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Effects of predators on sea urchin density and habitat use in a southern California kelp forest

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Abstract Grazing sea urchins can reduce kelp abundance and therefore strongly affect kelp forest community structure. Despite the ecological importance of sea urchins, direct field studies on the role that urchin predators play in shaping urchin populations are rare for southern California. We conducted surveys and manipulative experiments within kelp forests near San Diego, CA, (32–51′28″N, 117–16′00″W) from 2006 to 2009 to determine whether predators such as sheephead (*Semicossyphus pulcher*) and spiny lobsters (*Panulirus interruptus*) may be linked to purple urchin (*Strongylocentrotus purpuratus*) and red urchin (*Strongylocentrotus franciscanus*) distribution and habitat use, as well as purple urchin density-dependent mortality. Purple urchins were less dense and more cryptic inside a local marine protected area (MPA) that contained high predator abundance than in nearby heavily fished areas, whereas red urchins rarely were found outside the MPA. Urchin proportional mortality was inversely density dependent during the day when sheephead were active, despite fish aggregations in plots of high urchin density, but was density independent during the night when lobsters were active. Urchin mortality was reduced under understory algal cover during the day, but not during the night. 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.

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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. Sea urchins typically are an abundant member of kelp forest communities, and as herbivores that consume kelp they may play key roles in dictating kelp abundance and spatial patterns of kelp forest habitat structure (Ling et al. 2015). 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; Ling et al. 2015), at least in part due to reduced abundance of key predators including sea otters, lobsters, and large fishes (Wharton and Mann 1981; Tegner and Dayton 1981; Tegner and Levin 1983; Shears and Babcock 2002; Lafferty 2004). 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 and Palmisano 1974; Estes et al. 1998).

Predator abundance and type (Shears and Babcock 2002; Sala et al. 1998; Pederson and Johnson 2006; Ling et al. 2009; Clemente et al. 2013), urchin density and group size (Bernstein et al. 1981), urchin body size (Tegner and Levin 1983; Shears and Babcock 2002; Pederson and Johnson

2006; Guidetti 2006; Clemente et al. 2013), disease (Sala et al. 1998), and the amount of spatial refuge available to urchins (Hereu et al. 2005; Farina et al. 2009) all may dictate the potential for predators to control sea urchin populations. Urchin mortality rates typically are higher within marine protected areas that house larger predators than in nearby fished areas, which can be depleted of predators (Shears and Babcock 2002; Pederson and Johnson 2006). Whereas predatory fishes often are the primary predators of urchins, nocturnally foraging lobsters may cause more predator-induced urchin mortality in areas where they are locally abundant (Lafferty 2004; Pederson and Johnson 2006).

To avoid predators, urchins typically remain cryptic on rocky reefs, inhabiting crevices or the undersides of rocks and feeding on drift algae. Small urchins can also avoid predation by sheltering in the spine canopy of conspecific adults (Clemente et al. 2013). Urchins can emerge from shelters to actively graze on live macroalgae when predator densities are low or when drift algae becomes scarce (Harrold and Reed 1985). Sheltering behavior can deter predation by fishes and invertebrates, and mortality of urchins often is highest for larger juvenile or adult urchins that can no longer inhabit small crevices (Shears and Babcock 2002; Pederson and Johnson 2006). Very large urchins, however, may have a size refuge from many predators (Tegner and Levin 1983; Guidetti 2006). Though rocky crevices and similar "hard" shelters may provide the best refuges for urchins, algae and marine plants also may offer protection from predators; in the Northwest Mediterranean Sea, predation on urchins by fishes decreased with increasing algal (Hereu et al. 2005) and seagrass (Farina et al. 2009) structural complexity.

Urchin barrens are not prevalent in the Point Loma kelp forest (San Diego, CA, USA), the largest kelp forest in California. Though sea otters once likely regulated urchin abundance in this area (Dayton et al. 1998), they 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 (*S. franciscanus*), may be effectively controlled by California spiny lobster (*Panulirus interruptus*), a nocturnal predator, and fishes such as the California sheephead (*Semicossyphus pulcher*), a diurnal predator (Tegner and Levin 1983; Lafferty 2004). Red urchins support a large fishery in southern California, and their low density also may contribute to the lack of urchin barrens in this region. Fishing influences urchin predators as well: lobsters and sheephead are heavily fished and resulting reductions in the densities and sizes of these predators may reduce their ability to control urchin populations (Tegner and Levin 1983; Hamilton et al. 2011). Fishery-induced alterations in the size distribution of predators such as lobsters (Barsky 2001) can have community-wide

impacts because only large predators are able to consume large urchins (Tegner and Levin 1983; Clemente et al. 2013). Despite the increasing number of studies focusing on urchin mortality and habitat use, direct field studies on urchin population regulation are relatively rare. Evidence that top kelp forest predators regulate urchin populations primarily comes from inverse correlations between urchin and predator densities (Mayfield and Branch 2000; Lafferty 2004; Carter et al. 2007). Our study is one of the few direct manipulative experiments within kelp forests conducted in southern California.

