CALIFORNIA SPINY LOBSTER (*PANULIRUS INTERRUPTUS*) MOVEMENT BEHAVIOR AND HABITAT USE: IMPLICATIONS FOR THE EFFECTIVENESS OF MARINE PROTECTED AREAS

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California Spiny Lobster (*Panulirus interruptus*) Movement Behavior and Habitat Use: Implications for the Effectiveness of Marine Protected Areas

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ABSTRACT OF THE THESIS

California Spiny Lobster (*Panulirus interruptus*) Movement
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Marine protected areas (MPAs) are widely used to rebuild depleted populations for exploited species, but their effectiveness hinges on adequate knowledge of the factors dictating population dynamics for target organisms. Estimates of connectivity via larval dispersal often are included in MPA design, but movement patterns, habitat associations, and habitat-specific survival rates of juveniles and adults, which often are unknown, also will influence MPA effectiveness. California spiny lobsters (*Panulirus interruptus* Randall) are the target of intense commercial and recreational fishing in southern California, but we lack basic information about home range and habitat use of lobsters to determine if MPAs planned for the region will enhance abundance. Working within and outside of the La Jolla Ecological Reserve (LJER) in southern California, we (i) quantified lobster movement patterns and home ranges over short (nightly – weekly) and long (1 – 14 months) time scales using acoustic telemetry, (ii) surveyed lobsters to determine day and night habitat associations, and (iii) tethered lobsters to assess habitat-specific predation risk. Lobsters exhibited high site fidelity, proclivities for homing, and small home ranges (geometric mean of 651 m^2 and 5,912 m^2 per week based on 50% and 95% Kernel Utilization Distributions (KUDs), respectively) that encompassed only a fraction of a small MPA, even over periods of several months. Lobsters were strongly associated with rocky habitat during the day (when in shelters) but were associated with the red algae *Plocamium cartilagineum* at night (when feeding). Lobster relative survival rates were high across vegetated and unvegetated habitats at night, but lobsters were protected from predators by surfgrass (*Phyllopsadix torreyi*) habitat during the day. Our results highlight the need to consider how movement patterns vary over short and long time scales, and how patterns of habitat use may vary from day to night for nocturnally active species such as spiny lobsters when planning MPAs.

TABLE OF CONTENTS

PAGE

APPENDIX

LIST OF TABLES

LIST OF FIGURES

PAGE

INTRODUCTION

Marine fish stocks have declined globally since 1974, negatively affecting many fisheries and marine ecosystems (Wijkström et al. 2004). Marine Protected Areas (MPAs) have become popular worldwide as a tool to replenish depleted populations and maintain biodiversity. MPAs have been successful at increasing mean body size and abundance of many species (see reviews by National Research Council 1999, Fogarty et al. 2000, Roberts and Hawkins 2000, Halpern and Warner 2002, Halpern 2003), including fishes (*Paralabrax clathratus*: Lowe et al. 2003, *Plectropomus* spp and *Lutjanus carponotatus*: Williamson et al. 2004), lobsters (*Panulirus argus*: Cox and Hunt 2005, *Panulirus interruptus*: Iacchei et al. 2005, *Jasus edwardsii*: Shears et al. 2006), and other invertebrates (*Strombus gigas*: Stoner and Ray 1996, *Strongylocentrotus franciscanus* and *Haliotis corrugata*: Parnell et al. 2005). Enhanced biomass and diversity are evident even in small MPAs (e.g., Roberts and Hawkins 1997, Halpern 2003) and a survey of MPA effectiveness worldwide suggests that overall, changes in population size, species interactions, and community structure can occur rapidly and can persist after MPAs are established (Halpern and Warner 2002).

Optimally, MPAs are sited and designed with consideration for the biological and ecological processes that sustain populations, promote diversity, and maintain key interspecies interactions. Information on dispersal distances and connectivity within and among populations, species habitat use and movement patterns, and the strength and direction of interactions that moderate population dynamics is crucial to possess for species targeted for protection by the establishment of MPAs. This information, however, is lacking for most species (Ward et al. 1999) and MPAs may not succeed when movement patterns and habitat associations of the targeted species are not incorporated into the MPA design. For example, lingcod (*Ophiodon elongatus*) generally have small-scale movements, but relatively large MPAs are needed to protect lingcod populations because they move further seasonally to participate in spawning events (Martell et al. 2000). Additionally, two MPAs in New Zealand were not large enough to encompass the home range and habitat use of the spiny lobster *J. edwardsii*, resulting in over 50% of lobsters moving beyond the boundaries to access offshore habitat (Kelly 2001).

Lobsters are an important fishery species worldwide and are targeted for conservation in MPAs in several regions of the globe. Though many species may exhibit seasonal migrations between shallow coastal waters to deeper offshore waters (Herrnkind et al. 1975, Kelly and MacDiarmid 2003), lobsters typically exhibit relatively small home ranges and high fidelity to particular shelters or landscapes (Kelly and McDiarmid 2003, Frisch 2007) suggesting that MPAs incorporating suitable habitat may be effective at protecting a subset of the population from fishing mortality, particularly if they incorporate shallow and deep habitats (Barrows 1996, California Department of Fish and Game [CDFG], unpublished data). MPAs increased abundance and mean body size of the spiny lobsters, *P. interruptus* (Iacchei et al. 2005) and *J. edwardsii* (Davidson et al. 2002, Shears et al. 2006) in California and New Zealand, respectively. High site fidelity to reefs over long time scales played a large role in rebuilding *J. edwardsii* populations within the Leigh Marine Reserve in New Zealand (Kelly and MacDiarmid 2003). Lobsters also may use a variety of habitats within their home range, but more information is needed on fine-scale use of biotic and abiotic features within generalized habitat types. California spiny lobsters, for instance, inhabit shelters composed of stacked boulders, rock crevices or kelp holdfasts in the kelp forest during the day (Spanier and Zimmer-Faust 1988, Mai and Hovel 2007, Loflen 2007), but emerge from shelters at night to forage within understory algae, seagrass beds (Hovel and Lowe 2007), or within intertidal zones (Robles et al. 1990). Lobster habitat associations and risk of predator-induced mortality therefore may change diurnally, and surveys and experiments quantifying habitat use and survival must be conducted both during the day and during the night to effectively determine how available habitat within MPAs will influence lobster population dynamics.

California spiny lobsters (Crustacea: Decapoda: Palinuridae; *Panulirus interruptus*) are subject to intense fishing pressure in California and Mexico, and are the only marine invertebrate in California that is highly sought in both commercial and recreational fisheries (Barsky 2001). In southern California, commercial fishing for *P. interruptus* has existed for over a century, and lobster abundance and mean body size concomitantly has decreased (Dayton et al. 1998, Barsky 2001). California spiny lobster populations may strongly influence marine community structure by indirectly facilitating kelp via their consumption of herbivorous sea urchins (Tegner and Levin 1983, Lafferty 2004, Halpern et al. 2006) and by consuming competitively dominant California mussels *Mytilus californianus* on rocky shorelines (Robles 1997) and invasive Asian mussels *Musculista senhousia* in seagrass habitat (Cheng and Hovel, *in press*). The California Department of Fish and Game (CDFG) regulates both the commercial and recreational fishery of California spiny lobster with seasonal closures, size limits, gear restrictions, and licensing. Though fishery-dependent data suggest that the lobster population has not collapsed, it is difficult to determine how effective these measures are in protecting a subset of the population from fishing mortality, particularly due to the lack of a stock assessment (Barsky 2001) and due to the lack of information on larval connectivity among population subgroups.

Since California spiny lobsters are economically and ecologically important, they have been targeted as a species to protect within a new network of MPAs that are currently being established in compliance with the California Marine Life Protection Act (MLPA; CDFG, unpublished data). Little is known, however, about patterns of *P. interruptus* movement, habitat use, and the factors that influence survival, particularly at night when lobsters are active. Working within and around a small MPA in southern California, we used acoustic tagging and tracking, benthic surveys, and tethering experiments to (i) quantify lobster movement patterns and home ranges over short (nightly – weekly) and long (1 – 14 months) time scales, (ii) determine lobster habitat associations during the day and during the night, and (iii) determine if lobster survival varies with habitat type, time of day, and lobster size.

MATERIALS AND METHODS

STUDY SPECIES

California spiny lobsters inhabit kelp forest, estuarine, and intertidal habitats from Monterey Bay, California, USA, to Manzanillo, Baja California, Mexico (Barsky 2001). Lobsters have a pelagic larval duration of up to 9 months (Engle 1979), and generally settle near inshore surfgrass *Phyllospadix* spp. habitat (Barsky 2001). *P. interruptus* is a generalist feeder, but prefers mollusks, including California mussels and gastropods, as well as crustaceans when available (Winget 1968, Castañeda-Fernández-de-Lara et al. 2005). Adult and juvenile lobsters can be found singly within daytime shelters, but often are gregarious and are found in groups of two to several dozen in shelters composed of rock crevices, stacked cobble and boulders, and hollowed-out kelp holdfasts (Mai and Hovel 2007).

STUDY SITE

We performed all surveys and experiments in the La Jolla Ecological Reserve (LJER) and the area directly outside of the LJER (32°51'N, 117°16'W; Figure 1), adjacent to San Diego in southern California, USA. The LJER was established in 1971, and is one of the oldest 'no take' MPAs in southern California (Parnell et al. 2005). At 2.16 km^2, the LJER is far smaller than the median size of MPAs worldwide (ca. 16 km^2: McClanahan 1999). The LJER encompasses a variety of habitats including kelp forest, surfgrass beds, sandy plains and a submarine canyon (Figure 1). Spiny lobster abundance and mean carapace length (CL) are higher inside the LJER than in nearby kelp forest habitat (Parnell et al. 2005) and the border of the LJER is heavily fished (Parnell et al. 2007).

