UC San Diego
Research Theses and Dissertations

Title

The Effects of Predators and Habitat on Sea Urchin Density and Behavior in Southern California Kelp Forests

Permalink

https://escholarship.org/uc/item/3zv9w2w2

Author

Nichols, Kathryn D.

Publication Date

2009

Peer reviewed

THE EFFECTS OF PREDATORS AND HABITAT ON SEA URCHIN

DENSITY AND BEHAVIOR IN SOUTHERN CALIFORNIA

KELP FORESTS

_____

A Thesis

Presented to the

Faculty of

San Diego State University

_____

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

_____

by

Kathryn D. Nichols

Spring 2009

SAN DIEGO STATE UNIVERSITY

The Undersigned Faculty Committee Approves the

Thesis of Kathryn D. Nichols:

The Effects of Predators and Habitat on Sea Urchin Density and Behavior in

Southern California Kelp Forests

_____
Kevin Hovel, Chair
Department of Biology

_____
Matt Edwards
Department of Biology

_____
Kathleen Farley
Department of Geography

_____
Approval Date

DEDICATION

I would like to dedicate this thesis to my family. Particularly my parents who have always supported my every endeavor with encouragement, excitement and a belief in me that is unwavering.

Curiosity is the one thing invincible in nature.

–Freya Stark

ABSTRACT OF THE THESIS

The Effects of Predators and Habitat on Sea Urchin Density and
Behavior in Southern California Kelp Forests
by
Kathryn D. Nichols
Master of Science in Biology
San Diego State University, 2009

It is well documented that sea urchins can have vast impacts on kelp forest community structure as a result of kelp grazing. Despite the ecological importance of sea urchins, direct field studies on the relative effects urchin predators have on shaping urchin populations are rare for southern California. I conducted surveys at three kelp forest sites near San Diego, CA, including heavily fished and marine reserve sites, to measure sea urchin size, abundance, and habitat use as well as the abundance of potential sea urchin predators. I also examined whether purple sea urchin (*Strongylocentrotus purpuratus*) proportional mortality varied with urchin density, time of day, and algal cover in the La Jolla Ecological Reserve, where densities of potential predators such as sheephead and spiny lobsters are high. Transect surveys showed urchin behavioral changes among the three sites with urchins tending to be more cryptic inside the reserve as compared to sites adjacent to the reserve and in heavily fished areas. Fished species, including spiny lobsters and red urchins were found to be less abundant in non-reserve sites, while unfished purple urchins were more abundant in non-reserve sites possibly due to reduced predation pressure in these areas. Predator densities and mean sizes of predators were highest inside the reserve and lowest in the heavily fished site. In the experiment, urchin proportional mortality decreased with increasing urchin density. This trend was stronger in open plots than in plots covered with algae, in which proportional mortality was more variable. Substantial nighttime predation was observed and was not influenced by the presence of algal cover. Examining whether urchin mortality from predation is density-dependent and how habitat complexity influences this relationship is imperative because behavioral changes and increases in urchin populations can have vast ecological and economic consequences in kelp forest communities.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Canopy forming kelps, such as the giant kelp *Macrocystis pyrifera*, form important habitats for a variety of vertebrate and invertebrate fauna in temperate latitudes worldwide. Ecologists continue to debate the relative roles of predation and nutrient availability (i.e. "top-down vs. bottom-up" forces) in structuring kelp forest communities (e.g., Foster et al. 2006, Halpern et al. 2006, Steele et al. 2006). Though kelp responses to nutrient input may be rapid (Tegner et al. 1997, Edwards & Hernandez-Carmona 2005), trophic cascades resulting from changes in top predator abundance may lead to a loss of entire kelp forest communities. For instance, in Alaska, removal of the sea otter *Enhydra lutris* led to an increase in their urchin prey, which resulted in increased herbivory and a loss of kelp forest habitat (Estes & Palmisano 1974, Estes et al. 1998). If unregulated, urchins can change their behavior from primarily sheltering in cracks and crevices and feeding on drift algae to moving out of their shelters and actively grazing on live macroalgae. Large urchin "barrens" may form where urchins move out of their crevices and overgraze macroalgae, leading to greatly reduced species diversity. Urchin induced deforestation has been increasing over the past several centuries (Steneck et al. 2002), in part due to heavy fishing pressure on large predators, such as lobsters and large fishes, which may exert strong top-down control on urchins (Wharton & Mann 1981, Tegner & Levin 1981, 1983, Shears & Babcock 2002, Lafferty 2004).

Urchin barrens are not prevalent in San Diego, where sea otters have been locally extinct for over a century. Instead, densities of the two most abundant urchins, the purple urchin (*Strongylocentrotus purpuratus*) and the red urchin (*Strongylocentrotus franciscanus*) may be effectively controlled by California spiny lobster, *Panulirus interruptus* and fishes such as the California sheephead, *Semicossyphus pulcher* (Tegner & Levin 1983, Lafferty 2004). Lobsters and sheephead are heavily fished, resulting in reductions in the densities and sizes of these predators, which may reduce their ability to control urchin populations (Tegner & Levin 1983). However, red urchin densities have also been reduced by fishing pressure in

southern California (Kalvass & Rogers-Bennett 2002) and this may contribute to the lack of urchin barrens in this region.

Theories that top kelp forest predators are controlling urchin populations primarily are based on inverse correlations between urchin and predator densities, rather than on direct manipulative experiments within kelp forests (Tegner & Levin 1983, Mayfield & Branch 2000, Lafferty 2004; but see Carter et al. 2007). Two factors that may largely dictate predatory effects on urchins are urchin density and the amount of spatial refuge available to urchins. In laboratory experiments in New Zealand, the number of sea urchins consumed by rock lobsters was proportional to their density, suggesting that lobsters may be able to regulate urchin populations (Mayfield et al. 2001). In the Northwest Mediterranean Sea, predation on urchins by fishes decreased with increasing algal structural complexity (Hereu et al. 2005). Predatory fish presence can also result in the indirect effect of a reduction in urchin grazing and movement (Cowen 1983, Hereu 2005).

My objective in this study was to determine the effects of predator abundance and habitat structure on the behavior and proportional mortality of sea urchins in southern California kelp forests. Specifically, I conducted surveys and experiments within a marine reserve and two nearby heavily fished areas to (1) determine whether red and purple urchin abundance, behavior, and size vary with the abundance of their potential predators, and (2) determine how habitat structure and urchin density interact to affect urchin proportional mortality.

CHAPTER 2

METHODS

2.1 STUDY SITES AND STUDY SPECIES

My work took place at three sites within the kelp forests along the coast of San Diego, California: (1) inside the La Jolla Ecological Reserve (LJER), a 2.16 km2 no-take reserve established in 1971; (2) 500 m outside the LJER, adjacent to the reserve (ATR) and (3) 10 km to the south in the Point Loma (PL) kelp forest (see Figure 1 in Appendix A; all figures are shown in Appendix A). I selected these three sites to represent a gradient in predator abundance, largely caused by fishing pressure. The LJER contains high abundances of lobsters and large fishes (Parnell et al. 2005, Loflen 2007), whereas I expected recreationally and commercially fished areas outside the reserve to have lower predator abundance. The kelp forest near Pt. Loma is the largest contiguous kelp forest in California and is one of the most heavily fished areas for lobsters, sheephead and other large fishes in the state, such that these predators may have become functionally absent from this ecosystem (Dayton et al. 1998, Tegner & Dayton 2000). Dominant algae at each site include the surface canopy-forming giant kelp, *M. pyrifera*, and understory kelps *Pterogophora californica* and *Laminaria farlowii*. Other commonly encountered algae include *Egregia menziesii*, *Eisenia arborea*, and *Cystoseira osmundacea*.

In southern California, purple and red sea urchins are prominent herbivores that consume a variety of brown and red algae but prefer the kelp *M. pyrifera* (Morris 1980). One important urchin predator, the California spiny lobster, supports an extensive commercial and recreational fishery in southern California. Spiny lobsters inhabit shelters during the day and come out of their shelters at dusk to forage (Lindberg, 1955). Spiny lobsters are key predators of benthic invertebrates including mussels (Robles et al. 1990) and both red and purple urchins (Tegner & Levin 1983). Fishery induced alterations in the size distribution of lobsters (Barsky 2001) can have community wide impacts because only large lobsters are able to consume large urchins (Tegner & Levin 1983).

The California sheephead, *Semicossyphus pulcher* is a protogynous sequential hermaphrodite that occurs in temperate rocky reefs and kelp beds from Monterey Bay to the Gulf of California. Sheephead feed on macroinvertebrates including echinoids, bryozoans, molluscs, brachyurans, and polychaetes and are considered essential in regulating urchin populations (Cowen 1983, 1986). Sheephead are also important predators of spiny lobsters (Loflen 2007). They are diurnally active and return to home shelters at night (Topping et al. 2005). The density of sheephead has been shown to affect the microhabitat use of red urchins (Cowen 1983) and thus may also influence purple urchin microhabitat use. Microhabitat use of urchins may be important as it may affect the feeding and growth of urchins (Grupe 2006).