Our objective in this study was to determine the effects of predator abundance and habitat structure on the proportional mortality and habitat use of sea urchins in southern California kelp forests. Specifically, we conducted surveys and experiments within an MPA and two nearby heavily fished areas to determine (1) how habitat structure (understory algal cover), time of day (day vs. night), and urchin density interact to affect urchin proportional mortality, and (2) whether red and purple urchin abundance and habitat use vary with the abundance of their potential predators.

Methods

Study sites and study species

Our 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 MPA established in 1971; (2) adjacent to the reserve (ATR), ca. 500 m outside the LJER, and (3) 10 km to the south in the Point Loma kelp forest (PL) (Fig. 1). We selected these three sites to represent differences 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 we expected recreationally and commercially fished areas outside the reserve (ATR and PL) to have lower predator abundance. The kelp forest near Point 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, which may have dramatically reduced their predatory influence in this ecosystem (Dayton et al. 1998; Tegner and Dayton 2000). Dominant algae at each site include the surface canopy-forming giant kelp, *Macrocystis pyrifera,* and understory kelps *Pterygophora californica* and *Laminaria farlowii*. Other commonly encountered algae include *Egregia menziesii, Eisenia arborea*, and *Stephanocystis 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 et al. 1980). California spiny lobsters range from Monterey Bay,
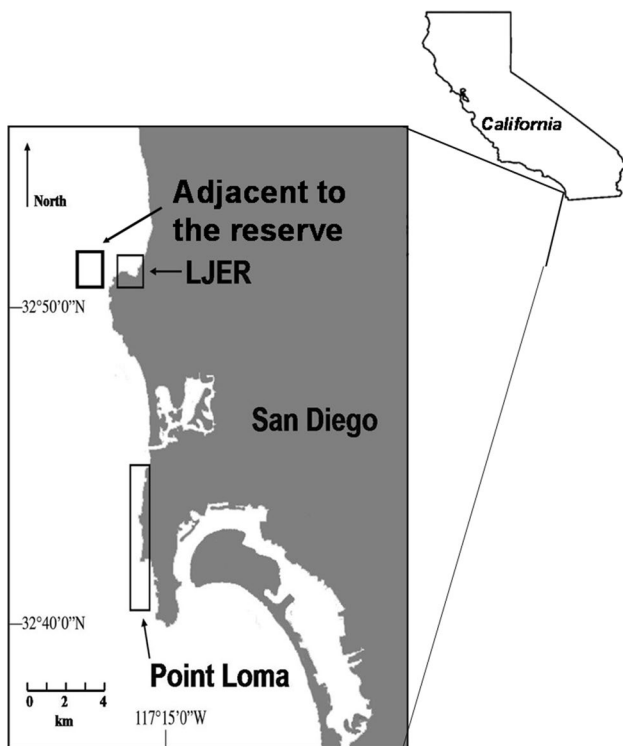
Fig. 1 Map of study sites in San Diego, CA, USA (32.69°N, 117.26°W), showing the location of the La Jolla Ecological Reserve (LJER), our site adjacent to the reserve (ATR), and the Point Loma kelp forest (PL)

California, to Magdalena Bay in Baja California, Mexico, where they inhabit shelters during the day and emerge from shelters at dusk to actively forage on benthic invertebrates, including mussels (Robles et al. 1990) and both red and purple urchins (Tegner and Levin 1983) during the night (Lindberg 1955; Withy-Allen and Hovel 2013). The California sheephead 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. Sheephead are diurnally active and return to home shelters at night (Topping et al. 2005).

Urchin proportional mortality

To determine how urchin density and algal cover interact to affect urchin mortality, we exposed purple urchins to predators inside the LJER where predator densities are high. We performed urchin mortality experiments during the day and at night to compare effects of major predators, sheephead (diurnal foragers) and lobsters (nocturnal foragers).

