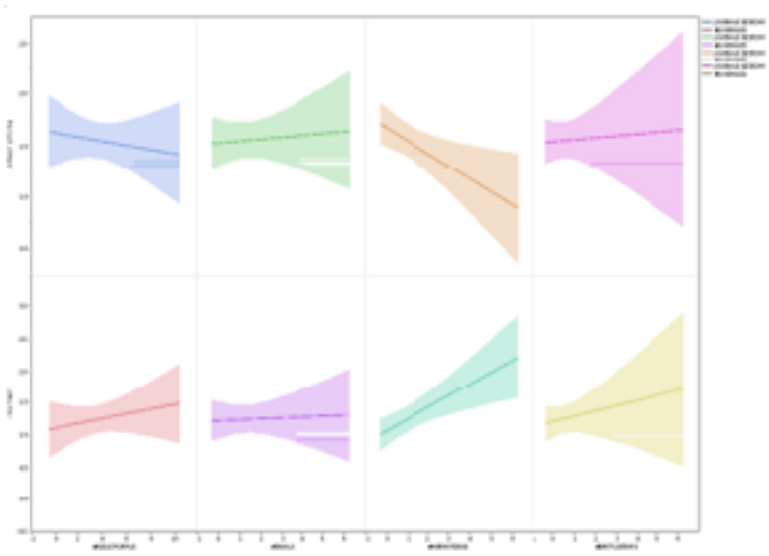

Figure 10: Regression analysis of the associations between the number and size of juvenile urchins vs. the number of other mobile species commonly observed in cracks.

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	1.6717807	0.092448	18.08	<.0001*
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Figure 11: Chi-square analysis for whether there is a significant association between the number of hermit crabs and juvenile urchin size. P-value<.0001 and estimate (slope) is negative, so there is a significant negative association.

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	1.0747619	0.111917	9.47	<.0001*
#HERMITCRAB	0.1833333	0.056988	3.22	0.0026*

Figure 12: Chi-square analysis for whether there is a significant association between the number of hermit crabs and the number of juvenile urchins. P-value<.0001 and estimate (slope) is positive, so there is a significant positive association.

Discussion

Habitat association within a species is a multidimensional subject that requires careful consideration of many interconnecting factors. Forces that affect urchin recruitment are largely under researched. Urchin populations and their grazing pressures can be a large driving force in determining the state of their surrounding habitat. Understanding the factors that correlate with their distribution and recruitment may provide valuable information on how these species interact with their environment and may lead to solutions for keeping their populations in check.

Our initial hypothesis looked at what juvenile urchins were settling on at the micro-scale. Our data supports our hypothesis that juveniles show a preference for certain substrate types including crustose coralline algae and diatomaceous film. We found juvenile urchins were seen significantly more often on crustose coralline algae, red encrusting algae, diatomaceous film, and

bare rock than any other substrate (Figure 5). Crustose coralline algae represents a roughly twenty percent higher rate of settlement than either red encrusting algae, diatomaceous film, or bare rock. All other substrates measured represented less than ten percent of the substrate juveniles were found on (Figure 5). This pattern reflects previous data that shows crustose coralline algae provides a favorable habitat for juvenile urchins. Crustose coralline algae supports the early growth of urchins by providing adequate food in the form of diatomaceous film and bacteria (Rowley 1989, Pierce & Scheibling 1990). Urchins therefore actively clear the coralline algae of epiphytes that reduce photosynthesis (Pearce & Sheibling 1990). This reveals a link between urchins and the presence of coralline algae because both benefit from each other. Coralline algae species have the highest juvenile settlement in relation to other algal species (Harold et al. 1991). This is consistent with our results showing a higher proportion of juvenile urchins with crustose coralline than any other substrate.