2.2 URCHIN, LOBSTER, AND FISH SURVEYS

To quantify the density of red and purple urchins and their chief predators, spiny lobsters and large fishes, I conducted transect surveys at the three sites from 1 June to 30 September 2007, and from 1 March to 31 July 2008. To sample for urchins and lobsters, I swam 20 m x 4 m transects in haphazardly chosen locations designed to encompass a variety of habitats in each of the three sites. In order to effectively represent the diversity of habitats in each of the three sites, each transect performed during a dive was swum in a haphazard direction originating from the same starting point. Sampling began 5 m away from the starting point to avoid over sampling at the center of the radial transects. During transect surveys, a team of two divers searched extensively for lobsters and urchins by flipping boulders and exploring all shelters and crevices. Using rulers test diameter (TD) was recorded to the nearest centimeter for urchins and lobster carapace length (CL) was recorded to the nearest 0.5 cm. I also recorded the habitat status of each urchin. Based on preliminary surveys I categorized each urchin into one of four categories: sheltered (if the urchin was found by turning over a boulder), burrowed (if the urchin was embedded into the rock in a pit or cavity form), ledge (if the urchin was found under an open ledge) and exposed. I compared mean abundances of purple urchins and lobsters counted in 2007 in PL and the LJER using t-tests. For 2008 data, lobster and urchin sizes and abundances were analyzed as dependent variables in separate one-way ANOVAs to test for mean differences among the three sites. Data were visually inspected for normality and I tested for homogeneity of variances using Cochran's test. I evaluated differences in means using Student-Newman-Keuls (SNK)

multiple comparisons here and in all subsequent ANOVAs. To examine possible differences in the distribution of lobster size among the sites I used a Kolmogorov-Smirnov (KS) test. To test whether urchin habitat use differed among sites I used a Yates corrected Pearson Chi-square.

To estimate fish abundances, a team of two divers slowly swam 25 m transects with a window approximately 4 m above the substrate and 4 m wide, identifying each fish encountered (Parnell 2005). There are numerous kelp forest fishes known to feed on juvenile urchins including black surfperch, *Embiotoca jacksoni*, rubberlip surfperch, *Rhacochilus toxotes*, and señorita, *Oxyjulis californica* (Kenner 1992). Other fishes including señorita, kelp bass, *Palabrax clathratus*, and rock wrasse, *Halichoeres semicinctus*, are known to scavenge urchins after sheephead attacks (Cailliet 2000, KDN *personal observation*). In order to assess possible differences in fish diversity among the sites, every species that was seen on transects was counted. Some of the fishes observed in the area are not only urchin predators, but also known predators of spiny lobsters. Giant black sea bass, *Stereolepis gigas*, one important spiny lobster predator, were seen regularly during the course of this research but were not observed on transects. Additionally, a horn shark, *Heterodontus francisci*, was observed consuming a sea urchin during nighttime experimental trials but not observed during daytime fish transects. I conducted transects between the hours of 0700-1300 on each of 8 days from 26 June to 1 October 2008 for a total of 20 haphazardly located transects at each site (for total counts see Table 1 in Appendix B; all tables are shown in Appendix B). I used separate one-way ANOVAs to analyze differences in fish abundances and Simpson's index of diversity (Ds) among the three sites.

2.3 HABITAT SURVEYS—RUGOSITY

In order to infer if available refuge habitat for urchins differs among sites, I estimated substratum complexity by quantifying rugosity along urchin and lobster transects. I quantified rugosity as the ratio l/L, where L is the actual distance between two points and l is the linear distance between such points (Luckhurst & Luckhurst 1978). At 12 haphazardly chosen points along 3-4 transects per site I laid a small linked, 3 m brass plated twist chain (Campbell #200) directly along the contours of the substrate (L) and then compared that

measurement to the total linear distance (l). I tested for differences in rugosity among the three sites using an ANOVA.

2.4 URCHIN PROPORTIONAL MORTALITY

To determine how urchin density and algal cover interact to affect urchin mortality, I exposed purple urchins to predators inside the LJER where predator densities are high. Spiny lobsters and sheephead likely cause most red and purple urchin predator-induced mortality in southern California (Tegner & Dayton 1981). Spiny lobsters occupy shelters during the day and forage at night, whereas sheephead occupy shelters at night and forage during the day (Topping et al. 2005). I therefore performed a subset of urchin mortality trials at night.

We exposed purple urchins to predators within standardized, artificial urchin habitat units (UHUs). Each 43 cm long x 38 cm wide UHU consisted of six, 10 cm diameter PVC pipes anchored vertically in cement, creating artificial urchin burrows 6-7 cm deep. I placed four UHUs together to create each plot, with each plot holding a maximum of 24 urchins. I used only purple urchins with test diameters of 6-8 cm in this experiment due to their high abundance in surveys and because they do not have a size refuge from predators such as lobsters (Tegner & Levin 1983).

Urchin proportional mortality experiments were conducted from July to October 2008. Three weeks before trials began, I placed two plots on rocky substrate in an open area with no macroalgal cover and two plots in an area of high macroalgal cover at a depth of approximately 10 m. For each trial, each plot received one of four urchin densities (4, 8, 16, or 24 urchins) chosen randomly. To conduct daytime urchin exposures; between 0900-1000 h I placed urchins in artificial crevices and I covered each urchin with a small piece of *M. pyrifera* to aid in camouflage and acclimation to the plot. I ensured urchins remained in artificial crevices for 1 min and then returned to plots to count the number of live urchins remaining after 20 min, 1 h, 2 h, 24 h and 48 h.

Because predators generally found urchins quickly (see Results), I conducted analyses on urchin proportional mortality after 1 h. Though the 24 and 48 h exposures encompassed both daylight and night, I wished to determine if any urchins survived exposure to predators over longer time periods. I conducted a total of 3-7 replicate trials for each combination of density x cover. Trials were identical for nocturnal urchin exposures, except

that exposures began at ca. 2000-2100 h when diurnal predators were inactive. Due to logistics, I was not able to conduct more than 1-3 replicate trials per urchin density at night.

Missing urchins may have been removed by predators or may have moved from plots on their own. I determined whether predators likely removed missing urchins by monitoring plots with underwater video. Three haphazardly selected plots were video taped for 90 min after divers completed urchin placement with a Sony TRV900 low-light digital video camera in an underwater housing. No urchins were seen moving from the plots after 90 min. Video analysis assisted us in determining which predators were removing urchins from the plots. I also tagged twenty urchins in plots with small, inconspicuous pieces of plastic sleeve insulation from electrical wire (Hereu 2005). For each urchin, two pieces of sleeve insulation were slipped over the largest ventral spines and secured with cyanoacrylate glue. When I returned to plots to count surviving urchins, I extensively searched surrounding areas for tagged and untagged purple urchins. Though I often found broken tests and partially consumed urchins, I found no live, tagged urchins outside of plots.

To analyze urchin proportional mortality data, I used an analysis of covariance (ANCOVA) to test how urchin proportional mortality varied with urchin density, algal cover and time of day. My daytime and nighttime data are unbalanced, which can reduce power and increase the possibility of overlooking an effect when the effect truly exists (Shaw & Mitchell-Olds 1993). In light of this, I chose to minimize my type II error by adopting a P level of 0.1 as suggested by Dayton et al. (1999). In highly variable coastal habitats with considerable natural variation, this level of probability is sufficient to suggest a meaningful relationship (Dayton et al. 1999). After running the full ANCOVA model with all interaction terms present, I used post hoc pooling to eliminate highly non-significant interactions from my model (Underwood 1997). Though Underwood (1997) suggests post-hoc pooling is appropriate when $P > 0.25$, all terms removed from my model had P values > 0.65. To test the assumptions of ANCOVA I used Levene's test to test for homogeneity of variances and I used KS tests to test for normality.

CHAPTER 3

RESULTS

3.1 URCHIN, LOBSTER AND FISH SURVEYS

In 2007 I sampled only the LJER and PL. The density of purple urchins was higher in PL (8.50 m-2 + 4.31 SE), than in the LJER (6.13 m-2 + 1.75 SE) but high variability made this trend relatively weak (t-test: $df = 1, 24, t = 0.59, P = 0.56$). In contrast, the densities of spiny lobsters and red urchins (the fished species) were higher within the reserve than in PL. I found an average of 7.75 (+ 4.49 SE) red urchins per transect in the LJER but no red urchins on any transect in PL. Spiny lobsters were five times as abundant inside the LJER as in PL (2.00 + 0.99 SE vs. 0.4 + 0.22 SE) but due to high variability among transects, the pattern was insubstantial (t-test: $df = 1, 24, t = 1.25, P = 0.22$).

In 2008, I quantified the abundance and sizes of spiny lobsters and both urchin species in the LJER, ATR, and in PL. I found strong evidence for a difference in the density of purple urchins among the three sites (Table 2, Figure 2), with PL having significantly higher densities of purple urchins than the LJER. Although the LJER had lower densities of purple urchins, the LJER had more representatives in each size class than in PL (Figure 3). Both the LJER and ATR sites had larger mean purple urchin sizes than PL (ANOVA: $df = 2, 715, F = 41.13, P < 0.001$). Size data for purple urchins from 2007 was similar to 2008, with the LJER having a higher mean urchin size than PL.

In 2008 densities of red urchins in PL were much lower than densities at the other two sites (Table 2, Figure 2). I found only 6 individuals on 20 transects in PL, but found 42 individuals in the LJER and 39 individuals in the ATR site. Although the distribution and range of size classes between the two sites was visually similar, mean red urchin size at the ATR site was slightly larger than in the LJER (t-test: $df = 1, 79, t = 3.24, P = 0.002$). The size distribution of red urchins in PL was not analyzed due to low sample sizes. Habitat rugosity may also influence urchin sizes and abundances (Figure 4).

