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Three-dimensional resource partitioning between American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) in a subtidal kelp forest

R.J. David Wells [a], R.S. Steneck [b], A.T. Palma [c,*]

[a] Department of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77551, USA
[b] University of Maine, Darling Marine Center, 193 Clark's Cove Road Walpole, ME 04573, USA
[c] Departamento de Ecología, Pontificia Universidad Católica de Chile and Center for Advanced Studies in Ecology and Biodiversity (CASEB), Alameda 340 Casilla 114-D, Santiago, Chile

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ABSTRACT

The American lobster (*Homarus americanus*) and the rock crab (*Cancer irroratus*) commonly coexist, and at high densities, compete for space in subtidal kelp forests in the Gulf of Maine. Competition between the two species was examined in field surveys using visual SCUBA quadrats and complementary laboratory experiments with both live and artificial kelp. Field surveys showed significantly higher crab densities ($0.50/m^2 \pm 0.08$ SE) found up the kelp versus on the ground ($0.22/m^2 \pm 0.04$ SE) when lobsters were present ($P = 0.002$). In contrast, crab densities were significantly higher on the ground ($0.44/m^2 \pm 0.07$ SE) as opposed to up the kelp ($0.23/m^2 \pm 0.06$ SE) when lobsters were absent ($P = 0.023$). However, the interaction between survey location*date was significant in five of the eight surveys, suggesting this pattern may not be ubiquitous in all subtidal kelp locations within our study region. Average size of crabs up the kelp or on the ground was not different when lobsters were present or absent ($P > 0.05$), and no size correlation was found between lobsters and crabs, irrespective of crab position. Experimental trials in the laboratory confirmed field surveys regardless of the order crabs and lobsters were added into the tank, or the use of live versus artificial kelp, and significant differences were observed in five of the six 5-day experimental trials. Our results suggest that when shelter availability may be limited, kelp could serve as an alternative habitat for rock crabs, perhaps to minimize competition between the two most abundant decapods in the shallow subtidal zone of New England.

1. Introduction

The American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) are two decapod species coexisting throughout the Gulf of Maine (Richards et al., 1983; Steneck et al., 2002). Both species occupy similar habitats and have relatively like diets (Richards, 1992; Moody and Steneck, 1993); however, previous studies have shown that lobsters are the dominant competitor (Cobb et al., 1986; Hudon and Lamarche, 1989). As a result of this negative interaction, rock crabs are often driven to use alternative habitats (Wang, 1982; Cobb et al., 1986) and preyed upon by lobsters (Hudon and Lamarche, 1989; Gendron et al., 2001; Sainte-Marie and Chabot, 2002). Coexistence of lobsters and other decapod species, such as the Jonah crab (*Cancer borealis*), has been investigated by others in the northwest Atlantic (Richards and Cobb, 1986; Richards, 1992). Specifically, Richards and Cobb (1986) found that Jonah crabs also utilize alternative shelters rather than compete directly with lobsters. As such, subordinate species (i.e. crabs) must adopt methods for niche segregation in order to coexist in areas occupied by lobsters.

Rock crabs have managed to use a suite of mechanisms to reduce the potential risk of predation. Palma et al. (1999) found that rock crabs settle indiscriminately (like many other brachyurans (i.e. Palma et al., 2006; Pardo et al., 2007)) among various habitats and suffer high post-settlement mortality compared to lobsters that preferentially settle in rocky, cobble bottoms. As such, early post-settled stages of rock crabs display color polymorphism rendering them inconspicuous to visual predators (Palma and Steneck, 2001). Further, coexistence of both rock crabs and lobsters is possible due to the differential utilization of food resources and substrate type, particularly due to the flexibility of alternative resources utilized by the rock crab (Hudon and Lamarche, 1989). Behavioral modifications of crabs may also minimize predation by and competition with lobsters, such as daytime activity of Jonah crabs and large rock crabs in contrast with peak nocturnal activity periods of lobsters (Novak, 2004). An alternative, and possibly overlooked mechanism, is the use of unconventional substrate types such as kelp fronds by rock crabs.

Shallow subtidal areas in the Gulf of Maine consist of rock, pebble, and sand habitats with areas of high kelp abundance. Two genera, *Laminaria* spp. and *Agarum* spp., are commonly found along subtidal areas of Maine (Steneck et al., 2002) and offer an additional form of structural complexity to the ecosystem. Because both lobsters and rock crabs have been shown to prefer areas with structural

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* Corresponding author. Tel.: +56 2 686 2971; fax: +56 2 354 2621.
E-mail address: apalma@bio.puc.cl (A.T. Palma).