We believe that food availability may be only one of many settlement cues for juvenile urchins and its influence may vary across substrates. Only one species of urchin, *S. droebachiensis*, has been proven to respond to chemical cues in the larval stage (Pearce and Sheibling 1990). Future studies should be conducted with other urchin species to determine if there is a chemical cue within crustose coralline algae, along with microbial film, that initiates a strong settlement cue to that substrate. Previous research shows that juvenile urchins discriminate between natural substrates and respond to a settlement cue other than or along with microbial film found on encrusting algae species (Rowley 1989). Laboratory cultures of *S. purpuratus* showed enhanced recruitment in the presence of crustose coralline algae compared to rocks encrusted with microbial film (Harold et al. 1991). Similarly, both coralline algae and red algal turf induced similar numbers of larvae of *S. purpuratus* to metamorphose, but that metamorphosis is significantly lower with microbial filmed rocks (Rowley 1989). The juveniles from coralline treatments were also able to grow larger post-metamorphosis than those associated with other substratum (Harold et al. 1991). This may indicate if *S. purpuratus* experience a stronger settlement cue associated with a chemical or the abundance of prefered microbial film found on coralline algae and red algal turf rather than the film found on rocks.

After determining what substrates juvenile urchins associate with, we investigated how this is influenced by what substrates are actually available to juveniles in two different habitats, kelp forest or barren. Our data supports the hypothesis that there are different algal assemblages between kelp forests and barrens that affect the recruitment of juvenile urchins to these sites. We found that barrens and kelp forest habitat outside of cracks are composed of very different algal and invertebrate assemblages.

When tested, the barrens were mostly composed of bryozoans, red encrusting algae, and crustose coralline (Figure 8). As a low-lying species, crustose coralline can be outcompeted for space and light by other foliose algae. However, crustose coralline algae is resilient to adult urchin grazing, resulting in a greater coverage of crustose coralline found beneath adult urchins or areas frequently grazed by adults (Cameron & Schroeter 1980). Both urchin grazing and crustose coralline maintain barrens by outcompeting other algae spores (Bulleri 2002). Adult urchins and crustose coralline can create a positive feedback loop by clearing competing substrate for juvenile urchins. In contrast to the barrens, kelp forest reef is composed of mostly articulated coralline algae and red turf, but also had a higher diversity of species present overall with significantly more cupcoral, brown algae, diatoms, sponges and tubeworms than the barrens site (Figure 8). The largest difference however, is the lack of crustose coralline. High proportions of crustose coralline algae are seen across the barrens and only within the cracks of a kelp forest (Figures 5 & 8). The lack of crustose coralline in kelp forest reef can be attributed to the presence of urchin predators. Urchins do not venture out of cracks in a kelp forest system where predators are present, and therefore do not actively graze foliose kelp species that compete with crustose coralline for space (Andrew & Choat 1985). This explains why crustose coralline dominates in urchin barrens where active urchin grazing is present. The presence of extensive crustose coralline algal cover may therefore contribute to the persistence of coralline algae—sea urchin communities (Breitburg 1984).

Turf algae is present in high proportions outside of cracks and on the reef. Urchins have also been observed to recruit to turf algae but at a much slower rate. The slower response observed for larvae settling on turf may indicate that larvae either prefer coralline algae, or respond to coralline and turf algae using different mechanisms (Rowley 1989). Previous studies indicate a high mortality rate of juveniles transplanted to a kelp forest reef habitat. In 18 weeks, juveniles experienced a 70% mortality rate compared to only 3% in a barren composed heavily of crustose coralline (Andrew & Choat 1985). This is possibly due to the slow recruitment rate of urchins to turf algae out on the reef and being confined to cracks and crevices where crustose coralline is present (Rowley 1989). In the presence or absence of predators, small urchins are more likely to hide in cracks rather than aggregate like adults do, which might be a response to small urchins susceptibility to a greater range of predators than adults (Bernstein et al. 1981). Although mortality rates are higher in a kelp forest, cracks can support juvenile recruitment just as well as the barrens.

Inside and outside of cracks, we observed urchins cohabitating the same spaces with various species. Juvenile urchins have been observed to recruit to adult spines or certain substrates such as crustose coralline (Andrew & Choat 1982). We hypothesized that there are patterns of association between juvenile urchins and other mobile species commonly found in cracks. In particular, we were interested in juveniles relationship to adults. However, no significant association was found between juvenile urchins and any species including adult urchins except hermit crabs (Figure 10). Previous studies have shown that when adults are removed, the abundance of gastropods that feed on similar substrates decreases (Andrew & Choat 1982). This shows that urchin presence can benefit certain herbivorous invertebrates due to an urchin-driven change in algal assemblage.