Lobster density in 2008 differed among the three sites (Table 2, Figure 5). I found significantly higher lobster density in the LJER than in PL, but lobster density in the LJER

and the ATR site did not differ statistically. Mean lobster size was greater in the LJER than in the ATR and PL sites (ANOVA: $df = 2, 152$, $F = 16.89$, $P < 0.001$). Results of my KS test showed the distribution of lobster sizes was significantly different in the LJER than in the other two sites ($P < 0.001$, Figure 6).

Purple urchin habitat status differed among sites (Yates corrected chi-square, $df = 6$, $\chi^2 = 73.127$, $P < 0.001$). In both sampling years, most urchins were found embedded in the rock or under ledges at all sites. In 2007, the proportion of purple urchins found in ledge habitat, which is relatively more exposed than burrowed habitat, was twice as high in the LJER (28%) as in PL (14%). In contrast, in 2008, purple urchin behavior was more similar between PL and the LJER, with the exception of finding a small number of exposed urchins at PL and none in the LJER or ATR sites. Analyses also showed an association between purple urchin size and habitat status with larger urchins tending to be less cryptic (Yates corrected chi-square, $df = 42$, $\chi^2 = 118.12$, $P < 0.001$). The red urchins I found in the LJER and ATR sites were found primarily in ledge habitat and small percentages of red urchins were exposed at these sites. The lack of highly cryptic behavior in red urchins may be a result of their possibly reduced predation risk due to their larger size.

We observed a total of 13 fish species in my surveys, and the abundance of fish predators did not precisely follow trends of fishing intensity among my three sites (Table 1). Though PL had the lowest abundance of fishes compared with the other two sites, I counted a high number of sheephead and kelp bass in the ATR site, and this site had a slightly higher abundance of these predators than inside the reserve (Table 1, Figure 5). However, I found that Simpson's index of diversity (Ds) was lower in PL than in the ATR or LJER sites (ANOVA: $df = 2, 57$, $F = 4.59$, $P = 0.01$).

3.2 HABITAT SURVEYS—RUGOSITY

Rugosity varied substantially among the three sites and was significantly lower in PL than in the LJER and ATR sites (ANOVA: $df = 2, 34$, $F = 3.67$, $P = 0.04$; Figure 4). Most of the locations I sampled in PL tended to be flat with very few boulders. Shelters at this site were typically long contiguous ledges, whereas in the LJER there are more large boulders and a greater diversity of substrate types. My ATR site infrequently had large boulders but did not contain as much substrate diversity as within the LJER.

3.3 URCHIN PROPORTIONAL MORTALITY

There was a significant effect of urchin density and a significant interactive effect of cover and time of day on purple urchin proportional mortality (Table 3). Urchin proportional mortality decreased with urchin density, algal cover reduced urchin mortality during the day (Figure 7) but not at night, and mortality was higher during the day than at night in the absence of cover, but was not different between day and night when cover was present (Figure 8). The main predators observed removing urchins from the plots during daytime trials were California sheephead. A distinctive behavioral pattern was observed, with a male sheephead removing the urchin from the plot, which then attracted female sheephead, kelp bass, señoritas and rock wrasses to scavenge the remains.

We observed several species of predators removing urchins from plots during the night. Numerous spiny lobsters were observed near plots consuming removed urchins, as was a horn shark. Not surprisingly, cover was not a strong predictor of proportional mortality at night (Figure 8). Overall, urchin mortality was higher during the day than during the night.

CHAPTER 4

DISCUSSION

In my study I found that (1) the abundance, behavior and size of two species of sea urchins and their potential predators differed among sites within kelp forests near San Diego, (2) habitat and urchin density influenced urchin proportional mortality, and (3) both sheephead and lobsters have the potential to strongly impact urchin mortality within the La Jolla Ecological Reserve.

Shelter is a key factor in determining predation rates on sea urchins (Hereu et al. 2005). In my study, I found predation by fishes decreased during the day when plots contained high macroalgal cover. Similarly, Hereu et al. (2005) found that predation by fishes was reduced in habitats with greater structural complexity. For predator-prey relationships, it is essential to consider whether mechanisms operate in a density-dependent manner, as this forms the foundation for population regulation (Hixon & Carr 1997, Anderson 2001). Density-dependent mortality in prey populations can be induced by predator responses, and habitat structure can influence this proportional mortality (Grabowski & Kimbro 2005).

Anderson (2001) found that per capita mortality of kelp perch *Brachyistius frenatus* in the laboratory was inversely density dependent to density independent with increasing habitat structure. In contrast, per capita mortality of kelp perch in the field was strongly density dependent, which was likely caused by an aggregative response by kelp bass, *Paralabrax clathratus* (Anderson 2001). Kushner and Hovel (2006) examined the aggregative and functional responses of the predatory gastropod *Pteropurpura festiva* to Asian mussel *Musculista senhousia* density in seagrass beds and found variable responses at different levels of seagrass habitat structure. *P. festiva* aggregated in plots with high mussel density, however proportional mortality was inversely density dependent at all levels of eelgrass habitat structure (Kushner & Hovel 2006).

Determining the degree of density dependence associated with urchin mortality from predation and how structural complexity influences predation and urchin behavior are

essential to understanding the dynamics that allow urchins to overgraze kelp forests. One widespread cause of density-dependent mortality is density-dependent predation due to a shortage of structural refuge available to prey (Forrester & Steele 2004). If spatial refuge is a limiting resource, as prey populations increase, their access to refuge should decrease and thus density-dependent mortality from predation will increase (Forrester & Steele 2004). For the small coral reef goby *Coryphopterus glaucofraenum*, limited shelter caused density-dependent mortality, but proportional mortality was density-independent in plots with abundant refuges (Forrester & Steele 2004).

Our results show urchin density is a strong factor in determining urchin proportional mortality. In addition to the ANCOVA, I ran a separate exploratory ANCOVA on solely my daytime data. In this analysis, density and cover came out as strong factors influencing proportional mortality ($P = 0.02$ and 0.03 respectively). As density increased, proportional mortality decreased (inverse density dependence). Forrester and Steele (2004) showed an accelerating per-predator consumption rate with increasing prey density. I cannot comment on the functional responses of the predators in my experiments. Future research is needed to quantify the number of predator visits to the plots to assess functional responses. The common type II response of predators (decelerating their consumption with increasing prey density) generally does not lead to prey population regulation. However, increases in prey density may lead to predator aggregation, which results in density-dependent mortality of prey, even if per-predator rates of consumption do not increase with increasing prey density (Anderson 2001).

In my experiment, per capita mortality rates of urchins exposed to predators did not increase with increasing urchin density (i.e. a potentially regulating predator response was not observed). However, when urchins were exposed to predators for 24-48 h (incorporating both diurnal and nocturnal predators) mortality approached 100%. I witnessed multiple predation events at night and the mean proportional mortality of urchins in my night time exposures in plots with algal cover was not dramatically different from the mean daytime proportional mortality in plots with algal cover. The fact that these means were not as radically different as might be anticipated considering the difference in the urchin consumption time of lobsters (longer) and sheephead (shorter), suggests that lobsters may be capable of exerting strong top down control in this system. In areas where predator densities

are high, over time, predator aggregative responses may help to prevent urchin barren prevalence in southern California. However, there may be a threshold urchin density in which predators cannot control new recruitment input into patches. Predation is not the only factor influencing urchin abundances; food availability, larval supply, recruitment, early post-settlement survival and disease can also shape their populations (Tegner & Dayton 1977, Watanabe & Harrold 1991, Pearse 2006).

We conducted my manipulative experiment within the LJER, which has numerous large predators present. Results of my study would likely be very different had I been able to replicate my experiment in the ATR site and in the heavily fished PL kelp forest. The LJER was chosen in order to be able to witness multiple predation events in a relatively short time period and be more apt to comment on the relative influences of diurnal vs. nocturnal predators.

Although the LJER is relatively small, it encompasses a large diversity of habitats and is helpful in protecting top predators. Lobster abundance and size, and fish diversity were greatest inside the LJER. The fact that I saw a large number of sheephead and kelp bass at my ATR site (Figure 5) may be due to the high mobility of these species and the proximity of my ATR sites to the reserve boundary. I were somewhat limited by depth and the presence of *M. pyrifera* in assessing sites that were more than 500 m from the reserve boundary, sampling more locations farther from the boundary would have been beneficial.

Marine reserves including 'no take' zones (areas where it is illegal to extract organisms in any way) have recently become a popular alternative to traditional management schemes (Halpern and Warner 2002), and have been shown to aid in the recovery of top predators (Kelly et al. 2000). Therefore 'no take' reserves may be a good strategy to reestablish lost interactions among species that have community wide effects (Guidetti 2006, Langlois et al. 2006). The LJER may be effective at protecting reproductively important populations of large lobster and sheephead (Parnell et al. 2005), and significant numbers of large, reproductively viable lobsters have been detected within the LJER (Loflen 2007).