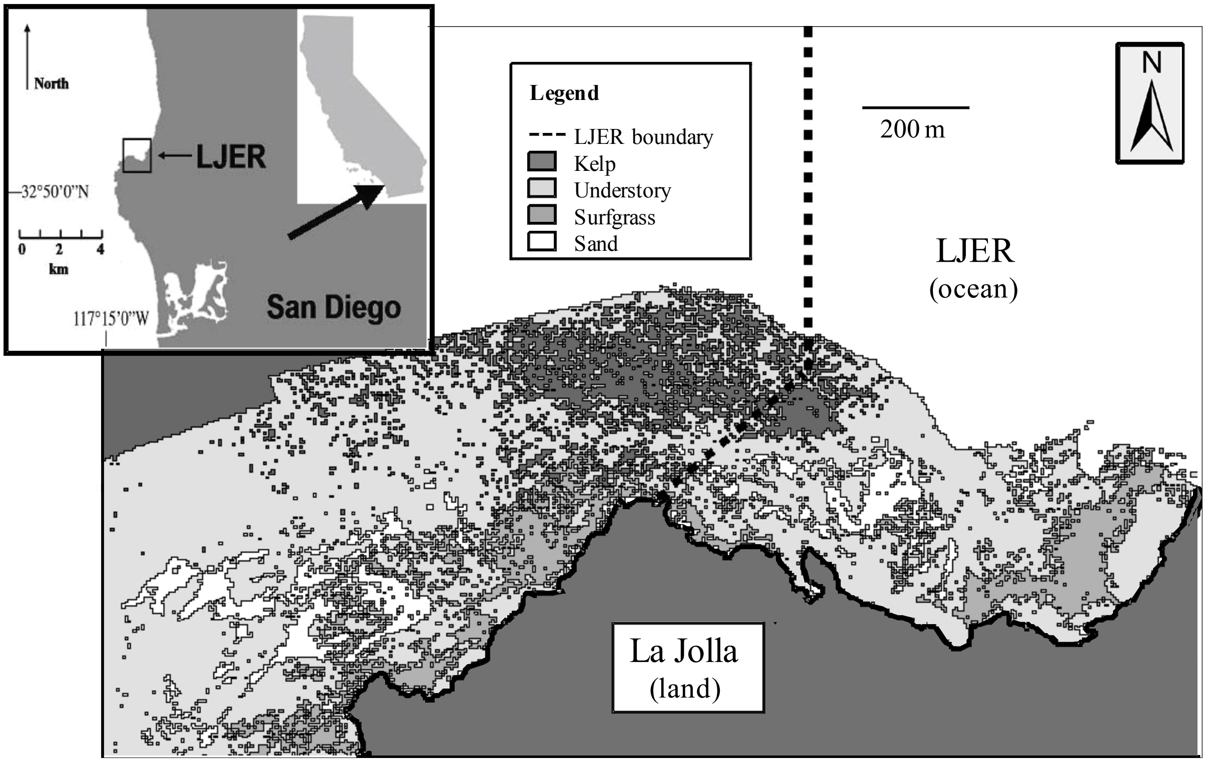

Figure 1. Map of the LJER near San Diego in southern California, including a vegetation layer from the San Diego Nearshore Mapping Program. Large white area is sand habitat that was not surveyed by the mapping program and the large gray area is land.

LOBSTER MOVEMENT

We used acoustic tagging and tracking to monitor lobster movements at night. Short-term nocturnal movements (over 1 – 3 nights) were monitored by active tracking from a small boat, and long-term lobster movements (1 – 14 months) were monitored using an array of acoustic receivers moored to the substratum. Adult lobsters between 7 – 15 cm CL were captured by hand using SCUBA and brought to the boat where they were fitted with an acoustic transmitter (Vemco V13H continuous transmitters for active tracking; Vemco R64 coded transmitters for passive tracking; Vemco Ltd., Nova Scotia, Canada) encased within a plastic holder that was tied to the lobster using thin wire wrapped around the carapace. We secured the transmitter to the carapace using cyanoacrylate glue and care was taken to ensure full range of motion of the walking legs. The CL and sex of each lobster was recorded upon tagging and lobsters were returned to shelters in the kelp forest within 60 min of capture.

Short-Term Lobster Movements

We tagged and tracked nine lobsters (four lobsters inside the LJER and five lobsters outside of the LJER) from June – September 2008 and 17 lobsters (12 lobsters inside of the LJER and five lobsters outside of the LJER) from June – August 2009 (N = 26). We allowed lobsters no less than 36 h to acclimate to transmitters and then returned to the area to track their nocturnal movements over three non-consecutive nights for up to one week, with an average of two days between tracking dates per lobster. Tracking began at ca. 1800 h each night and consisted of relocating up to seven individual lobsters every hour using a VEMCO VR60 boat mounted hydrophone and GPS. Tracking ended at ca. 0600 each morning when lobsters typically had ceased moving for ca. one hour. We visually relocated lobsters with SCUBA at the end of tracking trials with an underwater hydrophone to confirm each lobster was alive and to recover tags if possible.

Coordinates for active tracking were plotted on a geo-referenced map of the nearshore La Jolla area using both ArcView 3.2 and ArcGIS 9.0. We determined the total cumulative distance each lobster traveled by adding the distance between each consecutive positional fix from all three tracking nights separately over a period of seven days using the "Animal Movements Analyst Extension" (AMAE; Hooge et al. 2001) in ArcView 3.2. We also used AMAE to calculate minimum convex polygons (MCPs) and the 95% and 50% kernel utilization distribution (95KUD and 50KUD, respectively) for each lobster as separate measures of home range. Whereas MCPs connect the outermost positions at which animals are found during their movements, KUDs represent areas that a lobster has a 95% chance or 50% chance of being found within each night with 50KUD representing the “core” home range for each lobster (Worton 1989, Lowe et al. 2003). We used AMAE’s MCP bootstrap tests on position data for each individual lobster to examine the minimum number of points required for a robust estimate of home range (ca. 20 points), and removed four lobsters from the analyses for which we had less than the minimum data requirement.

To analyze short-term movement data, we performed separate two-way, fixed-factor analyses of covariance (ANCOVAs) to test whether lobster MCP, 95KUD, and 50KUD varied with lobster sex, site (inside the LJER vs. outside the LJER), or CL. We used Cochran’s test to test for heterogeneous variances and used normal probability plots to check for normality, and transformed data when necessary to meet the assumptions of ANCOVA in this and all relevant subsequent tests (Underwood 1997). If interactions were detected, we used lower-level ANCOVAs and linear regressions for post hoc analysis. We used the geometric mean as a measure of central tendency for movement data due to strong right-skew in distributions. We evaluated lobster homing behavior by calculating a linearity ratio for each lobster, which is the distance between the initial and final positional fix of the lobster divided by the total cumulative distance the lobster traversed during the entire track. Values near zero suggest the lobster was homing, while values near one suggest the lobster exhibited linear, nomadic behavior (Zeller 1997, Bellquist et al. 2008). We also calculated an aspect ratio to describe home range shape by dividing the maximum width of the MCP polygon by the maximum length for each lobster. If the aspect ratio was closer to one, the lobster had a circular home range, while a ratio closer to zero described an elongated home range (Topping et al. 2005, Bellquist et al. 2008). To determine the percentage of an individual lobster’s home range that could be encompassed by the LJER we divided home range size by the total area of the LJER (2.16 km²; Topping et al. 2005).

Long-Term Lobster Movements

We used benthic acoustic receivers stationed inside and outside of the LJER to continuously monitor the positions of an additional 26 lobsters from April 2008 – June 2009. In March 2008 we deployed 12 VEMCO VR2W underwater automated omni-directional receivers using concrete moorings, with each receiver separated by a distance of 200 – 500 m (Figure 2). Receivers were moored 1 m off the bottom and were located where detection ranges could cover surfgrass and kelp forest habitats within the LJER, up to one km outside of the LJER, and along the LJER boundary. We used range testing before deploying receivers to determine the appropriate distances between receivers. Acoustic tags on lobsters transmitted a unique identification code with a 60 – 85 kHz range with a continuous pulse interval of 1000 or 2000 ms to VR2W receivers. Eighteen lobsters were tagged and released in April 2008, and four additional lobsters were tagged and released both in August and November 2008 (N = 26). After lobsters were released, the date and time of day that each lobster ventured within range (ca. 100 − 300 m) of each receiver were recorded for up to 14 months, and the study ended in June 2009.