Our results revealed a positive relationship between hermit crabs and juvenile urchin abundance, but a negative relationship with juvenile size (Figures 11 & 12). Although no experiments were conducted to further investigate this relationship, with future research, a possible explanation could lie within hermit crab diet. Hermit crabs are detritivores and feed on similar drift algae and organic material as adult urchins, indicating possible competition between the two for crustose coralline as a preferred habitat (Breitburg 1984). By feeding on this organic material, hermit crabs could be clearing the way for bare rock, diatomaceous film, or crustose coralline that would make an ideal habitat for juvenile urchin settlement. This may allow greater numbers of juveniles to settle in cracks where hermit crabs are present. However, juvenile urchins also feed on this microbial film, so although hermit crabs might be clearing a path for them, they would also be competing with juveniles for food. Juvenile urchins therefore do not receive as many nutrients to facilitate growth when in the presence of hermit crabs. Further research should be done to confirm or deny a mutualistic relationship between urchins and hermit crabs because there does appear to be a clear correlation between the two species. In order to determine if episodes of high recruitment are responsible for an increase in urchin number, more information is needed concerning interspecific and intraspecific relationships between juveniles and other herbivores (Andrew and Choat 1982).

Although we attempted to account for all variables, there were some limitations to our study that should be addressed in further research. Our observations were conducted in fall, with several storms disturbing our study site. This might explain why urchins were observed only in cracks in the kelp forest, especially juveniles who are small enough to be swept away by heavy wave action. Similarly, invertebrate recruitment can change year to year, and without surveying for multiple years we do not know what is considered a normal recruitment for this area. These variables could be accounted for by performing surveys in the spring and summer when storms are less common and across multiple years. Another important influence of the seasons is various changes in urchin predation, for example fish have a larger presence and effect in the summer, which showed to alter urchin foraging behavior (Bernstein et al. 1982). Changes in foraging behavior as response to predation at certain population densities could have an extreme negative effect on an existing kelp forest and can maintain a stable urchin barren (Bernstein et al. 1982).

In addition, *Macrocystis* holdfasts are an important site of urchin recruitment and source of food and shelter for adults in kelp forest communities (Tegner et al. 1995). However, because

our study was conducted within a marine protected area (MPA), we were unable to disturb the kelp holdfasts in order to measure any juvenile recruitment; future observations could include juvenile recruitment to *Macrocystis* holdfasts as well as cracks and crevices. Furthermore, we were unable to take measurements of urchin density in either habitat. Previous research shows reduced mortality of juvenile urchins in barrens habitat contributes to a larger number of adults (Rowley 1989); therefore density rather than proportion is an important factor to consider in order to form a more complete description of this complex system. Our observations raised several questions about the nature of *S. purpuratus* recruitment and settlement. Currently, no research has concluded that larval *S. purpuratus* respond to chemical cues for settlement, nor has any research shown that crustose coralline algae release chemical cues into the water column. It could be that crustose coralline provides a more consistent supply of microbial film for juveniles to feed on, resulting in higher survivorship into juvenile stages, or the microbial film itself could possibly emit some chemical tracer that induces the settlement and subsequent metamorphosis of juvenile urchins. Additional research into the mechanisms that control urchin recruitment is vital to understanding the matrix of species interactions that influence habitats in these highly productive subtidal communities.

Species interactions shape and alter the states of their communities. Recruitment of key species may determine the future of their community altogether. Understanding why urchins recruit to particular habitats may provide insight into the mechanisms that cause their populations to influx or decrease and their impact on intertidal communities as a whole. We found support that juvenile urchins recruit to a preferred substrate, crustose coralline algae, both in kelp forests and in a barrens environment. If crustose coralline and adult urchins are confined to cracks and crevices, then the kelp forest persists; however, when adult urchins overgraze brown algae, crustose coralline outcompetes macro-algae species for future settlement space, enforcing a barren habitat. Unfortunately, these barren habitats act as a less diverse and productive alternative stable state that cannot be reversed without the intervention of a large disturbance event (Ebeling et al. 1985). As both a catalyst and a steward for barrens environments, monitoring the life cycle of urchins is necessary to monitor the overall health and resilience of kelp forest habitats. With climate change and human interference becoming an ever-increasing omnipresent threat to kelp forests and other vulnerable habitats, monitoring influential species and the environmental cues that affect their behavior and success must become a priority if we hope to preserve the worlds most productive habitats.