We exposed purple urchins to predators within standardized, artificial urchin habitat units (UHUs). UHUs allow

urchins to mimic natural sheltering behavior and avoid enhanced predation as a result of tethering (Peterson and Black 1994). Each 43 cm long × 38 cm wide UHU consisted of six, 10-cm-diameter PVC pipes anchored vertically in cement, creating artificial crevices 6–7 cm deep. We placed UHUs side by side to create each plot, with each plot holding a maximum of 36 urchins (for additional detail see Fig. 1A, a photograph of the plot in the Appendix). We 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 and Levin 1983). Urchin proportional mortality experiments were conducted from July to October 2008 and June to September 2009. Three weeks before trials began, we 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 either 4, 8, 16, 24, or 36 urchins to represent a gradient of low to high urchin density, chosen randomly.

To conduct daytime urchin predation trials, between 0900 and 1000 hours, we placed urchins in artificial crevices and covered each urchin with a small piece of *M. pyrifera* to aid in acclimation to the plot. We 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, 2, 24, and 48 h. Predators generally found urchins quickly (see "Results" section), and 1 h was sufficient time to see differences among treatments. Trials were identical for nocturnal urchin exposures, except that exposures began at ca. 2000–2100 hours when diurnal predators were inactive, and we returned to quantify urchin proportional mortality shortly before dawn (ca. 8-h exposures). We conducted a total of 3–7 replicate trials for each combination of density × cover × time of day. Urchin mortality rates were standardized to 1 h so that we could statistically compare daytime versus nighttime data.

To analyze urchin proportional mortality data, we used an analysis of covariance (ANCOVA) to test how urchin proportional mortality varied with urchin density (covariate), algal cover, and time of day. Our daytime and nighttime data are unbalanced, which can reduce power and increase the possibility of overlooking an effect when the effect truly exists (Shaw and Mitchell-Olds 1993). In light of this, we chose to minimize our 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, we used post hoc pooling to eliminate highly non-significant interactions from our model (Underwood 1997). Though Underwood (1997) suggests post hoc pooling is

appropriate when $P \geq 0.25$, all terms removed from our model had P values ≥ 0.65.

We used video to determine whether predators exhibit an aggregative response to increased urchin densities. One Sony HDR HC-9 camera in an underwater housing was used to record the number and species of predators visiting plots over a 1-h period during the day. The camera was placed at an oblique angle approximately 2.5 m from the plots. One plot was recorded for each level of urchin density. Upon replaying the video, predators were counted by pausing the tape every 15 s to identify and quantify predators ($N = 1430$ frames). We used linear regression to determine whether mean fish abundance (average number of fishes observed per frame) varied with urchin density.

Missing urchins may have been removed by predators or may have moved from plots on their own. We determined whether predators had likely removed missing urchins by (1) monitoring daytime plots with underwater video and (2) tagging a subset of urchins with small, inconspicuous pieces of plastic sleeve insulation from electrical wire (Hereu 2005). Three haphazardly selected plots were recorded for 90 min after divers completed urchin placement with the video camera. Upon reviewing the video, no urchins were seen moving from the plots. We tagged twenty urchins in plots by gluing two pieces of sleeve insulation onto the largest ventral spines. When we returned to plots to count surviving urchins, we extensively searched surrounding areas for tagged and untagged purple urchins. Though we often found broken tests and partially consumed urchins, we found no live tagged urchins outside of plots.

Urchin, lobster, and fish surveys

We conducted transect surveys (March 1 to July 31, 2008) to quantify the density of red and purple urchins and their chief predators, spiny lobsters, and large fishes in LJER, ATR, and PL. To sample for urchins and lobsters, we swam 20 m × 4 m transects in haphazardly chosen locations designed to encompass a variety of habitats in each of the three sites. We conducted a total of 19, 17, and 20 transects in the LJER, ATR, and PL, respectively, in eight unique locations on average per site. 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, lobster carapace length (CL) was recorded to the nearest 0.5 cm.

During surveys, we also recorded the habitat status for all urchins. Based on preliminary surveys, we categorized each urchin into one of four categories, ranging from least exposed to most exposed: concealed (the urchin was completely concealed under a boulder that needed to be flipped to expose urchins), burrowed (the urchin was visible but tightly embedded into a deep cavity within the rock), ledge (the urchin was found under a ledge that was accessible to at least some predators), or fully exposed (the urchin was out in the open with no concealment or cover). Concealed and burrowed urchins are extremely difficult for predators to find or remove, whereas urchins under ledges and exposed on rocks are comparatively vulnerable to predators. Therefore, for analysis, we combined the concealed and burrowed categories to form a "protected" category and combined the ledge and exposed categories to form an "exposed" category.