An exact home range cannot be determined using passive receivers because lobsters can be anywhere within the detection radius of each receiver when detected. We therefore used the receiver location as an approximate positional fix when lobsters were detected and calculated an estimated MCP for each lobster (methods adapted from Bellquist et al. 2008). We only calculated MCPs for lobsters that travelled within the detection range of ≥ 3

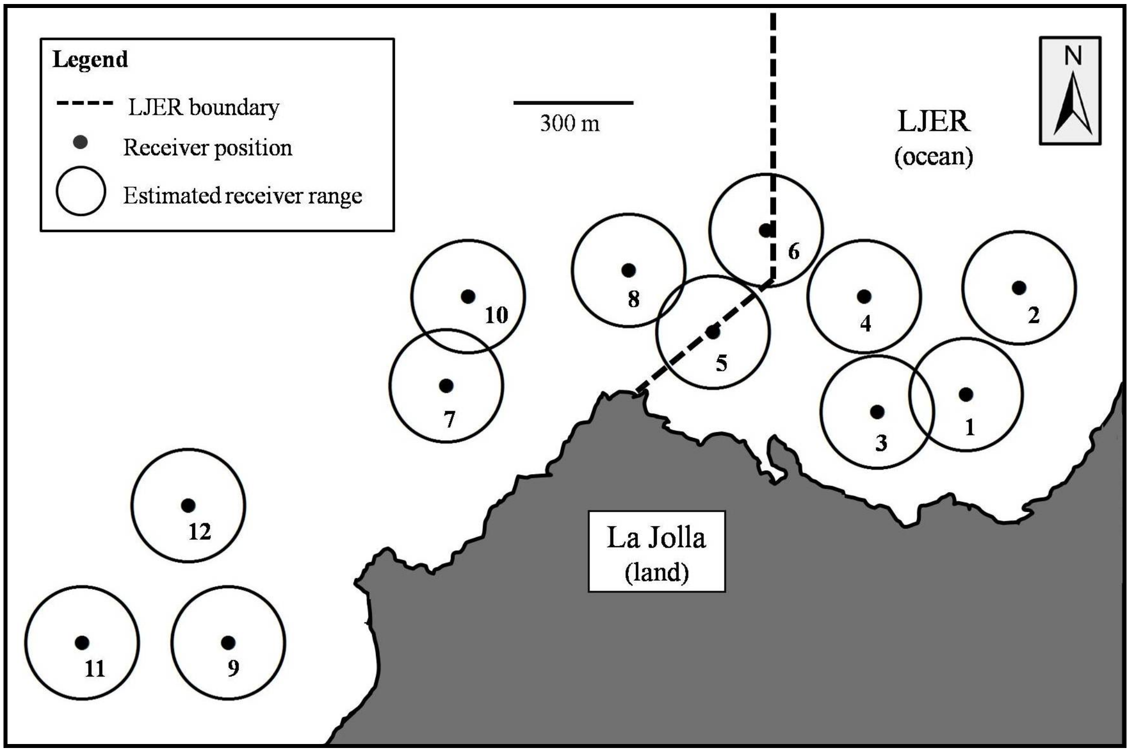

Figure 2. Map with locations of 12 omni-directional receivers (including ID #) and estimated detection range (ca. 300 m) inside the LJER, at the boundary, and outside (southwest) of the LJER. See Table 7 for a list of lobsters that were detected by receivers.

receivers. We used separate two-way, fixed-factor ANCOVAs to test whether estimated MCP area varied with sex, site, and CL, or sex, site, and duration of detections (time), and conducted post-hoc analyses using lower-level tests as described above. We further determined whether lobsters remained within the study site for a period of up to 14 months.

LOBSTER-HABITAT ASSOCIATIONS

We surveyed benthic habitats within the LJER from July – September 2009 to quantify lobster habitat use during the day, when lobsters typically are within shelters, and at night when lobsters typically are feeding outside of shelter. To represent the two primary vegetated habitats within the LJER, we haphazardly selected ten sites for surveys, with five sites dominated by kelp forest (*Macrocystis pyrifera*) habitat and five sites dominated by surfgrass (*Phyllospadix torreyi*) habitat. At each site, divers swam two 50 x 4 m transects to search for lobsters and to record habitat cover within 5 m x 4 m quadrats (n = 200 observations). All lobsters found on transects were counted and visually measured for CL and their general activity (feeding, walking, or remaining motionless) was noted. We surveyed the percent coverage of the most abundant substratum and vegetation encountered within each transect (also see Parnell et al. 2005). Substratum cover for abiotic habitat was quantified by visually estimating the percent cover of (1) boulder, (2) cobble, (3) flat rock, and (4) sand within quadrats. Vegetation cover for biotic habitat was quantified by visually estimating the percent canopy cover of common understory algae, which included (1) *Egregia menziesii*, (2) *Pterygophora californica,* (3) *Laminaria farlowii*, (4) *Eisenia arboria*, (5) *Plocamium cartilagineum*, (6) articulated coralline algae, (7) *Ulva lactuca*, and (8) *Cystoseira osmundacea*. These algal species represented > 95% of the algal cover within our sites. When lobsters were found within shelters, we categorized their shelters as "ledge" (a rock overhang) or "hole" (a crevice within stacked boulders). We used separate forward stepwise logistic regressions (one each for day and night surveys) to determine whether the odds of finding lobsters in a quadrat were correlated with habitat cover of each substratum and vegetation type within a quadrat (n = 200). Before conducting logistic regressions we used Pearson's correlations to test for correlations among the 12 substrate and vegetation variables. Only sand and boulder habitat were strongly (negatively) correlated, so we removed percent cover of sand from the analysis. To ensure independence of quadrats, we tested for autocorrelation among adjacent quadrats with an ACF time series test (SYSTAT 12) for each transect, and used the Pearson's correlation coefficients table to determine first order correlations. Any habitat types significantly correlated with the odds of finding lobsters in the logistic regression were investigated further using a classification tree analysis (CART). CART is a classification method based on hierarchal (if, then) components, is simple to interpret, and both non-parameteric and non-linear. The computational algorithm is complex and the classification tree is validated using v-fold cross validation (Breiman et al. 1984, De'ath and Fabricius 2000).

LOBSTER SURVIVAL

We used tethering to determine if relative lobster survival varied between juvenile and adult lobsters and among the following habitat types: (1) unvegetated substratum ("sand"), (2) *M. pyrifera* canopy with understory (*E. menziesii*, *P. californica*, or *E. arboria*) ("understory"), and (3) *P. torreyi* ("surfgrass"). Tethering is widely used to estimate relative survival rates for invertebrates and fishes, including lobsters (Mintz et al.1994, Lipcius et al. 1998, Diaz et al. 2005, Loflen 2007, Mai and Hovel 2007), but does not measure absolute mortality rates because tethered animals cannot flee from predators.

We captured lobsters by hand or trap and kept them in a large recirculating aquarium for no more than one week before using them in experiments. To tether lobsters we tied a 50 cm length of 23 kg braided fishing line around the carapace by cinching a noose, and then secured the noose to the lobster with cyanoacrylate glue. Approximately 30 cm of line extending from the carapace was attached to a washer, which was then affixed to a stake embedded in the substratum. Fifteen sites for tethering were chosen haphazardly inside and outside of the LJER. Trials were conducted from July 2008 – 2009. All trials included two size classes of lobsters, juveniles (< 5.5 cm CL) and adults (> 7 cm CL). We tethered at least four lobsters (2 juveniles and 2 adults) at each site within the three habitat types (n = 24 in understory, n = 22 in surfgrass, and n = 19 in sand; N = 65 lobsters). All lobsters at understory or surfgrass sites were tethered so that the lobster had access to vegetation coverage. Lobsters were tethered no less than 3 m apart and plots were not reused.

To quantify relative survival rates when lobsters are out of protective shelters at night, each tethering trial commenced shortly after dusk and then lobsters were checked shortly before dawn. Lobsters were recorded as either alive (an active lobster remaining on the tether), eaten (a fragment of the carapace remaining on the tether), missing (no lobster or fragment remaining on the tether), or molted (entire carapace remaining on the tether). We considered missing lobsters as eaten by predators because video analysis of tethered *P. interruptus* showed that large fish predators could remove lobsters entirely from tethers (Loflen 2007), and six lobsters tethered in predator exclusion cages remained affixed to tethers after one week (see also Mai and Hovel 2007). As relative survival was very high after a single night (see Results), lobsters again were checked 36 h and then 7 d after the trial began to determine relative survival rates for longer time scales, after which all remaining live lobsters were released. We used separate G tests of independence (one for each length of exposure: single night, 36 h, and 7 d) followed by Pearson Chi Square analyses to determine whether lobster relative mortality varied between juveniles and adults and among habitat types.

RESULTS

SHORT-TERM LOBSTER MOVEMENTS

Of 26 lobsters tagged for short-term tracking, we successfully located 20 lobsters for three non-consecutive nights within a given week between June 2008 and August 2009 (Table 1). Overall, lobsters moved short distances each night and maintained small home ranges (Table 1, Table 2). Mean distance moved per night was < 150 m, and only six lobsters had 95KUD home ranges > 10,000 m^2 (Table 1, Table 2, Figure 3). Seventeen of 20 lobsters tracked for one week had linearity ratios that were close to zero, suggesting that lobsters exhibited homing rather than nomadic behavior (Table 1, Figure 4). MCP home ranges were neither highly circular nor highly elongated, and covered only a small percent of the area available within the LJER (Table 2). Two lobsters crossed the LJER boundary over one night, and two additional lobsters crossed the boundary after one week (Figure 5). Of these lobsters, all except one was emigrating from the reserve, and only one lobster returned to the reserve within a week's time.

We found a marginally significant three-way interaction among site, sex, and CL for total cumulative linear distance travelled by lobsters over a period of three nights (Table 3). An interaction between site and CL was significant for females (df = 1, $F = 6.453$, $P = 0.044$), but not for males (df = 1, $F = 0.053$, $P = 0.826$). This interaction could not be further analyzed due to a small sample size of females released outside of the LJER.