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complexity (Palma et al., 1998, 1999), the kelp canopy may represent a mechanism by which both species can co-occupy a given unit of area. Hudon and Lamarche (1989) found high densities of both lobsters and rock crabs over boulders colonized by macroalgae and suggested that this complex habitat may result in a high carrying capacity. Further, intertidal and shallow subtidal areas of New England consisting of rocky ledges covered in algae of *Chondrus crispus* and *Mastocarpus stellatus* harbored large numbers of both decapods (Jones and Shulman, 2008). Similar findings were observed in soft-bottom habitats where lobsters occupied crevices or rocks while crabs burrowed in the sediment (Cobb, 1971; Aiken, 1980; Hudon, 1987). These alternative habitats (i.e. macroalgae, sediment burrows) may function as microhabitats and play an important role to the survival of subordinate species, such as the rock crab.

The objective of this study was to investigate three-dimensional resource partitioning of lobsters and rock crabs in subtidal kelp beds in the Gulf of Maine by considering the hypothesis that kelp serves as an alternative habitat for the smaller and subordinate rock crab in the presence of the competitively dominant American lobster. We tested this hypothesis through field surveys of rock crabs on or under kelp fronds when lobsters were present and absent. In addition, we performed laboratory-based experiments with and without lobsters using both live and artificial kelp to evaluate whether field based observations could be confirmed in the laboratory. Ultimately, our goal was to examine whether kelp may serve as an alternative habitat that rock crabs may utilize in the presence of lobsters, thereby providing a likely mechanism facilitating the coexistence of these abundant decapod species.

2. Materials and methods

2.1. Field surveys

Field studies were conducted during visual SCUBA surveys at four locations along the central coast of Maine (USA) from July through September of 1998 (Fig. 1). At each location, 1 m^2 quadrats were haphazardly placed over the substrate at a depth range between 4 and 12 m. Quadrats were located at least 10 m apart from one another to minimize the possibility of re-counting individuals in multiple quadrats. Initially at each quadrat, the percent kelp cover (percent total area of quadrat) and depth (m) were recorded. Within each quadrat, movable rocks were overturned and soft-sediment (i.e. sand) was carefully raked by hand to identify any hidden or buried individuals. In addition, the number of lobsters and crabs was recorded and the location of each was categorized as either on the ground or up the kelp. All lobsters and crabs were measured to the nearest mm carapace length (CL) and carapace width (CW), respectively, and released.

2.2. Laboratory experiments

Laboratory experiments consisted of two types: the first experimental trials used live kelp of both *Laminaria saccharina* and *Agarum cribosum*, and the second experimental trials used artificial kelp. Artificial kelp was used to test whether crabs were moving up the kelp for purposes other than alternative habitat use, such as feeding on the kelp fronds or associated biota. A total of six 5-day experimental trials