The LJER may be highly successful in preserving sheephead stocks because their home ranges can be quite small (minimum home range 938 m2, Topping et al. 2005). The combined effects of lobsters and sheephead on urchin populations may be extremely complex as sheephead are also important predators of lobsters (Loflen 2007). Marine reserves provide

an ideal opportunity for testing the top-down impact of predators and examining possible ecosystem-level fishing effects (Shears & Babcock 2002). In my study I only worked in one reserve, however as one of the oldest no take reserves in southern California, changes between my reserve sites and nearby fished areas are apparent.

Many studies have shown that predation is a key process in determining sea urchin behavior, population structure and dynamics (McClanahan & Muthiga 1989, Scheibling 1996, Hereu et al. 2005). I observed differences in mean sizes of purple urchins between the sites, however a 1 cm change (particularly from 6 to 7 cm) in the TD of purple urchins is not likely to strongly influence predation on this species. The large increase in purple urchin abundance in my non-reserve sites as compared with the LJER (Figure 2) can likely be attributed to the lower numbers of predators at these sites.

Rugosity does differ among the sites and visually; habitat differences between the LJER, ATR and PL are evident (KDN, *personal observation*). The LJER and ATR sites generally have larger boulders and higher rugosity than the flatter, more structurally simple PL kelp forest. However, I believe the differences in urchin abundances observed at these sites were not solely determined by differences in available habitat. Predatory fish presence can result in the indirect effect of a reduction in urchin grazing and movement (Cowen 1983, Hereu 2005). The fact that urchin behavior (quantified in the four habitat categories) changed among the sites supports the theory that the presence of predators may be influential for these populations. Although only a small percentage of urchins encountered in PL were totally exposed, this behavior suggests a lack of a predator threat in PL.

The red urchins I observed in both the LJER and ATR sites were typically large and not very cryptic, which suggests a possible size refuge for this species. Lobster predation is limited on larger sized urchins (Tegner & Levin 1983, Andrew & MacDiarmid 1991, Mayfield et al. 2001). Although a difference between the mean sizes of red urchins was detected between the LJER and ATR sites, I do not consider a 1-2 cm change in TD at the sizes I observed likely to substantially influence predation on this species. Red urchins were almost completely absent in PL. Thus, the commercial fishery for red urchins in PL may be partly filling the ecological role of large lobsters at this site (Dayton et al. 1998).

If indeed lobsters and sheephead are important predators that influence urchin behavior as evidenced by this research, the status of their populations becomes increasingly

critical due to potential cascading effects. If these species are overfished, they may become ineffective at controlling sea urchin populations, thus leading to trophic cascades. A reduction in macroalgae caused by this trophic cascade will lead to a decrease in those species that depend on this macroalgae, and a loss of diversity in kelp forest communities. The kelp forests in southern California alone support more than 200 species of algae, invertebrates, fishes, and mammals (Graham 2004). The distributions of many of these organisms are known to be linked tightly to the presence of *M. pyrifera*, due to a variety of trophic and habitat associations. This habitat also supports a broad array of extractive and non-extractive industries, including fisheries, aquaculture, and tourism.

Ecological data on top predators and the impacts they have on the community are important in kelp forests not only to foster an understanding of basic ecological processes but also to promote practical management schemes, particularly those dealing with fisheries management and reserve design (Parnell et al. 2006). My results help to elucidate the processes behind urchin population regulation in southern California, which is critical due to the possible community wide impacts an increase in urchin abundance may have.

The overall goal of my research was to fill the gaps in our knowledge of urchin-predator interactions in southern California by determining the potential effects of top kelp forest predators on urchin populations and how predation rates are influenced by urchin density and the presence of algal cover. Although in my experiment I saw inverse density dependence in the short term, if I examine longer time scales and consider my survey results, my results lend support for theories that predators are capable of altering urchin population dynamics. Previous work suggesting that top predators are controlling urchin populations are primarily based on inverse correlations between urchin and predator densities (Tegner & Levin 1983, Mayfield & Branch 2000, Lafferty 2004). My results provide direct evidence of urchin predator-induced mortality, and highlight the potential consequences reductions in predator numbers may have on urchin populations in southern California.

ACKNOWLEDGEMENTS

REFERENCES

Anderson, T.W., 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology 82(1), 245-257.

Andrew, N.L., MacDiarmid, A.B., 1991. Interrelations between sea urchins and spiny lobsters in northeastern New Zealand. Mar. Ecol. Prog. Ser. 70, 211-222.

Barsky, K. C., 2001. California's living marine resources: a status report, California spiny lobster. Ca Department of Fish and Game. 98-100.

Cailliet, G. M., 2000. Biological characteristics of nearshore fishes of California: Final report: a review of existing knowledge and proposed additional studies for the Pacific Ocean Interjurisdictional Fisheries Management Plan Coordination and Development Project. Ca Department of Fish and Game. Pacific States Marine Fisheries Commission.

Carter, S. K., VanBlaricom, G. R., Allen, B. L., 2007. Testing the generality of the trophic cascade paradigm for sea otters: a case study with kelp forests in northern Washington, USA. Hydrobiologia 579, 233-249.

Cowen, R. K., 1983. The effect of sheephead (Semicossyphus pulcher) predation on red-sea urchin (Strongylocentrotus franciscanus) populations an experimental analysis. Oecologia 58, 249-255.

Cowen, R. K., 1986. Site-specific differences in the feeding ecology of the California Sheephead, Semicossyphus pulcher (Labridae). Environmental Biology of Fishes 16, 193-203.

Dayton, P. K., M. J. Tegner, P. B. Edwards, Riser, K.L., (1999). Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecol. Monogr. 69, 219-250.

Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1998. Sliding baselines, ghosts and reduced expectations in kelp forest communities. Ecol. App. 8(2), 309-322.

Edwards, M. S., Hernandez-Carmona, G., 2005. Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño. Mar. Biol. 147, 273-279.

Estes, J.A., Palmisano, J.F., 1974. Sea Otters: their role in structuring nearshore communities. Science 185, 1058-1060.

Estes, J. A., Tinker, M. T., Williams, T. M., Doak, D. F., 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282, 473-476.

Forrester, G. E., Steele, M. A., 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology 85, 1332-1342.

Foster, M.S., Edwards, M.S., Reed, D.C., Schiel, D.R., Zimmerman, R.C., 2006. Top-down vs. bottom-up effects in kelp forests. Science 313, 1737-1739.

Grabowski, J.H., Kimbro, D.L., 2005. Predator-avoidance behavior extends trophic cascades to refuge habitats. Ecology 86(5), 1312-1319.

Graham, M. H., 2004. Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. Ecosystems 7, 341-357.

Grupe, B. M., 2006. Purple sea urchins (Strongylocentrotus purpuratus) in and out of pits: the effects of microhabitat on population structure, morphology, growth and mortality. M.S. thesis. University of Oregon, Oregon.

Guidetti, P., 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. Ecol. App. 16(3), 963-976.

Halpern, B.S., Cottenie, K., Broitman, B.R., 2006. Strong top-down control in Southern California kelp forest ecosystems. Science 312, 1230-1232.

Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5, 361-366.

Hassell, M. P., 1966. Evaluation of parasite or predator responses. J. Animal Ecol. 35, 65-75

Hereu, B., 2005. Movement patterns of the sea urchin Paracentrotus lividus in a marine reserve and an unprotected area in the NW Mediterranean. Mar. Ecol. 26, 54-62.

Hereu, B., Zabala, M., Linares, C., Sala, E., 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. Mar. Biol. 146, 293-299.

Hixon, M. A., Carr, M.H., 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277, 946-949.

Kalvass, P.E, Rogers-Bennett, L., 2002. Annual Status of the Fisheries Report- Red Urchins

California Department of Fish and Game. 9, 1-14.

Kelly, S., MacDiarmid, A.B., Babcock, R.C., 2000. Spiny lobster Jasus edwardsii, recovery in New Zealand marine reserves. Biol. Cons. 92, 359-369.

Kenner, M.C., 1992. Population dynamics of the sea urchin Strongylocentrotus purpuratus in a Central California kelp forest: recruitment, mortality, growth and diet. Mar. Biol. 112, 107-118.

Kushner, R. B., Hovel, K. A., 2006. Effects of native predators and eelgrass habitat structure on the introduced Asian mussel Musculista senhousia (Benson in Cantor) in southern California. J. Exp. Mar. Biol. Ecol. 332, 166-177.

Lafferty, K.D., 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. Ecol. App. 14(5), 1566-1573.

Langlois, T.J., Anderson, M.J., Babcock, R.C., Kato, S., 2006. Marine reserves demonstrate trophic interactions across habitats. Oecologia 147, 134-140.

Lindberg, R.G., 1955. Growth, population dynamics and field behavior of the spiny lobster, Panulirus interruptus. Univ. of Ca. Pub. Zoo. 59, 157-247.

Loflen, C. L., 2007. Behavioral responses by the California spiny lobster (Panulirus interruptus) to predation inside and outside a marine protected area. M.S. thesis. San Diego State University, San Diego.

Luckhurst B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. 49, 317-323.

Mayfield, S., Branch, G.M., 2000. Interrelations among rock lobsters, sea urchins, and juvenile abalone: implications for community management. Can. J. Fish. Aquat. Sciences 57, 2175-2185.

Mayfield, S., de Beer, E., Branch, G.M., 2001. Prey preference and the consumption of sea urchins and juvenile abalone by captive rock lobsters (Jasus lalandii). Mar. Freshw. Res. 52, 773-780.