Site of lobster release significantly influenced all lobster home range area estimators (Table 4, Table 5, Table 6). Lobsters had larger home ranges when captured and released

Table 1. Summary Information for 20 California Spiny Lobsters that Were Released Inside (I) and Outside (O) of the LJER and Actively Tracked for Three Non-Consecutive Nights. Distance Represents the Cumulative Linear Movements of Individual Lobsters for 3 Non-Consecutive Nights. Lobster 18 was Tracked for Two Non-Consecutive Nights

Lobster ID	Date Released	Total # of positional fixes	CL (mm)	Sex	Release site	Distance (m)	MCP (m²)	50% Kernel (m²)	95% Kernel (m²)	Aspect ratio	Linearity ratio
1	8/5/2008	20	81	F	O	465	15,302	7,720	46,949	0.17	0.42
2	8/5/2008	35	78	F	O	986	5,083	424	5,092	0.39	0.02
3	8/5/2008	32	80	M	O	560	5,083	565	6,044	0.29	0.17
4	8/5/2008	33	79	M	O	619	9,233	1,751	13,794	0.15	0.24
5	8/5/2008	33	83	M	O	415	2,853	387	3,760	0.90	0.14
6	6/22/2009	31	74	M	O	620	4,772	877	8,779	0.39	0.09
7	6/22/2009	26	75	M	O	300	14,004	2,633	24,708	0.33	0.20
8	6/22/2009	20	79	M	O	447	61,150	62,382	248,712	0.17	0.70
9	8/10/2009	34	84	F	I	478	2,075	411	2,634	0.79	0.00
10	8/10/2009	34	95	M	I	391	985	161	1,583	0.89	0.03
11	8/10/2009	33	76	F	I	379	1,712	183	2,294	0.86	0.05
12	8/10/2009	33	78	M	I	714	1,763	139	2,305	0.74	0.04
13	8/10/2009	27	151	M	I	411	1,089	142	1,644	0.78	0.02
14	8/24/2009	21	129	M	I	249	4,046	1,057	8,976	0.26	0.08
15	8/24/2009	35	81	F	I	426	10,580	1,529	12,221	0.33	0.20
16	8/24/2009	34	78	F	I	409	2,541	137	1,165	0.55	0.02
17	8/24/2009	35	74	F	I	283	778	65	1,045	0.48	0.04
18	8/24/2009	21	81	F	I	500	7,624	1,609	8,081	0.27	0.56
19	8/24/2009	34	86	F	I	473	14,004	3,425	22,476	0.31	0.19
20	8/24/2009	35	70	F	I	546	934	56	765	0.80	0.11

Table 2. Maximum, Mean (± SE), and Minimum Values of 20 Actively Tracked California Spiny Lobsters Within and Outside of the LJER. Left of the Dotted Line are Values for Home Range Estimators with Geometric Mean Calculations. Distance per Night is the Average Cumulative Linear Distance Travelled During Three Non-Consecutive Nights. Distance is the Total Cumulative Linear Distance Travelled During Three Non-Consecutive Nights. Right of the Dotted Line Are Calculations Based on MCP Home Ranges Using Arithmetic Mean Values

	Distance per night (m)	Distance (m)	MCP (m^2)	50KUD (m^2)	95KUD (m^2)	Aspect ratio	Linearity ratio	% of LJER area
Maximum	475	986	61,150	62,382	248,712	0.90	0.7	2.83
Mean	143	460	4,160	651	5,912	0.49	0.17	0.38
(+) SE	153	494	5,380	961	8,166	0.06	0.04	0.14
(−) SE	133	428	3,217	442	4,280	0.06	0.04	0.14
Minimum	48	249	778	56	765	0.15	0	0.04

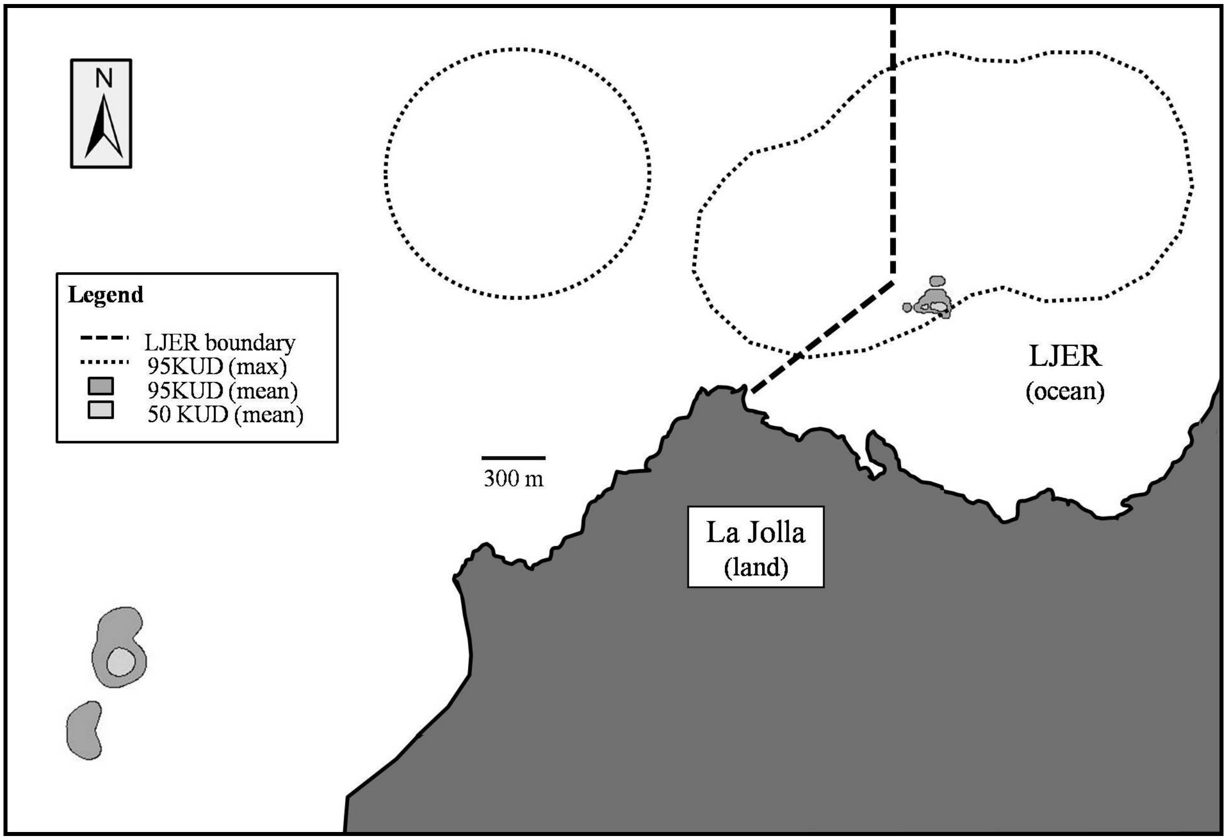

Figure 3. Home range estimates for three lobsters actively tracked for three non-consecutive nights. The dotted lines represent the 95KUD for the maximum home range of a single lobster (Lobster 8). We selected one lobster each to represent the geometric mean of lobsters released inside or outside of the LJER. The polygon within the LJER is the 95KUD and 50KUD for Lobster 9. The larger polygon outside of the LJER is the 95KUD and 50KUD for Lobster 4. See Table 1 for area calculations of these lobsters.

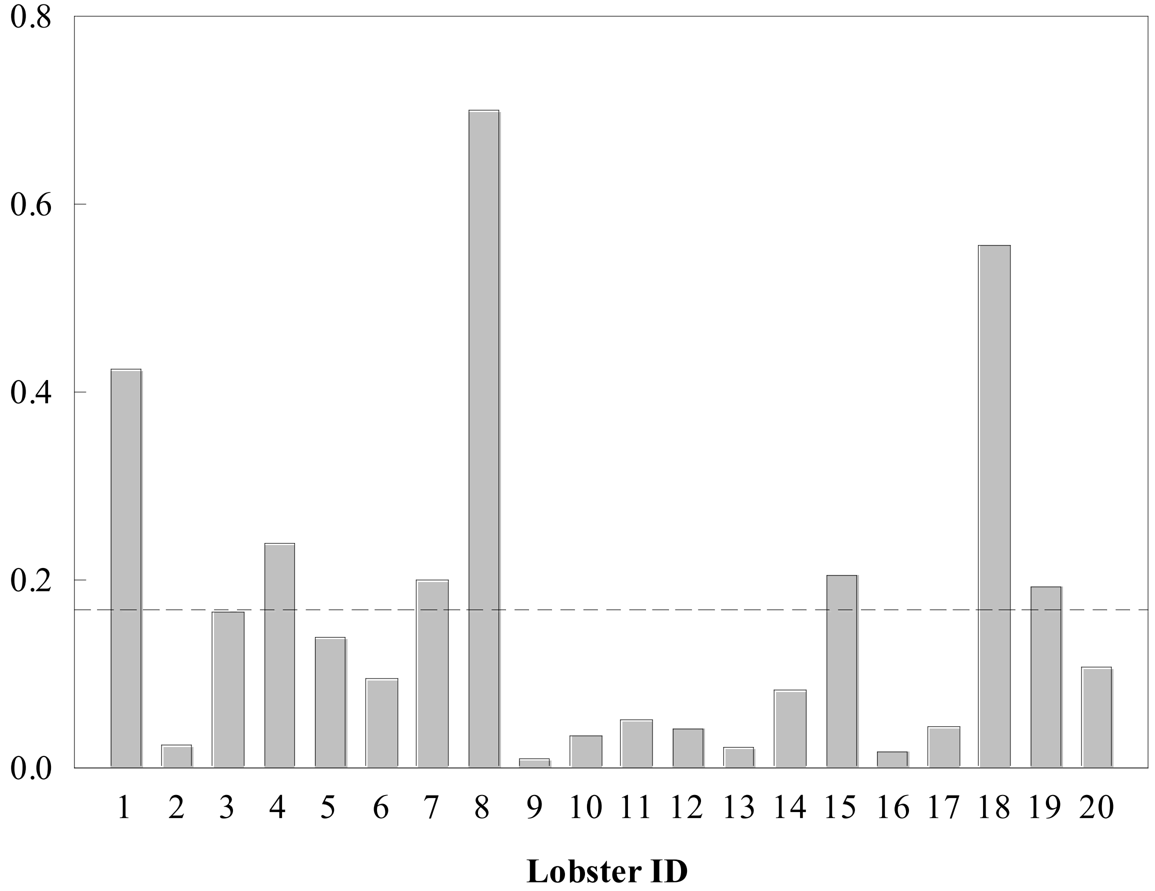

Figure 4. Linearity ratio values for short-term movement. Lobsters with linearity ratio values closer to zero were homing, and values closer to one were interpreted as straight-line, nomadic movement. The dashed line represents the arithmetic mean value for all 20 lobsters.