We used separate one-way ANOVAs to test for differences in lobster and urchin density and lobster size among the three sites. Data were visually inspected for normality, and we tested for homogeneity of variances using Cochran's test in this and all subsequent ANOVAs. We evaluated differences in means using Student–Newman–Keuls (SNK) multiple comparisons. To test whether purple and red urchin habitat status differed among sites, we used separate Pearson's Chi-square tests.

To estimate fish abundance, a team of two divers conducted 25 × 4 × 4 m transects and identified each fish encountered (Parnell et al. 2005). There are numerous kelp forest fishes known to feed on juvenile or adult urchins including black surfperch, *Embiotoca jacksoni*, rubberlip surfperch, *Rhacochilus toxotes*, and señorita, *Oxyjulis californica* (Kenner 1992). Other fishes including kelp bass, *Paralabrax clathratus*, and rock wrasse, *Halichoeres semicinctus*, are known to scavenge urchins after sheephead attacks (Cailliet 2000; KDN *personal observation*). 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. We conducted transects between the hours of 0700–1300 from June 26 to October 1, 2008, for a total of 20 haphazardly located transects at each site (for total counts see Table 3). We used separate one-way ANOVAs to analyze differences in fish abundances and Simpson's index of diversity (D_s) among the three sites.

Habitat surveys: rugosity

In order to infer whether available refuge habitat for urchins differs among sites, we estimated substratum complexity by quantifying rugosity along urchin and lobster

Table 1 Analysis of covariance (ANCOVA) results for the effects of starting urchin density, presence of algal cover, and time of day (day vs. night) on purple urchin *Strongylocentrotus purpuratus* proportional mortality

Source[a]	df	MS	F	P
Time of day	1	1.78	48.3	<0.001
Cover	1	0.34	9.1	0.003
Urchin density	1	0.19	5.24	0.024
Time of day × cover	1	0.41	11.1	0.001
Time of day × urchin density	1	0.16	4.42	0.04
Cover × urchin density	1	0.06	1.64	0.20
Residual	104	0.03		
Total	110			

[a] Three-way interaction term removed from final model

transects. We 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 and Luckhurst 1978). At 12 haphazardly chosen points along 3–4 transects per site we 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). We tested for differences in rugosity among the three sites using a one-way ANOVA.

Results

Urchin proportional mortality

There was a significant interactive effect of urchin density and time of day, and a significant interactive effect of cover and time of day on purple urchin proportional mortality (Table 1). Urchin proportional mortality decreased with urchin density during the day but was density independent during the night (Fig. 2), and algal cover reduced purple urchin proportional mortality during the day, but not at night (Fig. 3).

The main predator observed removing urchins from the plots during daytime trials was the California sheephead. Video recordings showed a marginally significant increase in sheephead abundance with urchin density (Linear regression, $r^2 = 0.71$, $F_{1,4} = 7.2$, $P = 0.07$; Fig. 4). A distinctive behavioral pattern was observed, with a male sheephead removing an 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. Additionally, a horn shark, *Heterodontus francisci*, was
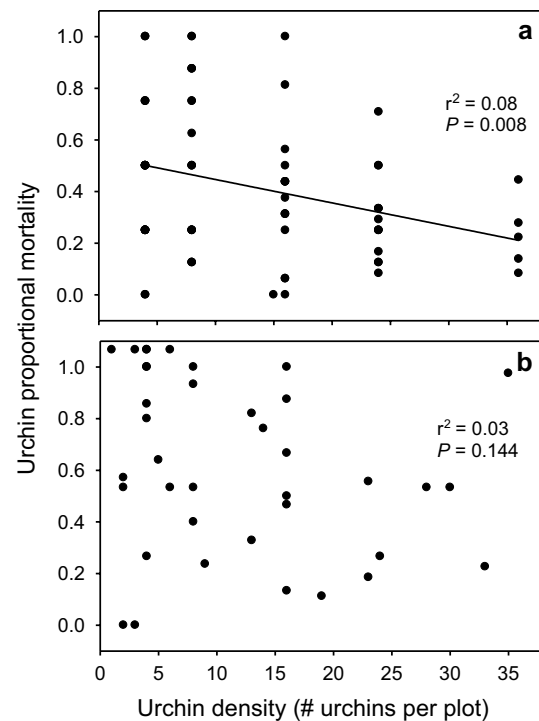

Fig. 2 Purple urchin (*Strongylocentrotus purpuratus*) proportional mortality **a** during the daytime, and **b** during the night in the La Jolla Ecological Reserve (LJER)

observed consuming a sea urchin during nighttime experimental trials though not observed during daytime fish transects.