McClanahan, T. R., Muthiga, N. A., 1989. Patterns of predation on a sea-urchin, Echinometra mathaei (Deblainville), on Kenyan coral reefs. J. Exp. Mar. Biol. Ecol. 126, 77-94.

McClanahan, T. R., 1995. Fish predators and scavengers of the sea-urchin, Echinometra mathaei in Kenyan coral-reef marine parks. Env. Biol. of Fishes 43, 187-193.

Morris, R.H. Abott, D.P., Haderlie, E.C., 1980. Intertidal invertebrates of California. Stanford University Press. Stanford, CA.

Parnell, P.E., Lennert-Cody, C.E., Geelen, L., Stanley, L.D., Dayton, P.K., 2005. Effectiveness of a small marine reserve in southern California. Mar. Ecol. Prog. Ser. 296, 39-52

Parnell, P.E., Dayton, P.K., Lennert-Cody, C.E., Rasmussen, L.L, Leichter, J.J., 2006. Marine reserve design: optimal size, habitats, species affinities, diversity and ocean microclimate. Ecol. App. 16(3) 945-962.

Pearse, J. S., 2006. Ecological role of purple sea urchins. Science 314, 940-941.

Robles, C.D., Sweetnam, D.A., Eminike, J., 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. Ecology 71(4), 1564-1577.

Scheibling, R. E., 1996. The role of predation in regulating sea urchin populations in eastern Canada. Oceanologica Acta 19, 421-430.

Shaw, R. G., Mitchell-Olds, T., 1993. Anova for unbalanced data: an overview. Ecology 74, 1638-1645.

Shears, N.T., Babcock, B.C., 2002. Marine Reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132, 131-142.

Steele, M.A., Schroeter, S.S., Carpenter, R.C., Kushner, D.J., 2006. Top-down vs. bottom-up effects in kelp forests. Science 313, 1738.

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. Env. Cons. 29(4), 436-459.

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

Tegner, M.J., Levin, L.A., 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. J. Exp. Mar. Biol. Ecol.73, 125-150.

Tegner, M.J., Dayton, P.K., 1981. Population structure, recruitment and mortality of two sea urchins (Strongylocentrotus franciscanus and S. purpuratus) in a kelp forest. Mar. Ecol. Prog. Ser. 5(3), 255-268.

Tegner, M.J., Dayton, P.K., Edwards, P.B., Riser, K.L., 1997. Large-scale, low frequency oceanographic effects on kelp forest succession: a tale of two cohorts. Mar. Ecol. Prog. Ser. 146, 117-134.

Tegner, M.J., Dayton, P.K., 2000. Ecosystem effects of fishing in kelp forest communities. J. of Mar. Science 57, 579-589.

Topping, D.T., Lowe, C.G., Caselle, J.E., 2005. Home range and habitat utilization of adult California sheephead Semicossyphus pulcher (Labridae), in a temperate no take marine reserve. Mar. Biol. 147, 301-311.

Underwood, A.J., 1997. Experiments in ecology. Cambridge Univ. Press, New York.

Watanabe, J. M., Harrold, C., 1991. Destructive grazing by sea urchins Strongylocentrotus spp. in a central California USA kelp forest: potential roles of recruitment depth and predation. Mar. Ecol. Prog. Ser. 71, 125-141.

Wharton, W.G., Mann, K. H., 1981. Relationship between destructive grazing by the sea urchin, Strongylocentrotus droebachiensis, and the abundance of American lobster, Homarus americanus, on the Atlantic coast of Nova Scotia. Can. J. Fish. Aquat. Sciences 38, 1339-1349.
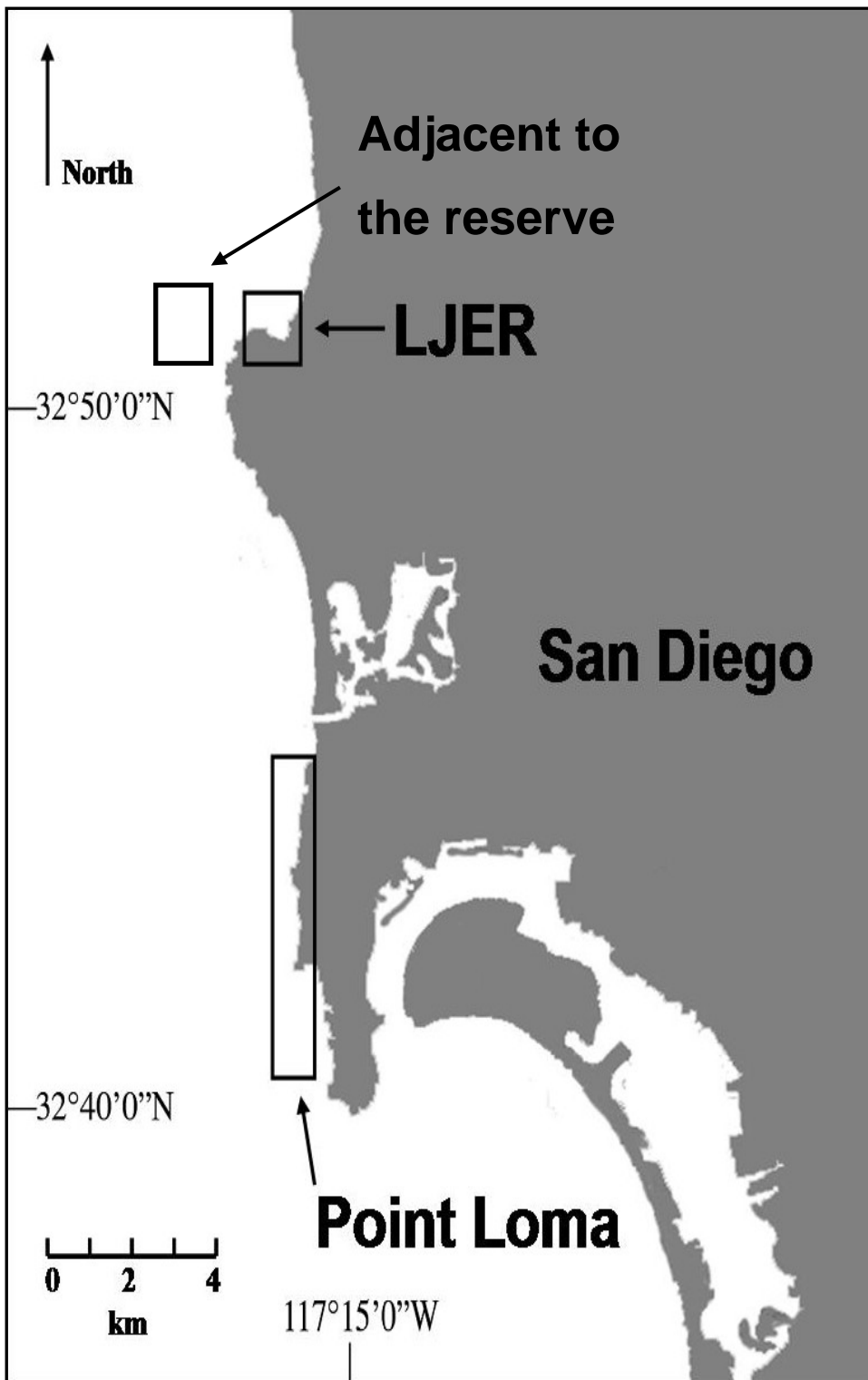
APPENDIX A