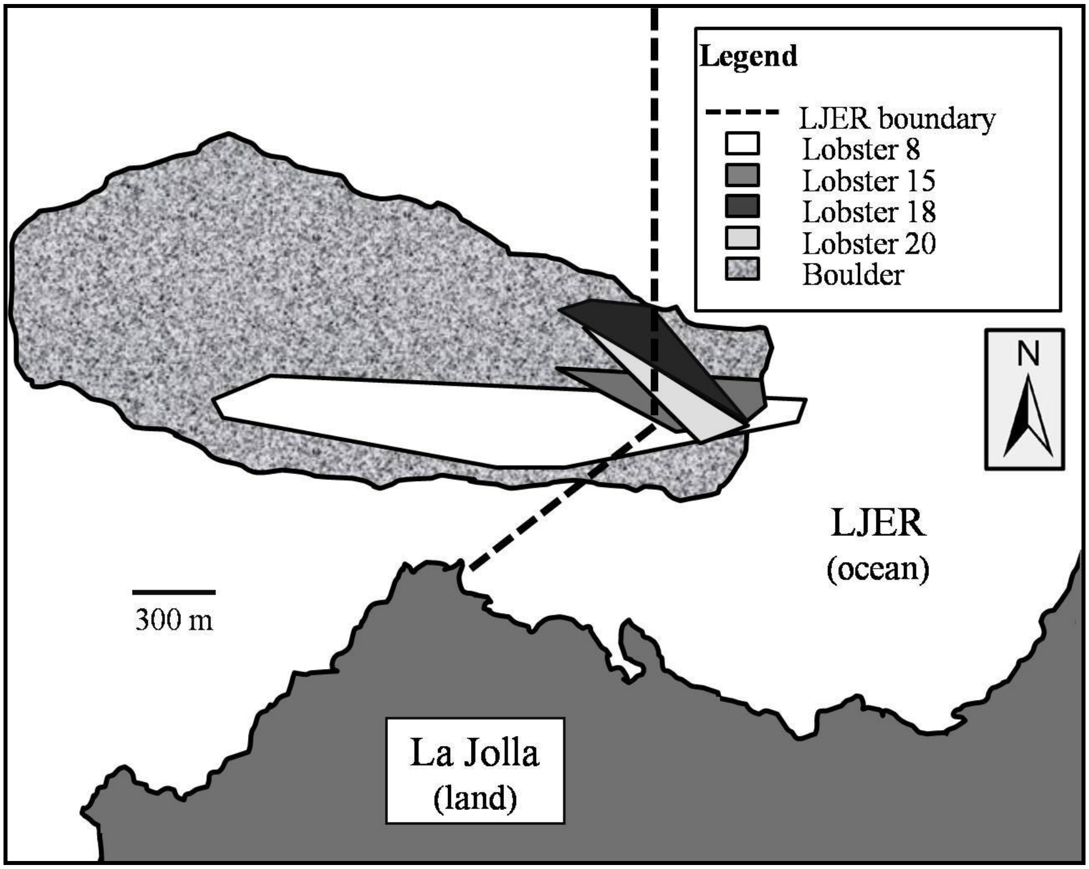

Figure 5. MCPs of 3 lobsters that utilized the contiguous boulder habitat to cross the boundary of the LJER over a period of 7 days. Three of these lobsters were released inside of the LJER and one lobster was released outside of the LJER.

Table 3. Analysis of Covariance (Fixed, Full Model) of the Effects of Sex, Site, and CL On Cumulative Linear Lobster Movement for 20 Lobsters Tracked for Three Non-Consecutive Nights Over a Period of Seven Days. No Factors Were Removed from the Model Due to a Marginally Significant Interaction Among Site, Sex, and CL

Source	SS	df	Mean Square	*F*-ratio	*P*-value
Sex	0.23	1	0.23	2.7	0.126
Site	0.261	1	0.261	3.067	0.105
CL	0.247	1	0.247	2.909	0.114
Sex (x) CL	0.227	1	0.227	2.664	0.129
Sex (x) Site	0.315	1	0.315	3.704	0.078
Site (x) CL	0.252	1	0.252	2.966	0.111
Site (x) Sex (x) CL	0.299	1	0.299	3.513	0.085
Error	1.02	12	0.085		

Table 4. Analysis of Covariance (Fixed, Reduced Model) of the Effects of Sex, Site, and CL Among 50KUD Area Calculations for 20 Lobsters Tracked Over Three Non-Consecutive Nights Over a Period of Seven Days

Source	SS	df	Mean Square	*F*-ratio	*P*-value
Sex	13.121	1	13.121	7.358	0.016
Site	9.532	1	9.532	5.346	0.035
CL	14.319	1	14.319	8.03	0.013
Sex (x) CL	13.929	1	13.929	7.811	0.014
Error	26.747	15	1.783		

Table 5. Analysis of Covariance (Fixed, Reduced Model) of the Effects of Sex, Site, and CL Among 95KUD Area Calculations for 20 Lobsters Tracked Over Three Non-Consecutive Nights Over a Period of Seven Days

Source	SS	df	Mean Square	*F*-ratio	*P*-value
Sex	7.487	1	7.487	6.13	0.026
Site	7.506	1	7.506	6.146	0.026
CL	7.941	1	7.941	6.502	0.022
Sex (x) CL	7.855	1	7.855	6.431	0.023
Error	18.32	15	1.221		

Table 6. Analysis of Covariance (Fixed, Reduced Model) of the Effects of Sex, Site, and CL Among MCP Area Calculations for 20 Lobsters Tracked Over Three Non-Consecutive Nights Over a Period of Seven Days

Source	SS	df	Mean Square	*F*-ratio	*P*-value
Sex	5.262	1	5.262	7.223	0.017
Site	4.702	1	4.702	6.455	0.023
CL	5.111	1	5.111	7.016	0.018
Sex (x) CL	5.675	1	5.675	7.79	0.014
Error	10.927	15	0.728		

outside of the LJER than when captured and released inside of the LJER. There was also a significant interactive effect of sex and CL for all home range area estimators (Table 4, p. 20; Table 5, p. 20; Table 6, p. 20). Home range area was positively correlated with lobster CL for females (50KUD: df = 1,10, $t = 3.661$, $P = 0.006$; 95KUD: df = 1,10, $t = 2.976$, $P = 0.018$; MCP: df = 1,10, $t = 3.229$, $P = 0.012$) but not for males.

LONG-TERM LOBSTER MOVEMENTS

Of 26 lobsters fitted with coded transmitters for long-term tracking, one was not detected after being released, 21 were detected for at least 30 days after being released, and 18 were used to calculate estimated MCP values since they were detected by ≥ 3 receivers (Table 7, Table 8). Though estimated home ranges were on the order of 10 – 100 times larger than for lobsters tracked for one week, lobsters still homed to specific sites and generally exhibited high site fidelity even over periods of several months. All receivers detected at least one lobster during the duration of the study. The receiver farthest from the reserve, in the southwest region, only detected 1 lobster for the duration of the study. The two receivers positioned at the boundary line detected more lobsters than all other receivers. Two lobsters were only detected by one receiver, while one lobster travelled to 8 distinct receivers (Table 7, Table 8). Seven of 25 lobsters crossed the boundary of the LJER. Four of these lobsters emigrated from the LJER and three immigrated to the LJER.

We found a marginally significant three-way interaction among site, sex, and CL (Table 9). This was most likely a result of larger females moving smaller distances within the LJER, although this relationship was weak (df = 1,6, $t = -1.988$, $P = 0.118$). There was no effect of duration of detections (time) on estimated MCP (Table 10).

Table 7. Summary Information for 21 California Spiny Lobster Released Inside (I) and Outside (O) of the LJER in 2008 that Were Passively Tracked for > 30 days. Estimated MCPs Are Only Included for Lobsters that Were Detected Within the Range of ≥ 3 Receivers

Lobster ID	Date released	Release site	Size (CL)	Sex	Duration of detections (days)	Total detections	Receiver ID # for detections	Estimated MCP (m^2)
1	4/18	I	80	M	50	1,042	2,3,5,6,7,8,10,12	575,488
2	4/18	O	79	F	45	2,064	5,6,8	31,378
3	4/18	O	75	M	146	11,612	5,6,8	31,378
4	4/18	O	77	M	210	31,378	5,6,8	31,378
5	4/18	O	75	F	126	883	3,5,6,8,12	395,831
6	4/22	I	82	F	271	5,043	1,2,3,4,5,6	182,101
7	4/22	I	71	F	116	1,646	4,5,6,8	66,958
8	4/22	I	73	M	69	2,102	3,4,5,6	82,674
9	4/22	I	75	F	176	10,053	1,3,4,5,6,8	141,645
10	4/22	O	77	F	246	16,501	7,9,10,12	159,027
11	4/22	O	80	F	135	2,707	7,9,12	105,861
12	4/22	O	73	F	55	1,538	7,9,10,11,12	212,089
13	4/22	O	81	M	55	4,155	7,10,12	53,166
14	5/2	I	78	M	75	203	4,5,6	35,580
15	5/2	I	79	M	88	759	3,4,5,6	82,674
16	7/24	O	84	M	70	2,880	7,10,12	53,166
17	7/24	O	81	M	33	2,031	7,10	—
18	7/24	I	75	F	201	64,286	2,3,4,5,6,8	191,073
19	11/14	O	78	F	199	5,795	2,4,6,8,10	98,750
20	11/14	I	70	M	170	4,463	3	—
21	11/14	I	83	M	129	565	3	—