Literature Cited

Andrew, N. L., & Choat, J. H. (1982). The influence of predation and conspecific adults on the abundance of juvenile Evechinus chloroticus (Echinoidea: Echinometridae). *Oecologia, 54*(1), 80-87.

Andrew, N. L., & Choat, J. H. (1985). Habitat related differences in the survivorship and growth of juvenile sea urchins. *Marine Ecology Progress Series, 27*, 155-161.

Barker, M. (1977). Observations on the settlement of the brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinaterias calamaria* (Gray) (Echinodermata: Asteroidea) in the laboratory and on the shore. *Ecology,* 30: 95-108.

Barnes, J, Gonor, J. (1973). The larval settling response of the lined chiton: *Tonicella lineata*. *Marine Biology*, 20 259- 264.

Bernstein, B. B., Williams, B. E., & Mann, K. H. (1981). The role of behavioral responses to predators in modifying urchins (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Marine Biology, 63*(1), 39-49.

Breitburg, D. L. (1984). Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology, 65*(4), 1136-1143.

Bulleri, F., Bertocci, I., & Micheli, F. (2002). Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. *Marine Ecology Progress Series, 243*, 101-109.

Cameron. R.A. & Schroeter S.C. (1980). Sea urchin recruitment: effects of substrate selection on juvenile distribution. *Marine Ecology*, 2:243-247.

Ebert, T. A. (1968). Growth rates of the sea urchin: *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology,* 49: 1075- 1091.

Ebeling, A. W., Laur, D. R., & Rowley, R. J. (1985). Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Marine Biology, 84*, 284294.

Fowler-Walker, M., & Connell, S. (2002). Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy-benthic associations. *Marine Ecology Progress Series, 240*, 49-56.

Gerard. V. A. (1976). Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay. California. Dissertation. University of California, Santa Cruz. California. USA.

Hamilton, S., White, J., Caselle, J., Swearer, S., & Warner, R. (2006). Consistent long-term spatial gradients in replenishment for an island population of a coral reef fish. *Marine Ecology Progress Series, 306*, 247-256.

Harold.C. Lisin.S. Light. K.H. Tudor Shirely.(1991). Isolating Settlement from recruitment of sea urchins. *Journal of Experimental Marine Biology and Ecology,* 147:81-94.

Leinaas, H. P., & Christie, H. (1996). Effects of removing sea urchins (Strongylocentrotus droebachiensis): stability of the barren state and succession of kelp forest recovery. *Oecologia, 105*(4), 524-536.

Pearce, C. M., & Scheibling, R. E. (1990). Induction of Metamorphosis of Larvae of the Green Sea Urchin, Strongylocentrotus droebachiensis, by Coralline Red Algae. *The Biological Bulletin, 179*(3), 304-311.

Pearce, C. M., & Scheibling, R. E. (1990). Induction of metamorphosis of larvae of the green sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. *The Biological Bulletin, 179*(3), 304-311.

Pusack, T. J., Christie, M. R., Johnson, D. W., Stallings, C. D., & Hixon, M. A. (2014). Spatial and temporal patterns of larval dispersal in a coral-reef fish metapopulation: evidence of variable reproductive success. *Molecular Ecology, 23*(14), 3396-3408.

Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J., & Hardin, J. (1984). Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs, 3*(2), 69-76.

Rowley, R. J. (1989). Settlement and recruitment of sea urchins (Strongylocentrotus spp.) in a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes? *Marine Biology, 100*(4), 485-494.

Schroeter, S. (1978). Experimental studies of competition as a factor affecting the distribution and abundance of purple sea urchin, Strongylocentrotus purpuratus (Stimpson). Ph. D. Thesis, Biology, University of California, Santa Barbara.

Shepherd, S., & Turner, J. (1985). Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. *Journal of Experimental Marine Biology and Ecology, 93*(3), 285-298.

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation, 29*(4).

Tegner, M., Dayton, P. (1977). Sea urchin recruitment patterns and implications of commercial fishing. *Science*, 196, 324-326

Tegner, M., Dayton, P., Edwards, P., & Riser, K. (1995). Sea urchin cavitation of giant kelp (*Macrocystis pyrifera*) holdfasts and its effects on kelp mortality across a large California forest. *Journal of Experimental Marine Biology and Ecology, 191*(1), 83-99.