FIGURES

Figure 1. Map of study sites in San Diego, CA, USA (32.69° N, 117.26° W), showing the location of the LJER, ATR, and PL.
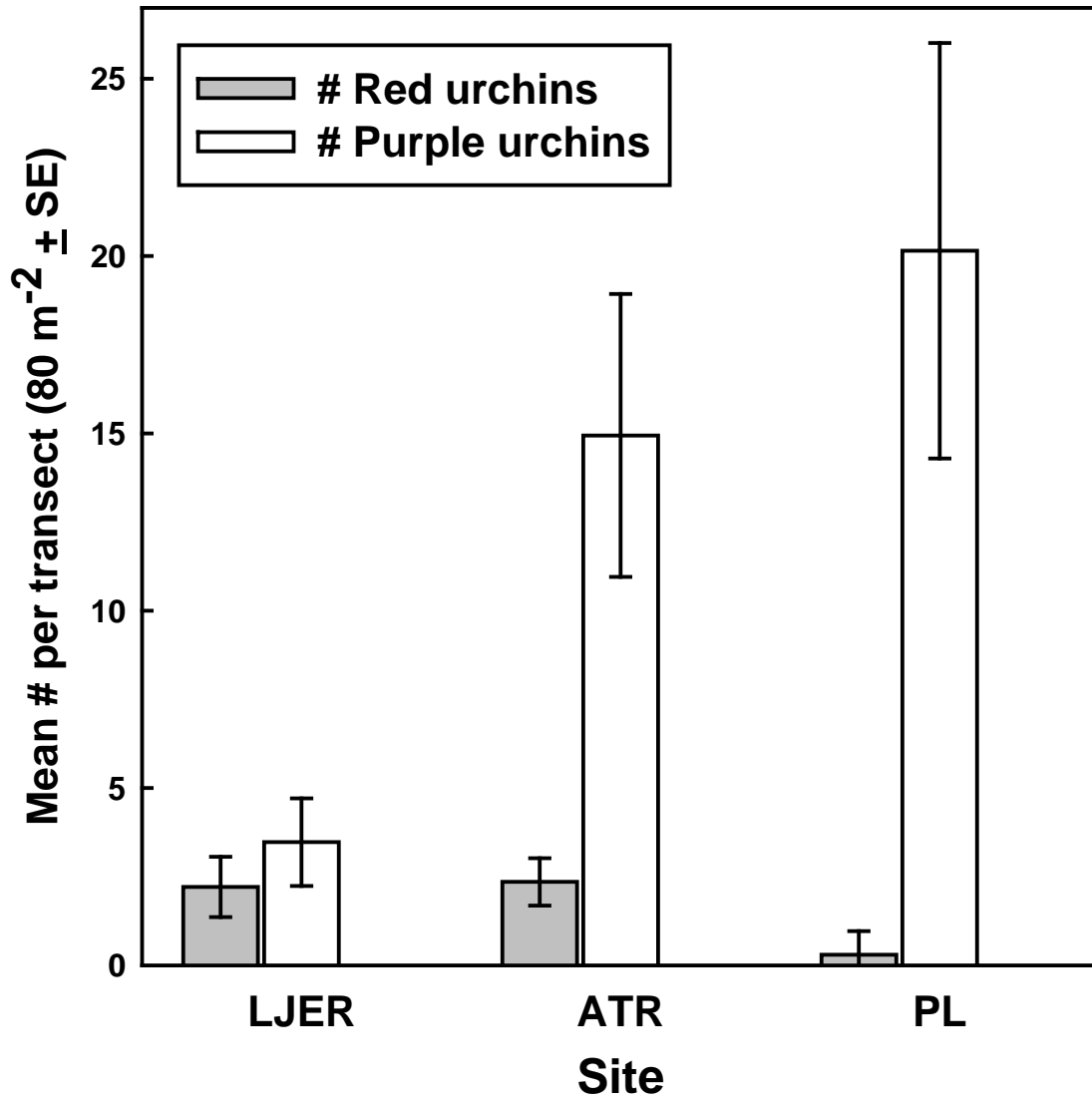
Figure 2. Mean density of red urchins (*Strongylocentrotus franciscanus*) and purple urchins (*Strongylocentrotus purpuratus*) in the LJER, ATR, and PL in 2008.
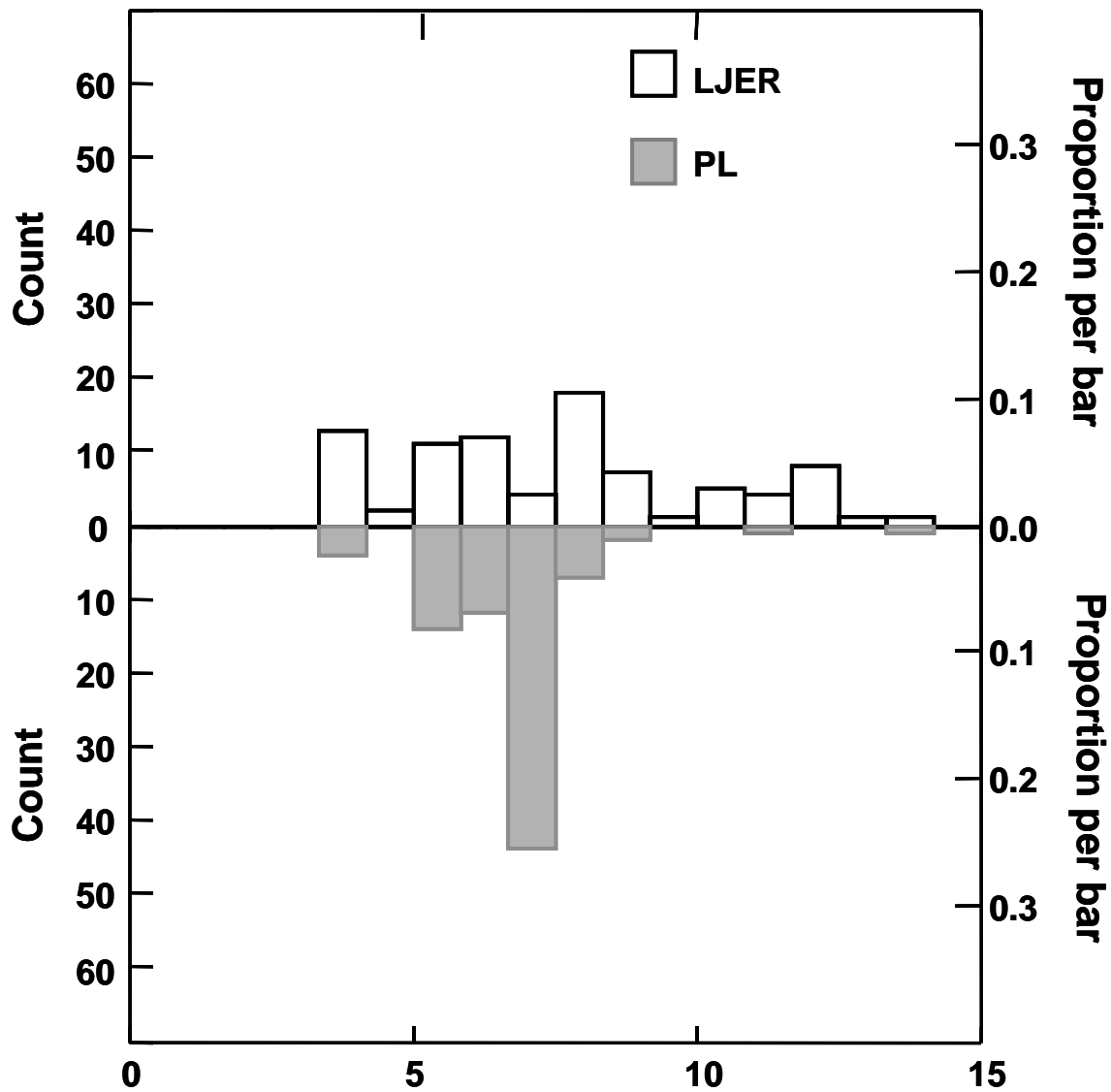
Figure 3. Size-frequency distribution of purple urchins (*Strongylocentrotus purpuratus*) in PL and in the LJER in 2007.
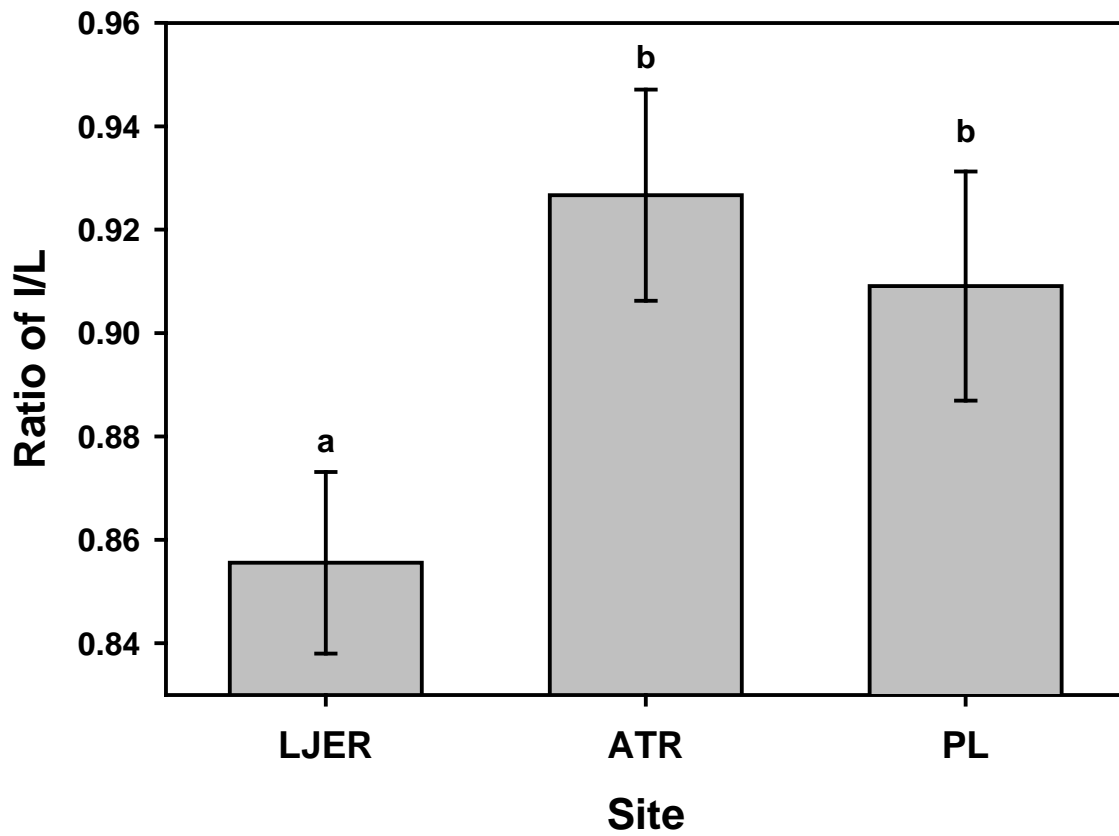
Figure 4. Mean rugosity (ratio of L/l) in the three sites in 2008. Rugosity decreases as the value approaches 1. Letters above bars denote groups that differed in SNK post-hoc analyses.
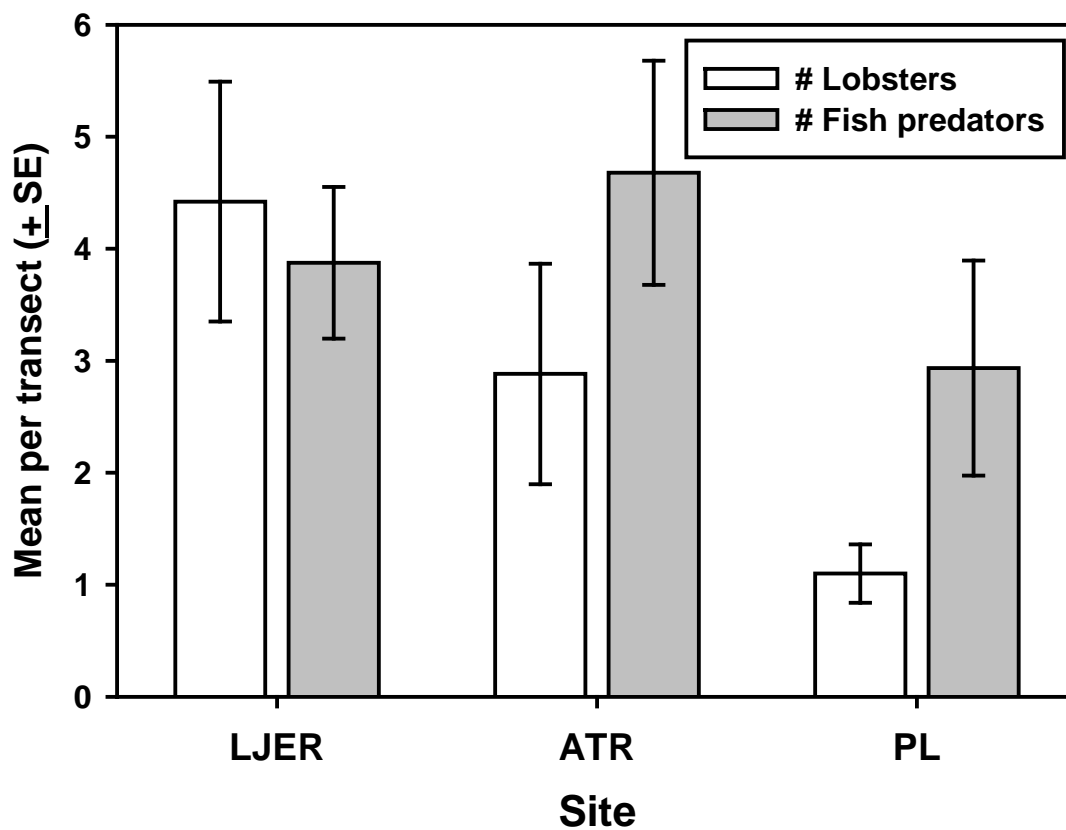
Figure 5. Urchin predator abundance. Mean number of spiny lobsters (*Panulirus interruptus*) and predatory fish (*Palabrax clathratus*) and sheephead (*Semicossyphus pulcher*) found per 20 m transect in the LJER, ATR, and PL in 2008.