Table 8. Maximum, Mean (± SE), and Minimum Values of 18 Passively Tracked California Spiny Lobsters Released Within and Outside of the LJER that Were Detected for > 30 days and Within the Range of ≥ 3 Receiver Locations. Left of the Dotted Line are Values for the Estimated MCP with Geometric Mean Calculations. Right of the Dotted Line Are Calculations Based on MCP Home Ranges Using Arithmetic Mean Values

	Estimated MCP (m^2)	Duration of detections (days)	Total detections	# of receivers visited	% of LJER area
Maximum	575,488	246	64,286	8	26.6
Mean	96,847	127	8, 176	3.95	6.5
(+) SE	117,554	15	3,220	0.4	1.5
(−) SE	79,805	15	3,220	0.4	1.5
Minimum	31,378	33	203	1	1.4

Table 9. Analysis of Covariance (Fixed, Full Model) of the Effects of Sex, Site, and CL Among Estimated MCP Area Calculations for 18 Lobsters Tracked for ≥ 30 Days and Were Detected by ≥ 3 Receivers. No Factors Were Removed from the Model Due to a Marginally Significant Interaction Among Site, Sex, and CL

Source	SS	df	Mean Square	*F*-ratio	*P*-value
Sex	1.583	1	1.583	2.2	0.169
Site	0.075	1	0.075	0.104	0.754
CL	0.142	1	0.142	0.198	0.666
Sex (x) CL	1.446	1	1.446	2.01	0.187
Sex (x) Site	2.939	1	2.939	4.083	0.071
Site (x) CL	0.065	1	0.065	0.09	0.770
Site (x) Sex (x) CL	3.004	1	3.004	4.174	0.068
Error	7.198	10	0.72		

Table 10. Analysis of Covariance (Fixed, Reduced Model) of the Effects of Sex, Site, and Time (Duration of Detections) Among Estimated MCP Area Calculations for 18 Lobsters Tracked for ≥ 30 Days and Were Detected by ≥ 3 Receivers

Source	SS	df	Mean Square	*F*-ratio	*P*-value
Sex	1.759	1	1.759	2.297	0.152
Site	0.001	1	0.001	0.002	0.969
Time	0.014	1	0.014	0.019	0.893
Error	10.723	14	0.766		

LOBSTER-HABITAT ASSOCIATIONS

Lobster habitat association differed between daytime and nighttime surveys. Ninety-one percent of lobsters were found in shelter during the day (100% in shelter in kelp habitat and 79% in shelter in surfgrass habitat; N = 160) whereas only 14% of lobsters were found in shelter at night (7% in shelter kelp habitat and 22% in shelter in surfgrass habitat; N = 218). We found more lobsters at night than during the day, likely due to unseen lobsters within shelters during the day.

The odds of finding lobsters within quadrats increased with boulder percent cover during the day (Table 11a), and increased with percent cover of the understory alga *Plocamium cartilagineum* (hereafter referred to as *Plocamium*) at night (Table 11b). The odds of finding lobsters did not vary with any other habitat type. During the day, we could predict lobster presence with 76% accuracy when boulder cover was > 55% and when cover of *Plocamium* was > 22.5% (Figure 6a). It is important to note that while the effect of *Plocamium* during the day was not statistically significant in the forward stepwise logistic regression (Table 11a), *Plocamium* can still play a role in predicting lobster presence during the day. At night, we could predict with 64% accuracy that lobsters would be present when *Plocamium* cover was above 25% (Figure 6b). Both boulder and *Plocamium* were not significantly autocorrelated within transect surveys (Appendix).

LOBSTER SURVIVAL

Lobster relative survival was extremely high after one night both for juveniles and adults (92% of all lobsters remaining alive), precluding statistical analysis (Figure 7). After 36 h of exposure to predators, lobsters had significantly higher relative survival in surfgrass as compared to sand habitat, but there was no effect of lobster size and no interactive

Table 11. Forward Stepwise Logistic Regression Results for (A) Day and (B) Night Habitat Associations Within and Outside of the LJER. Odds Ratios Indicate How the Odds of Finding Lobsters Increase with a 1% Increase in Habitat Cover. Numbers in Parentheses Are Lower and Upper Wald Confidence Limits

	Source	df	Parameter	P	Odds ratio
(A)	Intercept	1	-2.423	<0.001	
	Boulder	1	0.033	<0.001	1.033 (1.016, 1.051)
	Plocamium	1	0.022	0.119	1.022 (0.994, 1.051)
(B)	Intercept	1	0.169	0.697	
	Plocamium	1	0.032	0.028	1.032 (1.003, 1.062)

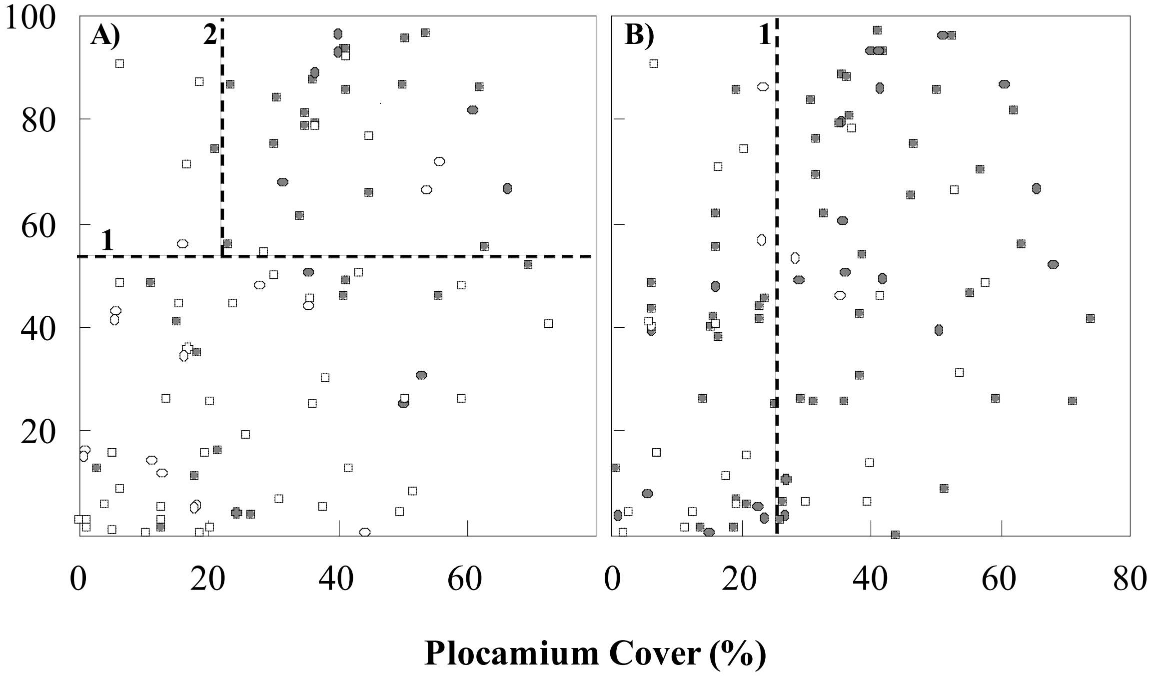

Figure 6. The percent cover of boulder and *Plocamium* habitats as compared to lobster presence during A) day and B) night time periods. Dark circles represent lobster presence and white circles represent lobster absence. Dashed lines denote the percent cover level at which lobster presence is predicted at higher proportions determined by CART analysis (day, cut 1: > 55% boulder and cut 2: > 22.5% *Plocamium*; night, cut 1: > 25% *Plocamium*).

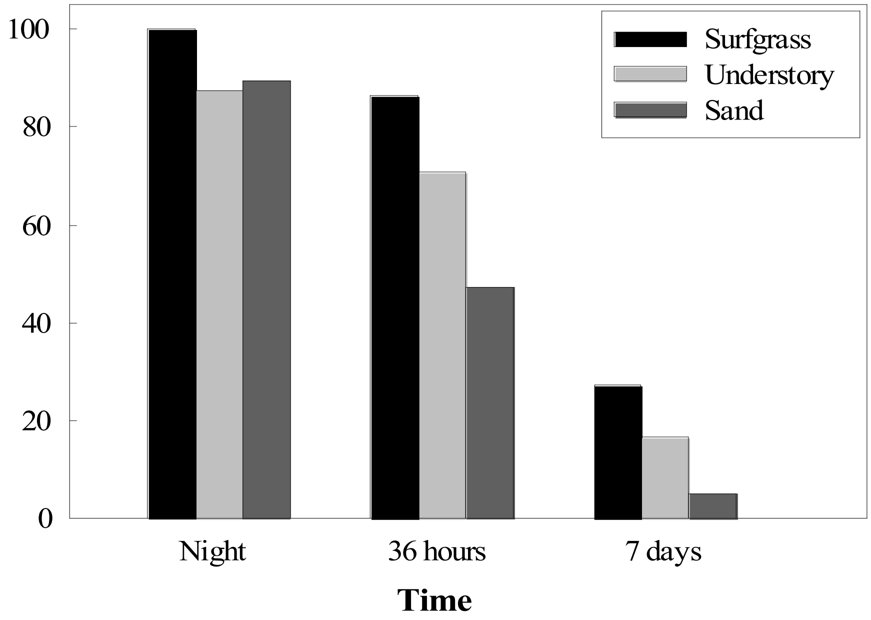

Figure 7. Lobster relative survival rates in different habitats (surfgrass, understory, sand) over time (overnight, 36 hours, and 7 days).

effect of habitat and lobster size on relative survival rates (Table 12). Finally, after 7 d of exposure to predators, only 17% of lobsters remained alive. There were too few juveniles and adults remaining alive (6 lobsters and 5 lobsters, respectively) to include lobster size in the analysis. We therefore pooled juvenile and adult lobsters and found no difference in relative survival among habitat types (G-test: df = 2, G = 4.3, P = 0.12; Figure 7).