Urchin, lobster and fish surveys

We found strong evidence for a difference in the density and habitat use of purple urchins and red urchins among the three sites (Table 2). Purple urchins were significantly denser in PL than in LJER, but densities did not differ between ATR and LJER and ATR and PL (Fig. 5). For red urchins, densities in PL were significantly lower than densities at the other two sites (Fig. 5). We found only six individuals on 20 transects in PL, but found 42 individuals in LJER and 39 individuals in ATR. For both species, most urchins found on transects were in rock burrows (64.7 %). Fewer were under ledges (22.5 %) sheltered under boulders (11.3 %), or exposed (1.3 %), with exposed urchins found only at PL. Purple urchin habitat status (protected vs. exposed) did not differ among sites (Pearson's Chi square, $\chi^2 = 1.36$, $P = 0.50$). For red urchins, we found a significant difference in habitat status between LJER and ATR (PL was not included in red urchin analyses due to low sample size). Most red urchins (74 %) were exposed in LJER, whereas only 33 % of red urchins were exposed to predators in ATR (Pearson's Chi square, $\chi^2 = 13.4$, $P = 0.003$).
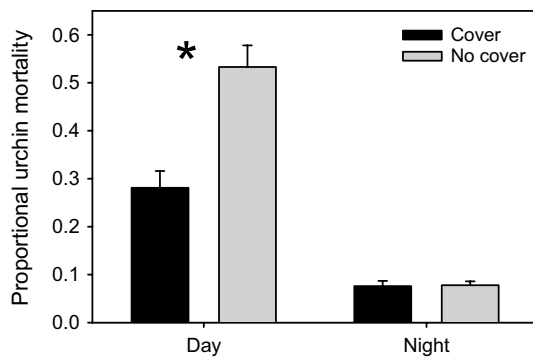
Fig. 3 Proportional mortality for purple urchins (*Strongylocentrotus purpuratus*) exposed to predators in the La Jolla Ecological Reserve during the day and during the night, either under cover of understory algae or in the open (no cover). *Asterisk* denotes significant difference in proportional mortality between cover and no-cover treatments
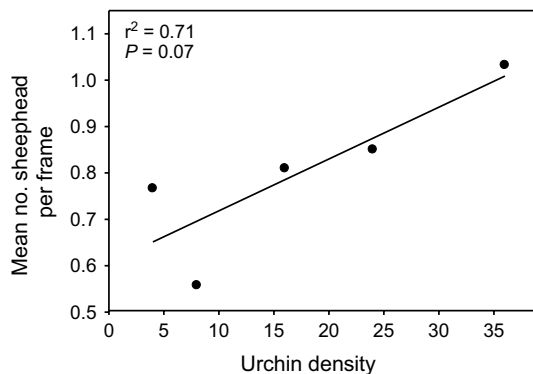

Fig. 4 Mean number of fish seen per frame in video recordings of purple urchins (*Strongylocentrotus*) exposed to predators in the La Jolla Ecological Reserve

Table 2 Analysis of variance (ANOVA) results for 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	17,896.228	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		

For lobsters, we found significantly higher lobster density in LJER than in PL, but lobster density in LJER and ATR, and in PL and ATR did not differ significantly (Table 2;
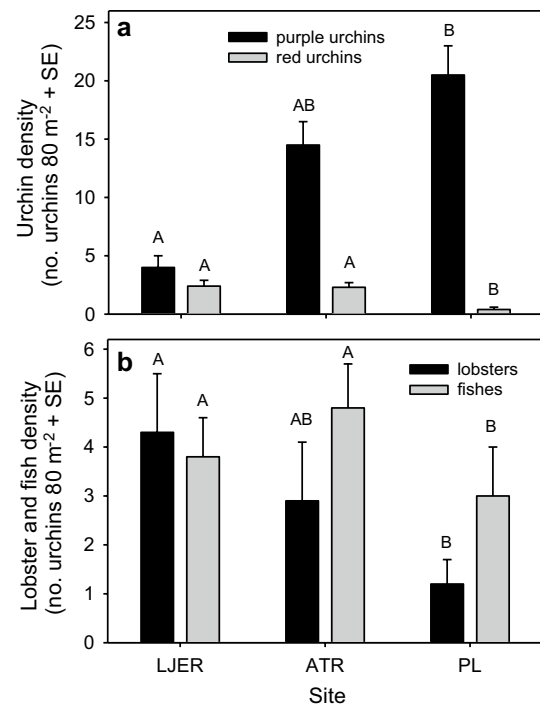

Fig. 5 Mean density of **a** red urchins (*Strongylocentrotus franciscanus*) and purple urchins (*Strongylocentrotus purpuratus*), and **b** California spiny lobsters (*Panulirus interruptus*) and predatory fishes from transect surveys conducted in the La Jolla Ecological Reserve (LJER), adjacent to the reserve (ATR), and Point Loma (PL). Unlike *letters above bars* denote treatments that differed significantly at $P < 0.05$ in post hoc tests conducted separately for each species or group

Fig. 5). Mean lobster CL was greater in LJER than in ATR and PL (ANOVA, $F(2152) = 16.89$, $P < 0.001$). LJER housed some very large lobsters that were absent from PL and ATR where lobster fishing is prevalent (Fig. 6).