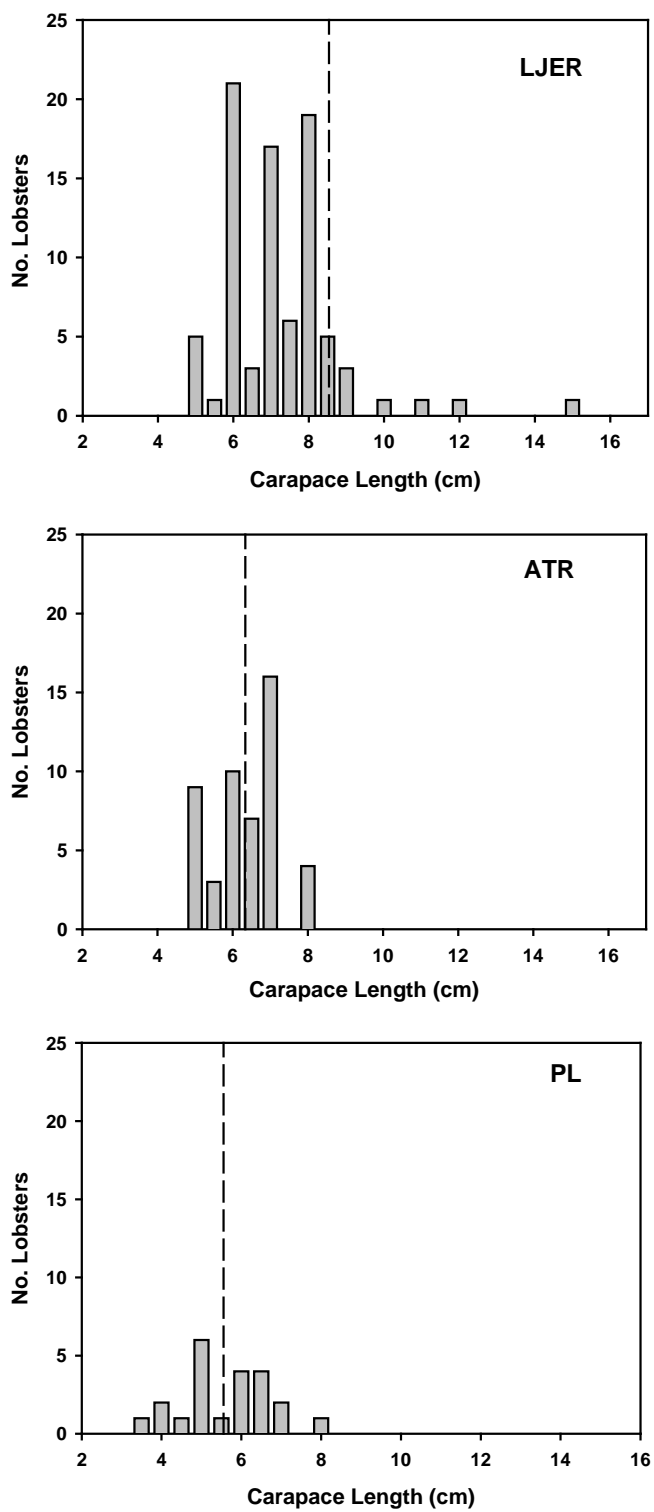
Figure 6. Spiny lobster (*Panulirus interruptus*) size-frequency distribution in the LJER, ATR, and PL in 2008. The dashed vertical line represents the mean CL for each site.
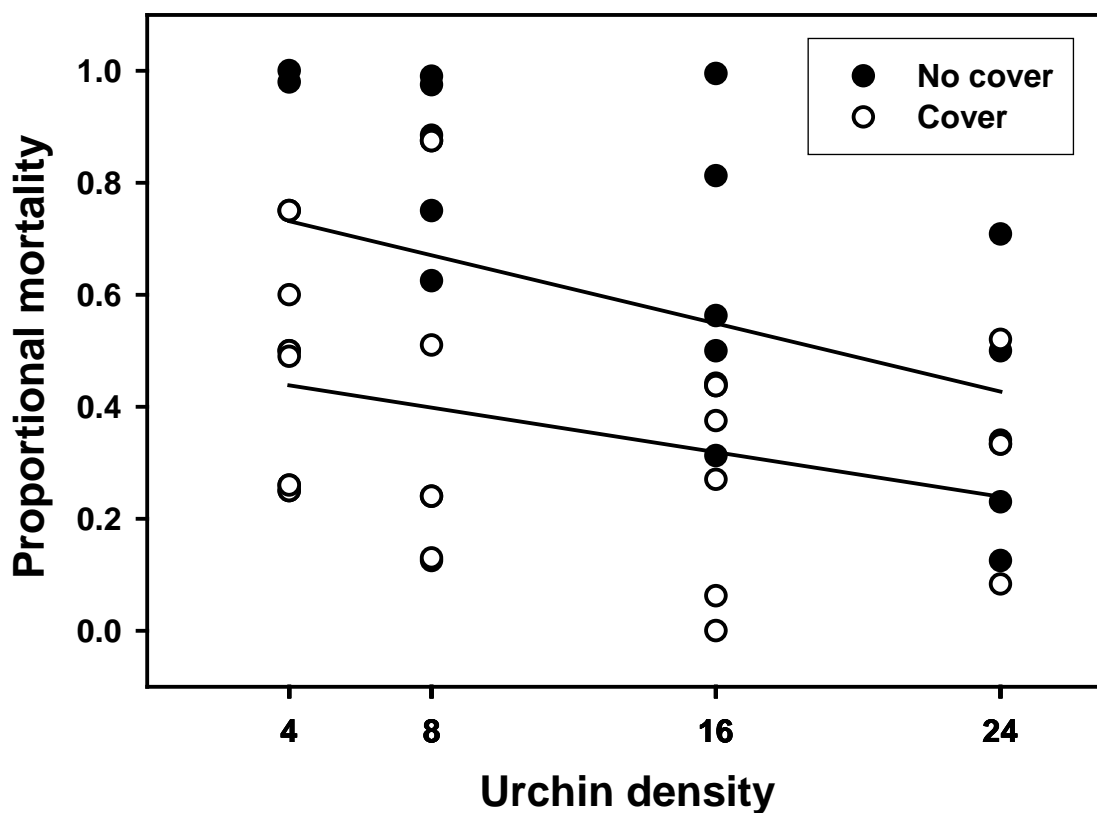
Figure 7. Purple urchin proportional mortality during the daytime 1-hour exposures for plots without algal cover (closed circles) and plots with algal cover (open circles). Lines represent linear regression trend lines (top line is the regression trend line for plots without algal cover, lower line is for plots with algal cover). Data were jittered to show all individual data points.
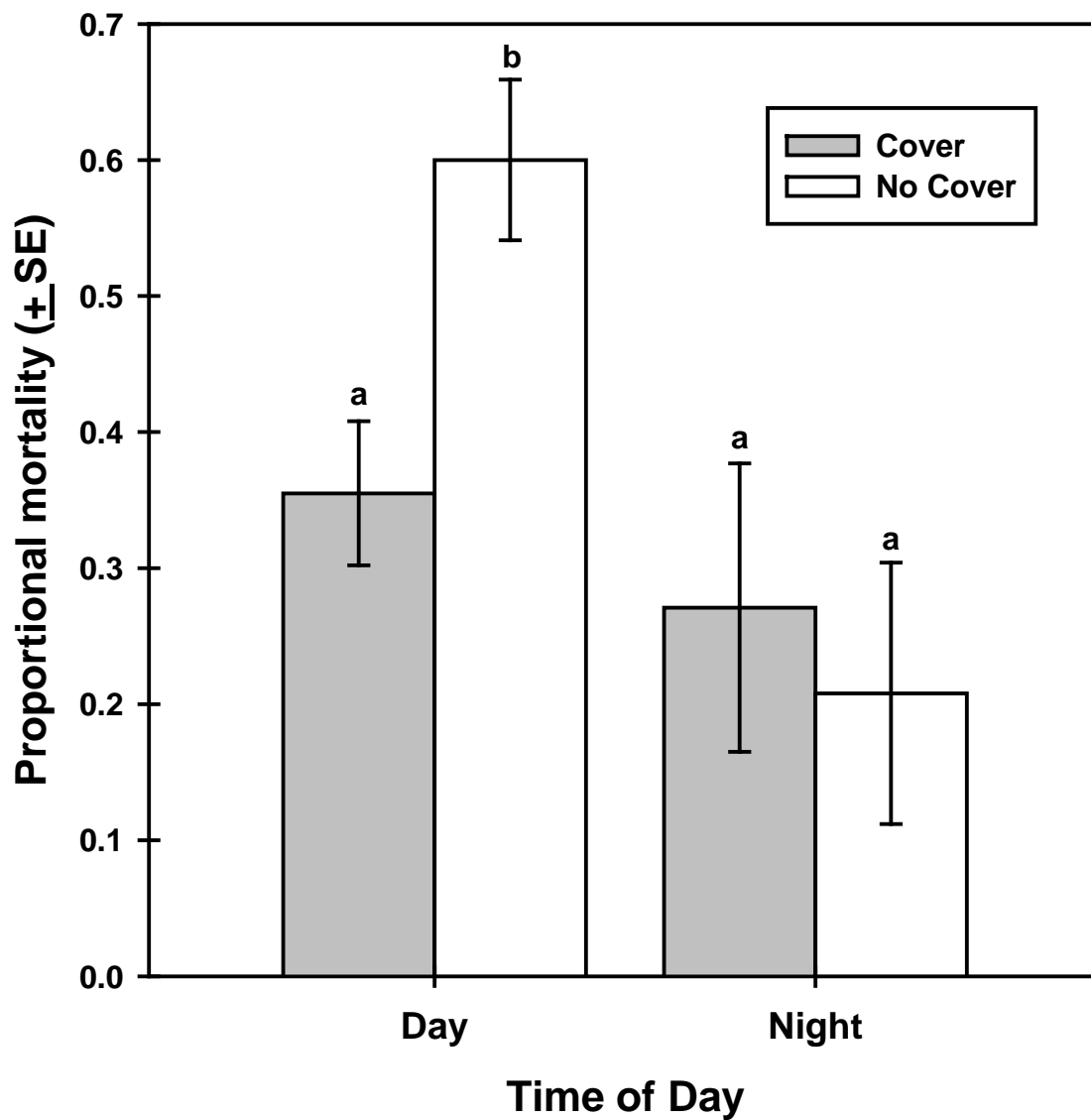
Figure 8. Total purple urchin (*Strongylocentrotus purpuratus*) proportional mortality during the daytime and nighttime 1-hour exposures for plots with and without algal cover. Letters above bars denote groups that differed in SNK post-hoc analyses.