Table 12. (A) G-Test Results for the Effect of Habitat and Lobster Size on Lobster Survival After 36 Hours, and (B) Pearson's Chi Square Results for Effect of Habitat After 36 Hours of Tethering Experiments Within and Outside of the LJER

	Source	df	Value	P
(A)	Habitat	2	6.05	0.04
	Size	1	0.89	0.34
	Habitat*size	2	2.70	0.26
(B)	Sand vs. understory	1	2.4426	0.12
	Surfgrass vs. understory	1	1.6272	0.20
	Sand vs. surfgrass	1	7.1595	<0.01

DISCUSSION

Optimal MPA design depends on having information on several ecological characteristics of target species. Despite their economic and ecological importance, prior to this study there was limited information available about California spiny lobsters to make educated management decisions. In this study we investigated three factors that can greatly influence the effectiveness of an MPA for mobile benthic species: (1) movement behavior, (2) habitat associations, and (3) habitat-specific survival rates. Our results suggest that California spiny lobsters in and around a small marine reserve in southern California exhibit high site fidelity with relatively small home ranges. *P. interruptus* was highly associated with boulder substrate for refuge during the day, but was strongly associated with *Plocamium* at night. Overnight survival rates were high, even in sandy plains, and surfgrass served to protect spiny lobsters from diurnal predators. We therefore predict that California spiny lobsters likely will benefit even from relatively small MPAs, provided they include high amounts of suitable habitat, particularly boulders, *Plocamium*, and surfgrass.

LOBSTER MOVEMENT

Our short-term and long-term tracking results suggest that California spiny lobsters have a small home range that is strongly influenced by habitat. Though California spiny lobsters are known to move into shallower water at night to forage (e.g., from kelp forest to shallow surfgrass habitat: Robles et al. 1990, Barsky 2001) lobsters in an around the LJER instead moved short distances within kelp, boulder and understory habitat and homed back to areas around their starting shelters. Our home range estimates for California spiny lobsters (maximum of 0.57 km^2) were substantially smaller than values suggested for some other Palinurid species, such as *J. edwardsii* at various sites in New Zealand, in which lobster home ranges encompassed linear distances of 3.1 – 5 km within one year (Annala 1981, McKoy 1983, Annala and Bycroft 1993, Kelly 2001). A tag and recapture study in the Mediterranean Sea for a period of 10 years found that ca. 61% of *P. elephas* remained within 2 km per year of the initial release site (Follesa et al. 2009). In contrast, the Australian spiny lobster *P. versicolor* moved only ca. 500 m per year from release sites (Frisch 2007).

Homing behavior was evident for lobsters tracked over several nights as well as for lobsters passively tracked for months, as they generally traveled to similar subsets of receivers every month. Because lobsters homed to similar areas every month, there was no effect of detection time of individual lobsters on the home range area with long-term tracking (also suggested for *J. edwardsii* in Kelly and MacDiarmid 2003). Homing behavior is common in other Palinurid species (*P. cygnus*: Chittleborough 1974; *P. argus*: Herrnkind et al. 1975; *J. edwardsii*: Kelly and MacDiarmid 2003; *P. versicolor*: Frisch 2007; *P. elephas*: Follesa et al. 2009) and may serve to optimize lobster ability to locate prey, avoid predators, and return to high-quality shelters (Herrnkind 1980). Other benthic organisms, such as echinoderms, also exhibit homing behavior to more easily find refuge when the level of predation is high and the availability of shelter is limited (Cook 1979, Nelson and Vance 1979).

Seasonal migrations from shallow (summer) to deeper water (winter) also are commonly observed in lobsters (Hernnkind 1980, MacDiarmid 1991, Kelly et al. 1999). Though our study was not intended to determine whether California spiny lobsters make seasonal migrations, we did not observe long-term movement patterns consistent with the idea that lobsters move to deeper offshore waters in the fall and back to shallower water in the spring.

Lobsters moved farther and had larger home ranges outside of the MPA than inside of the MPA during short-term tracking. As we worked in and around only one MPA, we are not able to suggest if this trend will be evident for MPAs in general. However, two factors that may strongly influence organismal movement (predator density and habitat availability) vary between the LJER and adjacent kelp forest habitat. Specifically, the LJER has higher densities of large fish predators (Parnell et al. 2005, Loflen 2007), and dense clustering of a variety of habitats as compared to outside the LJER (Parnell et al. 2005, 2007). Though it is possible that lobsters move shorter distances within the reserve because predators are abundant there, we observed low predation rates even on small California spiny lobsters tethered without habitat cover at night, and we suggest that lobsters simply did not need to move long distances to access resources inside of the reserve (see also *Habitat associations* below). It is common for Palinurids that reside in reef habitat with extensive shelter and food to exhibit homing behavior and move only a few kilometers or less over several months, while nomadic movement patterns occur when resources are more widely dispersed (Herrnkind 1980). This idea is supported by the difference in movement behavior witnessed with California spiny lobsters in the nearby Point Loma kelp forest (ca. 15 km south of the LJER), where acoustically tagged lobsters exhibited more linear, nomadic movements from deeper kelp forest habitat to shallower surfgrass habitat overnight, which is most likely a result of more isolated resources in that location (Hovel and Lowe 2007).

We found a positive correlation between home range area and lobster size for female lobsters, but not for male lobsters, over a period of one week. Female Palinurids often move greater distances than do males (MacDiarmid 1989, Kelly 2001, Bertelsen and Hornbeck 2009; but see Frisch 2007), and may become increasingly active when brooding, particularly before larvae are released (MacDiarmid 1989). Results from our long-term tracking, however, suggested a weak inverse correlation between estimated home range area and female body size within the LJER. We observed no evidence for an influence of brooding cycles on patterns of female lobster movement, but a definitive test of this would require fine-scale monitoring over larger spatial and temporal scales than we included in our study. Though we did not monitor movements of juvenile lobsters (i.e. < 7.0 cm CL), which often move farther than adults (e.g. *P. cygnus*: Phillips 1983, *P. argus*: Davis and Dodrill 1989, *P. gilchristi*: Groeneveld and Branch 2002, *P. delagoae*: Cockcroft et al. 1995; *J. edwardsii*: Kelly and MacDiarmid 2003), we were able to track adult lobsters over a broad range of sizes (7.0 cm to 15.1 cm CL). Studies on other species using similar adult size ranges have not found significant effects of size on movement patterns, including *P. argus* (Bertelsen and Hornbeck 2009) and *P. elephas* (Follesa et al. 2009).

Our results suggest that relatively small reserves should be effective at protecting California spiny lobsters from fishing mortality, provided reserves encompass suitable lobster habitat and spillover rates are low (Kelly et al. 2002, Goni et al. 2006, Parnell et al. 2007). The maximum home range size in our study was an estimated MCP of 575,488 m^2, which is only 27% of the size of the LJER, and this represented ca. two months of movement. Although the size of the LJER is much larger than lobster home range areas, the MPA encompasses only ~0.8% of the kelp forest habitat and ~11% of the boulder-reef habitat in the La Jolla area (Parnell et al. 2005), and lobsters therefore may cross the MPA boundary to access more habitat. A swath of contiguous, high rugosity boulder and kelp habitat crosses the present LJER boundary and connects the LJER with adjacent, heavily fished La Jolla kelp forest habitat (Figure 1, p. 6). Spillover rates for fishes (Collinge 1996, Bartholomew et al. 2008) and lobsters (Freeman et al. 2009) increase when MPA boundaries intersect contiguous habitat. Our long-term tracking data indicate that California spiny lobsters used the contiguous corridor to cross the reserve boundary (Figure 5, p. 20), and therefore, reserve effectiveness could be enhanced if the boundary was extended westward to the edge of boulder habitat. Six out of 21 lobsters that were released inside of the LJER during both short-term and long-term monitoring definitively spilled over the reserve boundary. Providing spillover rates are low, an MPA can still be effective in protecting the majority of the lobster population while also enhancing local fisheries (Freeman et al. 2009).

LOBSTER-HABITAT ASSOCIATIONS

Nocturnally active species such as spiny lobsters may associate with and prefer different habitats during the day (when taking refuge from predators) vs. during the night (when foraging or switching shelters or home ranges). While it is well documented that lobsters often associate with rocky structures while stationary during the day (see review in Herrnkind 1980), the factors that influence lobster habitat selection when lobsters are mobile at night are less well known. Vegetation cover, however, may influence lobster habitat selection, even for species that commonly are associated with rocky reefs. Juvenile *Homarus americanus* may obtain refuge from predators under kelp (*Laminaria* spp.: Bologna and Steneck 1993), and California spiny lobsters commonly are found in surfgrass (Barsky 2001, Hovel and Lowe 2007) and in eelgrass *Zostera marina* habitat (KWA and KAH, personal observation) as well as under canopies of kelp (see also Parnell et al. 2005). Parnell et al. (2007) suggested that California spiny lobsters associate with reefs and algae such as *Eisenia* *arboria, Cystoseira osmundacea,* red turf algae, and articulated coralline algae during the day. Such associations are evident with other species, including *J. edwardsii* that associate with an understory alga, *Ecklonia radiata* (MacDiarmid et al. 1991), and *P. argus* which prefer shelters near seagrass *Thalassia testudinum* (Sosa-Cordero et al. 1998, Acosta 1999).