We observed a total of 13 fish species in our surveys, and the abundance of fish predators did not precisely follow trends of fishing intensity among our three sites (Table 3; Fig. 5). PL had significantly lower fish abundance than the other two sites, but we counted a high number of sheephead and kelp bass in ATR, which had a slightly (but not significantly) higher abundance of predators than in LJER (ANOVA, $F(2,57) = 3.35$, $P = 0.04$). Simpson's index of diversity (D_s) was significantly lower in PL than in ATR or LJER (ANOVA, $F(2,57) = 4.59$, $P = 0.01$).

Habitat surveys: rugosity

Rugosity varied substantially among the three sites and was significantly higher in LJER (0.43 ± SE = 0.05) than in ATR (0.22 ± SE = 0.06) and PL (0.27 ± SE = 0.08; ANOVA, $F(2,34) = 3.67$, $P = 0.04$). Most of the locations we sampled in PL tended to be flat with very few boulders.
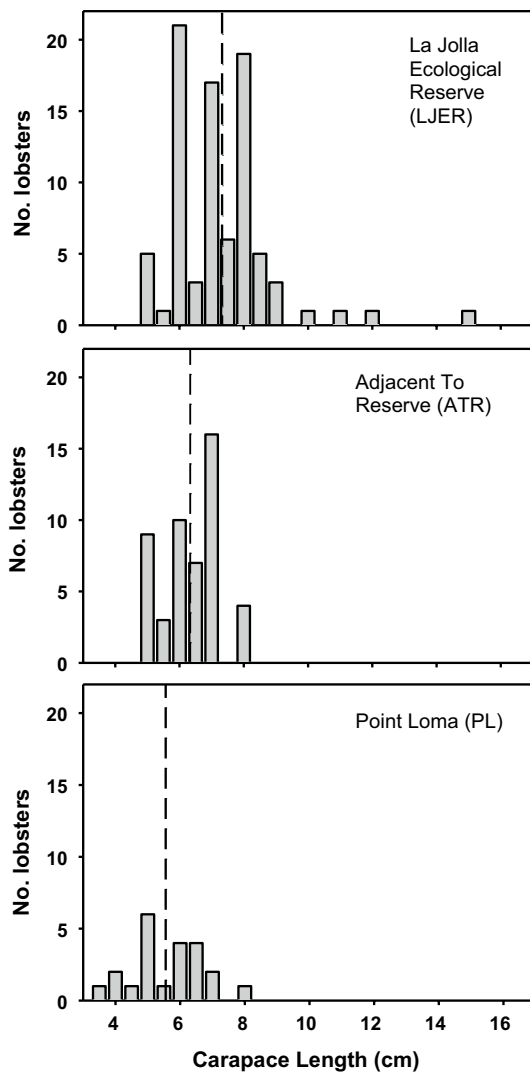
Fig. 6 California spiny lobster (*Panulirus interruptus*) size-frequency distribution in La Jolla Ecological Reserve (LJER), adjacent to the reserve (ATR) and Point Loma (PL) in 2008. The *dashed vertical line* represents the mean CL for each site

Shelters at this site were typically long contiguous ledges, whereas in LJER, there are more large boulders and a greater diversity of substrate types. ATR infrequently had large boulders but did not contain as much substrate diversity as within LJER.

Discussion

Determining the degree of density dependence associated with urchin mortality from predation, and how habitat structure influences predation and urchin behavior are essential to understanding the effects of urchin grazing on algae and the implications this has for kelp forest dynamics and stability. In our experiment, per capita mortality

Table 3 Number of fish counted on each of 20 transects per site in the La Jolla Ecological Reserve (LJER) adjacent to the reserve (ATR) and Point Loma (PL) in 2008

Common name	Scientific name	LJER	ATR	PL
California sheephead	*Semicossyphus pulcher*	5	21	8
Kelp bass	*Paralabrax 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