APPENDIX B

TABLES

Table 1. Number of Fish Counted on Each of 20 Transects per Site in 2008 (N = 60)

Common name	Scientific name	LJER	ATR	PL
California sheephead	*Semicossyphus pulcher*	5	21	8
Kelp bass	*Palabrax clathratus*	42	36	8
Rock wrasse	*Halichoeres semicinctus*	15	9	2
Señorita	*Oxyjulis californica*	14	8	14
Black surfperch	*Embiotoca jacksoni*	7	16	2
Rubberlip surfperch	*Rhacochilus toxotes*	1	4	0
Kelp surfperch	*Brachyistius frenatus*	16	1	5
Opal eye	*Girella nigricans*	6	3	0
Garibaldi	*Hypsypops rubicundus*	5	4	0
Blacksmith	*Chromis punctipinnis*	7	7	0
Sargo	*Anisotremus davidsonii*	2	0	0
Barred sand bass	*Paralabrax nebulifer*	0	4	2
Tope shark	*Galeorhinus zyopterus*	2	0	0

Note. Predators shown in bold were considered potential urchin predators.

Table 2. Analysis of Variance on the Effects of Site on Urchin and Lobster Densities in 2008

Source	SS	df	MS	F-ratio	P
A) Purple urchin abundance					
Site	2810.326	2	1405.163	4.161	0.021
Error	17896.228	53	337.666		
B) Red urchin abundance					
Site	50.474	2	25.237	3.527	0.036
Error	379.240	53	7.155		
C) Lobster abundance					
Site	107.786	2	53.893	4.187	0.020
Error	682.186	53	12.872		

Table 3. Analysis of Covariance (Full Model) of the Effects of Starting Density, Algal Cover and Time of Day in Predicting Urchin Proportional Mortality for Day and Night Time Exposures

Source	Type III SS	df	MS	F-ratio	P
Time of day	0.283	1	0.283	4.467	0.040
Density	0.153	1	0.153	2.409	0.127
Cover	0.069	1	0.069	1.091	0.301
Time of day x density	0.028	1	0.028	0.443	0.509
Cover x density	0.010	1	0.010	0.161	0.690
Time of day x cover	0.224	1	0.224	3.540	0.066
Error	3.102	49	0.063		

Table 4. Analysis of Covariance (Reduced Model) of the Effects of Starting Density, Algal Cover and Time of Day in Predicting Urchin Proportional Mortality for Day and Night Time Exposures

Source	Type III SS	df	MS	F-ratio	P
Time of day	0.498	1	0.498	7.834	**0.007**
Density	0.421	3	0.140	2.210	**0.099**
Cover	0.089	1	0.089	1.407	0.241
Time of day x cover	0.209	1	0.209	3.296	**0.076**
Error	3.113	49	0.064		

ABSTRACT OF THE THESIS

The Effects of Predators and Habitat on Sea Urchin Density and
Behavior in Southern California Kelp Forests
by
Kathryn D. Nichols
Master of Science in Biology
San Diego State University, 2009

It is well documented that sea urchins can have vast impacts on kelp forest community structure as a result of kelp grazing. Despite the ecological importance of sea urchins, direct field studies on the relative effects urchin predators have on shaping urchin populations are rare for southern California. I conducted surveys at three kelp forest sites near San Diego, CA, including heavily fished and marine reserve sites, to measure sea urchin size, abundance, and habitat use as well as the abundance of potential sea urchin predators. I also examined whether purple sea urchin (*Strongylocentrotus purpuratus*) proportional mortality varied with urchin density, time of day, and algal cover in the La Jolla Ecological Reserve, where densities of potential predators such as sheephead and spiny lobsters are high. Transect surveys showed urchin behavioral changes among the three sites with urchins tending to be more cryptic inside the reserve as compared to sites adjacent to the reserve and in heavily fished areas. Fished species, including spiny lobsters and red urchins were found to be less abundant in non-reserve sites, while unfished purple urchins were more abundant in non-reserve sites possibly due to reduced predation pressure in these areas. Predator densities and mean sizes of predators were highest inside the reserve and lowest in the heavily fished site. In the experiment, urchin proportional mortality decreased with increasing urchin density. This trend was stronger in open plots than in plots covered with algae, in which proportional mortality was more variable. Substantial nighttime predation was observed and was not influenced by the presence of algal cover. Examining whether urchin mortality from predation is density-dependent and how habitat complexity influences this relationship is imperative because behavioral changes and increases in urchin populations can have vast ecological and economic consequences in kelp forest communities.