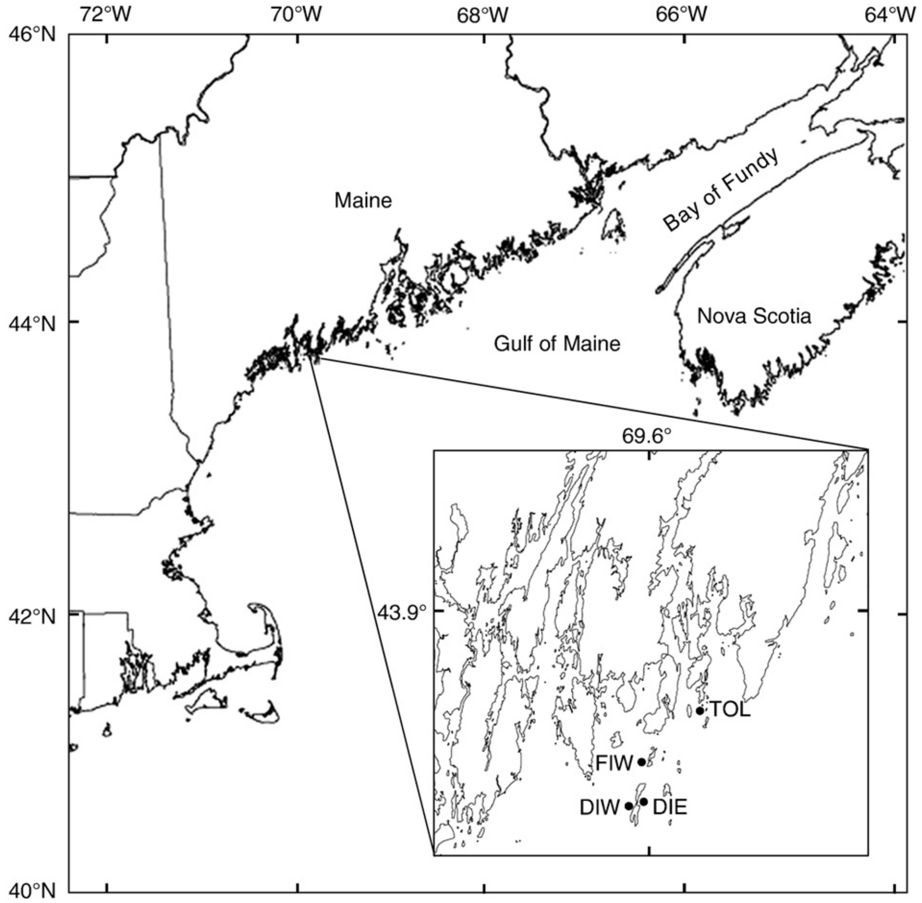

Fig. 1. Locations of the four field survey stations along the central coast of Maine. Survey stations include; Thread of Life (TOL), Fisherman's Island West (FIW), Damariscove Island West (DIW), and Damariscove Island East (DIE).

were conducted; four trials using live kelp and two with artificial kelp. In addition, two different orders by which both species were added to or removed from the tank were performed to examine if behavioral differences contributed to results. During the three trials (two with live kelp and one with artificial kelp), only crabs were present during days 1 and 5, while both crabs and lobsters were together for days 2–4. For the other three trials (two with live kelp and one with artificial kelp), both crabs and lobsters were added simultaneously and monitored for days 1–4, then lobsters were removed leaving only crabs on day 5.

For all experiments we attempted to mimic the field density of lobsters, crabs, and kelp. Densities of both lobsters and crabs were determined based upon our July field surveys, found in Palma et al. (1999). Thus, a total of six lobsters and eight crabs were initially used for each experimental trial. Care was also taken to select the average size of each species for experimental trials based upon field surveys. Specifically, selected sizes ranged between the 25th and 75th percentiles from field surveys: lobsters (38 to 70 mm CL) and crabs (26 to 40 mm CW), similar to the respective sizes of large lobsters (31 to 92 mm CL) and medium crabs (26 to 37 mm CW) found coexisting in the Gulf of St Lawrence (Hudon and Lamarche, 1989). Lobsters and crabs were placed in separate holding tanks immediately following field collections for a 24 h period and fed mussels (*Mytilus trossulus*) before experimental trials. Prior to experiments, lobsters and crabs were measured to the nearest mm CL and CW, respectively. A small ($1*1$ cm) orange tape was glued to the crab carapace to aid in visual identification due to difficulty in identifying crabs when on or under the kelp canopy. All species (lobsters, crabs, kelp) were replaced after each experimental trial.

Visual observations of crabs and lobsters were recorded every 2 h over a 16 h period (8 observations per day), totaling 40 observations per experimental trial. Time of day, when observations started and ended varied; however, observations were performed during both daylight and night time hours during each day, but no time-related differences in the percent number of crabs up the kelp were detected (t-test, $P=0.943$). Observations consisted of lobsters and crabs categorized as either on the tank bottom (on ground) or up the kelp. Dimensions of the square experimental tank were 3×3 m and 157 cm height with a constant seawater flow rate of 15 l/min, and a 2.3 cm diameter PVC pipe drained the tank to allow seawater to fill the tank to a height of 81 cm. Tank setup contained kelp in half the tank, while the other half was bare. Artificial kelp was made from black 6 Mil polyethylene sheeting and half was punched with holes to mimic the morphology and texture of *A. cribosum*. Kelp species (*L. saccharina* and *A. cribosum*) did not affect the number of crabs observed up the kelp when both lobsters and crabs were present (t-test, $P=0.075$).