Species in bold were considered potential urchin predators

rates of urchins exposed to predators did not increase with increasing urchin density (i.e., a potentially regulating predator response was not observed). This was surprising given the high density and high average sizes of major urchin predators in LJER; sheephead and spiny lobsters. In our experiments, sheephead appeared to aggregate on plots with high urchin density, but videos of sheephead feeding revealed that a common pattern of behavior was for a large male sheephead to begin consuming an urchin, after which smaller female sheephead and other species such as kelp bass would come in to devour smaller urchin pieces, resulting from the crushing of the urchin by the large male. Fish size and type influence their ability to consume urchins as only larger fish may be able to break the urchin test (Clemente et al. 2010). The high numbers of fish observed during the day on high urchin density plots did not often result in a large proportion of urchins being consumed over periods of 1 h. We also did not observe an increase in purple urchin proportional mortality with urchin density at night, when lobsters are actively foraging. Similar to our results, in Nova Scotia, Canada, urchin *Strongylocentrotus droebachiensis* aggregations reduced the number of attacks by the predatory crab *Cancer irroratus* (Bernstein et al. 1981).

Though our predation experiment results suggest that predators such as lobsters and large fishes may not be able to substantially reduce urchin density when urchins achieve very high densities, our results and those of others suggest that predators may effectively control urchin density and behavior at relatively low urchin densities (Hereu et al. 2012; Clemente et al. 2011). The fact that urchin proportional mortality was lowest at our highest urchin density suggests that dense patches of urchins experience low

per capita urchin mortality. Predators may not be able to achieve high enough foraging rates to substantially reduce urchin densities when urchins are found in dense aggregations. In future experiments including higher urchin densities may be advisable, however, urchin proportional mortality in our experiments was high at low urchin densities, which are akin to densities normally found in healthy kelp forests. In our surveys, purple urchins were least dense in the LJER where lobsters and fishes were abundant (and lobsters were larger), and were most dense in PL where lobsters and fishes were less abundant (and lobsters were smaller). Several studies have shown correlations between predator abundance and urchin behavior in marine reserves, with predators being more abundant and effective and urchins, exhibiting more cryptic behavior within reserves as compared to non reserve sites (Sala and Zabala 1996; Sala et al. 1998; Clemente et al. 2011). This pattern also exists among sites in kelp forests of the Channel Islands in southern California (Lafferty 2004).

A dramatic increase in spiny lobster *Jasus lalandii* abundance was correlated with strong reductions in sea urchin *Parechinus angulosus* abundance in South Africa (Mayfield and Branch 2000), though in contrast to our results, laboratory experiments with these species revealed that the number of sea urchins consumed by spiny lobsters was proportional to their density (Mayfield et al. 2001). Laboratory feeding experiments with California spiny lobster, purple urchins, and red urchins led Tegner and Levin (1983) to propose that spiny lobster predation in southern California kelp forests was sufficient to dictate urchin size-frequency distributions. Additionally, Cowen (1983) compared sea urchin abundance between sheephead removal and non-removal sites of southern California kelp forests and concluded that sheephead strongly control red urchin abundance and sheltering behavior. It is also important to note that predation may synergistically act with other factors influencing urchin abundance, such as food availability, larval supply, recruitment, and disease (Tegner and Dayton 1977; Watanabe and Harrold 1991; Pearse 2006, Foster and Schiel 2010).

Shelter is a key factor in determining predation rates on sea urchins (Cowen 1983; Sala et al. 1998; Hereu et al. 2005). Though urchins commonly seek shelter in crevices or under boulders, they also may use understory algae as a refuge. We hypothesized that macroalgal cover would reduce urchin mortality during the day by hiding urchins from visually oriented predators, but might increase urchin mortality at night because spiny lobsters, a primary nocturnal predator of urchins, often seek cover under macroalgae (Mai and Hovel 2007; Hovel and Lowe, unpublished data) or even seek out macroalgae after emerging from shelter to forage on attached invertebrates (Withy-Allen and Hovel 2013). Daytime predation by fishes was reduced when plots contained high macroalgal cover, but there was no difference in urchin mortality between cover and no-cover treatments at night. Similarly, Hereu et al. (2005) found that predation by fishes on juvenile urchins (*Paracentrotus lividus*) was reduced under algae and in rocky crevices in a Mediterranean Sea marine reserve.