Not unexpectedly, we found that lobsters were most likely to be found within quadrats with high boulder cover during the day, and we frequently observed lobsters within deep crevices or overhangs formed by boulders. We did not find any significant relationships between algae and lobster presence during the day, although there was a trend for a higher proportion of lobsters sheltering near low-lying *Plocamium* algae. In contrast, California spiny lobster abundance in the nearby Point Loma kelp forest was most strongly correlated with abundance of understory algae such as *P. californica*, although this varied seasonally (Mai and Hovel 2007). Strong associations with vegetated habitats, including seagrasses (e.g. eelgrass *Zostera marina* and surfgrass *Phyllospadix* spp.) and algal clumps, are commonly observed for juvenile lobsters (Butler et al. 1997, Sosa-Cordero et al. 1998, Acosta 1999). Though nearly all studies on lobster-habitat associations are conducted during the day, when most species are inactive, Karnofsky et al. (1989) found that American lobsters *Homarus americanus* spent much of the night combing through various species of algae, potentially searching for small invertebrate prey. We found that the odds of finding California spiny lobsters at night increased with cover of the understory red alga *Plocamium cartilagineum*, on which we frequently observed them foraging on small invertebrates, and in laboratory experiments juvenile California spiny lobsters preferred *Plocamium* over surfgrass*, Halidrys dioica,* and other red algae (Parker 1972, Engle 1979). Juveniles of the California sea hare *Aplysia californica* are common on *Plocamium* and can be consumed by spiny lobsters (Pennings 1991), but whether sea hares are important to spiny lobster diets has yet to be explored.

The accessibility of preferred nocturnal habitat may help explain the relatively small home ranges we observed for *P. interruptus*. *Plocamium* is a perennial red alga ranging in height from 4 – 25 cm and is found on a variety of substrata in intertidal and subtidal zones (Mondragon and Mondragon 2003). Most lobsters we observed needed to travel no more than several meters from shelter to access *Plocamium*, which was abundant resource within our study site, and some lobsters occupied shelters close enough to *Plocamium* to feed during the day (KWA *personal observation*). It is important to note, however, that our dive surveys were conducted during the summer, and therefore we did not quantify whether lobsters associate with the same types of habitats throughout the year.

LOBSTER SURVIVAL

Lobster relative survival was extremely high across all habitat types over the course of a single night, both for juveniles and for adults, which was surprising given relatively high predator densities within the LJER (Parnell et al. 2005, Loflen 2007). Nocturnal predators of California spiny lobsters may include giant black sea bass (*Stereolepis gigas*), California moray (*Gymnothorax mordax*), two spotted octopus (*Octopus bimaculatus*), California scorpion fish (*Scorpaena guttata*), cabezon (*Scorpaenichthys marmoratus*), or leopard sharks (*Triakis semifasciata)* (Allen 1916, Lindberg 1955). Although densities of octopus and cabezon have decreased over time within the LJER (Parnell et al. 2005), we commonly observed other predators, such as *S. gigas*, within the MPA (also see Loflen 2007). The LJER also houses high densities of diurnal predators such as the California sheephead *S. pulcher*, which are rarer in Pt. Loma (Parnell et al. 2005, Loflen 2007). Lobster relative survival was relatively low in the LJER after 7 d (17% of all lobsters survived), even within protective surfgrass habitat. In contrast, lobsters tethered in Pt. Loma, a site with fewer large, predatory fish (Loflen 2007) for 7 d had a 61% probability of survival when tethered under algae (*L. farlowii* and *P. californica)* and a 48% chance of survival when tethered in the open (Mai and Hovel 2007).

Though we were unable to determine the relative effects of the total time of exposure to predators vs. the inclusion of daylight in reducing relative survival as exposure time increased from a single night to 36 h and 7 d, our results suggest that diurnal predators are a much larger threat to lobsters than are nocturnal predators, but that lobsters can achieve some refuge from predators in surfgrass habitat during the day. Seagrasses are primary nursery habitats in shallow coastal waters worldwide where they provide refuge to a variety of fishes and invertebrates (Heck and Crowder 1991, Beck et al. 2001) including juvenile California spiny lobsters that selectively settle in surfgrass habitat (Barsky 2001). Understory algae also may provide refuge for lobsters (Mai and Hovel 2007), but the trend for higher relative survival in understory algae vs. sand was not significant in our study. Surfgrass is generally denser than understory habitat, and is found in shallow water, which may make it more difficult for visually oriented predators to find prey and may result in less visitation by large predators than in the kelp forest (Parnell et al. 2005). We found more lobsters outside of shelter during the day in surfgrass habitat vs. kelp forest habitat. Similarly, California spiny lobsters are found outside of shelter during the day and the night in estuarine habitats where large predators are rare (Cheng and Hovel *in press*), and significantly more lobsters were found outside of shelter during the day in Pt. Loma (low predator abundance) than in La Jolla (high predator abundance; Loflen 2007). Since California spiny lobsters prey on invertebrates within seagrass habitats (Robles et al. 1990, Barsky 2001, Cheng and Hovel *in press*), lobsters that utilize surfgrass as a refuge during the day may have a foraging advantage over lobsters that shelter within boulders.

CONCLUSIONS

Though patterns of dispersal and recruitment often are incorporated into MPA design (when known), movement behavior, habitat use, and predator-prey interactions play key roles in population dynamics and therefore in the effectiveness of MPAs, which may not succeed if they are designed in the absence of these pieces of information (e.g. Martell et al. 2000, Kelly 2001). MPAs should be larger than home ranges of target organisms, consist of a variety of habitat types (Simberloff and Abele 1982, CDFG unpublished data), and should consider how predator-prey interactions likely will change after an MPA is established due to shifts in predator and prey abundance and species composition (Shears and Babcock 2002, Diaz et al. 2005). As a primary fishery species in the southern California region, California spiny lobsters are one of the principle species that may benefit from the implementation of an MPA network that is being established statewide in California (CDFG unpublished data). Our results suggest that California spiny lobsters have relatively small home ranges, but that movement patterns within a MPA will most likely depend on habitat availability, and that habitats deemed important for lobsters differ from day to night. The most effective MPAs for California spiny lobsters therefore may be those that include a variety of habitats, including rocky reef, understory algae, and surfgrass habitat. MPAs can be relatively small and still encompass lobster home ranges. Thus, simply creating large MPAs, without regard to habitat availability, will not be of much benefit to lobsters.

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APPENDIX

TESTING FOR AUTOCORRELATION AMONG HABITAT TRANSECTS

Table 13. All Transects Were Tested for Autocorrelation Among Boulder and Plocamium Habitat (rCrit = 0.666). Autocorrelation Was Significant for Two Transects in Boulder Habitat. Removal of These Two Autocorrelated Transects from the Forward Stepwise Logistic Regression Had No Affect on the Outcome of the Test, and Therefore We Determined that Our Results Were Not an Artifact of Autocorrelation. (*) Denotes Significance at Alpha ≤ 0.05

Transect	Boulder (r)	*Plocamium* (r)
1	0.495	0
2	-0.192	-0.348
3	0.468	0.085
4	-0.116	0.473
5	0.047	0.037
6	-0.318	-0.43
7	0.232	0.664
8	0.678 *	0.603
9	0.117	0.619
10	-0.254	0.572
11	0.495	0.18
12	0.682 *	-0.136
13	0.142	-0.09
14	-0.116	0.473
15	0.035	-0.253
16	-0.318	-0.43
17	0.246	0.664
18	0.051	0.426
19	0.117	0.619
20	-0.254	0.572

ABSTRACT OF THE THESIS

California Spiny Lobster (*Panulirus interruptus*) Movement Behavior and Habitat Use: Implications for the Effectiveness of Marine Protected Areas

by

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Marine protected areas (MPAs) are widely used to rebuild depleted populations for exploited species, but their effectiveness hinges on adequate knowledge of the factors dictating population dynamics for target organisms. Estimates of connectivity via larval dispersal often are included in MPA design, but movement patterns, habitat associations, and habitat-specific survival rates of juveniles and adults, which often are unknown, also will influence MPA effectiveness. California spiny lobsters (*Panulirus interruptus* Randall) are the target of intense commercial and recreational fishing in southern California, but we lack basic information about home range and habitat use of lobsters to determine if MPAs planned for the region will enhance abundance. Working within and outside of the La Jolla Ecological Reserve (LJER) in southern California, we (i) quantified lobster movement patterns and home ranges over short (nightly – weekly) and long (1 – 14 months) time scales using acoustic telemetry, (ii) surveyed lobsters to determine day and night habitat associations, and (iii) tethered lobsters to assess habitat-specific predation risk. Lobsters exhibited high site fidelity, proclivities for homing, and small home ranges (geometric mean of 651 m^2 and 5,912 m^2 per week based on 50% and 95% Kernel Utilization Distributions (KUDs), respectively) that encompassed only a fraction of a small MPA, even over periods of several months. Lobsters were strongly associated with rocky habitat during the day (when in shelters) but were associated with the red algae *Plocamium cartilagineum* at night (when feeding). Lobster relative survival rates were high across vegetated and unvegetated habitats at night, but lobsters were protected from predators by surfgrass (*Phyllopsadix torreyi*) habitat during the day. Our results highlight the need to consider how movement patterns vary over short and long time scales, and how patterns of habitat use may vary from day to night for nocturnally active species such as spiny lobsters when planning MPAs.