An interesting result from our experiment was that the presence of habitat structure had no influence on the relationship between urchin proportional mortality and urchin density. Urchin proportional mortality decreased with urchin density at the same rate with and without understory algae present. In contrast, many other studies have shown that habitat structure can influence whether prey mortality rates are density dependent. For example, kelp perch *Brachyistius frenatus* proportional mortality was inversely density dependent when kelp habitat structure was low, but was density independent when moderate or high amounts of kelp were added to laboratory mesocosms (Anderson 2001). Similar results were found in field experiments on the small coral reef goby *Coryphopterus glaucofraenum*, in which limited shelter caused density-dependent mortality, but proportional mortality was density independent in plots with abundant refuges (Forrester and Steele 2004). A difference between our experiment and Forrester and Steele (2004) was that gobies used discrete rocky crevices in their study, but urchins were provided with more diffuse algal cover in our study, preventing the "musical chairs" type of shelter limitation in which particular individuals are without shelter. Similar to our study, proportional mortality of the invasive Asian mussel *Musculista senhousia* was inversely density dependent at all levels of eelgrass *Zostera marina* habitat structure in southern California, even though their primary predator (the gastropod *Pteropurpura festiva*) aggregated in plots with high mussel density and displayed different functional responses among different levels of seagrass habitat structure (Kushner and Hovel 2006).

In our surveys, we saw no difference in purple urchin habitat use among sites. Most urchins we found were under rocks or embedded within small crevices, and nearly all remaining urchins were found under ledges. However, our low-predator-density site (PL) was the only site at which urchins were found completely exposed on top of rocks (2.5 % of purple urchins found in PL). Kelp forest urchins typically remain cryptic and feed on drift algae and may only leave hiding places when drift algae becomes scarce (Harrold and Reed 1985). However, there is evidence that predator abundance may influence urchin behavior (Sala et al. 1998). On southern California rocky reefs, red urchins *Strongylocentrotus franciscanus* were less cryptic in areas where sheephead *Semicossyphus pulcher* were removed and where sheephead densities were low (Cowen 1983). Sheephead removal also resulted in increased

urchin abundance (Cowen 1983). In the northwest Mediterranean Sea, daily and monthly movement of the urchin *Paracentrotus lividus* was reduced by high predator abundance (Hereu 2005). Lobster predation is limited on large urchins (Tegner and Levin 1983; Andrew and MacDiarmid 1991; Mayfield et al. 2001). The red urchins we observed in both the LJER and ATR sites were typically large and not very cryptic, which suggests a possible size refuge for this species. The proportion of red urchins found exposed was higher in LJER than in the ATR, even though predator density and urchin density were similar between these two sites, and rugosity was higher in the LJER, potentially providing more crevices.

A caveat of our study is that there are a variety of factors that may vary between our sites, which may influence purple and red urchin habitat use and behavior (e.g., predation, habitat structure, recruitment, food supply, and competition). Since both predator density and rugosity varied among the three sites, we cannot explicitly tease apart the effect of fishing pressure and rugosity on urchin abundance and habitat use, as rugosity is positively correlated with reef fish abundance and species richness (Luckhurst and Luckhurst 1978, Friedlander and Parish 1998) and urchin density is correlated with habitat structure (Guenther et al. 2012). For red urchins, fishing strongly influences abundance, and red urchins were almost completely absent in PL. Fishers also may select exposed urchins over cryptic urchins, leading to fewer exposed urchins in ATR than in LJER. Thus, in areas outside of marine reserves, the commercial fishery for red urchins may be partly filling the ecological role of large lobsters and fishes (Dayton et al. 1998). Ideally, our study would have encompassed a larger geographic area and multiple marine reserves allowing us to explicitly tease out the effects fishing pressure may have on this system. While we believe the no-take LJER established in 1971 has been effective, particularly in increasing local diversity and predator abundances in the area, replicating our study in multiple reserves would strengthen our understanding of the relationships we observed.

Though the role of sheephead and lobsters in regulating urchin population abundance has come into question (Foster and Schiel 2010), their ecological role as predators reflects the complexity of trophic interactions that sustain the kelp forest food web (Tegner and Levin 1983; Cowen 1986; Hamilton et al. 2011, Guenther et al. 2012). 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. The factors influencing the ecological stable state of a kelp forest community are numerous (Steneck et al. 2002); understanding which factors impact urchin communities most significantly can help to avoid undesirable urchin barrens and promote ecologically resilient communities.

Studying urchin population regulation and potential density dependence over large scales is important to understand potential global regime shifts (Ling et al. 2015). Though predation is one of many factors influencing urchin populations, the fishing of predators can have dramatic effects on urchin behavior (Sala et al. 1998) and the influence of fishing pressure on top predators may be particularly important in kelp forest systems (Halpern et al. 2006). 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). Our results help to elucidate the processes behind urchin population regulation, which is critical due to the possible community-wide impacts an increase in urchin abundance may have.

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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