2.3. Data analysis

T-tests were used to assess for differences in densities and sizes of crabs observed on the ground versus up the kelp, both when lobsters were present and when lobsters were absent from field quadrats. Linear regressions were used to investigate the relationship between densities of lobsters and crabs both up the kelp and on the ground. A logistic regression was used to predict the presence or absence of crabs up the kelp using several predictor variables including the presence of lobsters, percent kelp in each quadrat, and depth of quadrat surveys. Spearman rank order correlation coefficients were used to investigate the association of lobster size to crab size. Laboratory experimental trials were analyzed using repeated measures analysis of variance (ANOVA) models. For each 5-day trial, the average percent of crabs found up the kelp (by day) was used as the dependent variable, with day as the repeated measure variable. The percent of crabs was used as the dependent variable because predation by lobsters on crabs occurred in several trials. Experimental trials were analyzed individually ($n=8$ observations per trial) because of equality of variance (sphericity) violations when all trials were combined. *A posteriori* differences among means were detected with Tukey's honestly significant difference (HSD) test. The equal variance assumption was assessed by examining plots of residuals versus predicted values, and normality was tested with a Shapiro–Wilk test for all tests. Statistical significance was determined at $P\leq0.05$ for all analyses using SigmaStat 3.1 (SYSTAT, 2004) and SAS 9.1 (SAS Institute Inc., 2006).

3. Results

3.1. Field surveys

A total of 8 field surveys were performed over the course of the study. These included 4 surveys at Thread of Life (TOL), 2 at Damariscove Island West (DIW), 1 at Damariscove Island East (DIE), and 1 at Fisherman's Island West (FIW) (Table 1, Fig. 1). Results of field surveys indicate that when lobsters were present in quadrats (59% of total field surveys), crabs were more frequently found up the kelp (33% of quadrats) than on the ground (18% of quadrats) (Fig. 2). In contrast, when lobsters were absent (41% of total field surveys), crabs were found up the kelp in 17% of the quadrats and on the ground in 34% of the quadrats (Fig. 2). Crabs were absent in the remaining quadrats. A significant difference was found when lobsters were present, with higher crab densities of $0.50/\mathrm{m}^2$ (±0.08 standard error (SE)) found up the kelp versus on the ground ($0.22/\mathrm{m}^2\pm0.04$ SE) ($P=0.002$, power $=0.837$). In contrast, crab densities were significantly higher on the ground ($0.44/\mathrm{m}^2\pm0.07$ SE) versus up the kelp ($0.23/\mathrm{m}^2\pm0.06$ SE) when lobsters were absent from field quadrats ($P=0.023$, power $=0.528$). Specific survey results from each location*date show that when lobsters were present, crab densities were higher up the kelp than on the ground during all 8 field surveys; however, only 5 location*date surveys were significant (Table 1). Although relatively weak, a positive relationship was found between densities of lobsters and densities of crabs up the kelp ($P=0.013$) ($\#\,\text{crabs}=0.258+[\#\,\text{lobsters}*0.166]$, $r^2=0.270$). In contrast, a negative relationship between densities of lobsters and crabs was observed on the ground ($P=0.006$) ($\#\,\text{crabs}=0.397-[\#\,\text{lobsters}*0.126]$, $r^2=0.330$). Further, results from the logistic regression indicate that the presence of lobsters had a significant effect on the probability of observing crabs up the kelp ($P=0.008$), while both percent kelp ($P=0.206$) and depth ($P=0.068$) were non-significant.

Average size of crabs was similar regardless of location up the kelp or on the ground during field surveys (Table 2) ($P=0.152$). Further, no difference was found between crab sizes up the kelp (33.13 ± 1.71 mm CW) or on the ground (38.82 ± 4.04 mm CW), when lobsters were present ($P=0.136$). Moreover, when lobsters were present, no correlation was found between sizes of lobsters and crabs up the kelp

Table 1
Summary of field survey sites, dates of surveys, total number of quadrats performed, densities of crabs observed up the kelp both when lobsters were present and absent, and respective statistical results from *t*-tests.

Site	Survey date	Number of quadrats	Crab density up kelp (number/m^2)		*P*-value	Power
			Lobsters present	Lobsters absent		
TOL	July 14	38	0.57 (±0.20)	0.24 (±0.12)	0.024*	0.541
TOL	July 17	17	0.33 (±0.19)	0.20 (±0.20)	0.684	0.050
TOL	August 15	53	0.36 (±0.12)	0.08 (±0.05)	0.045*	0.407
TOL	August 16	63	0.55 (±0.15)	0.13 (±0.08)	0.018*	0.582
DIW	July 24	16	0.58 (±0.26)	0.25 (±0.25)	0.499	0.050
DIW	August 21	13	0.75 (±0.49)	0.20 (±0.20)	0.415	0.050
DIE	September 12	15	0.90 (±0.23)	0.00 (±0.00)	0.030*	0.524
FIW	September 12	15	0.92 (±0.42)	0.00 (±0.00)	0.024*	0.574

* Significance was determined at the $P\leq0.05$ level.

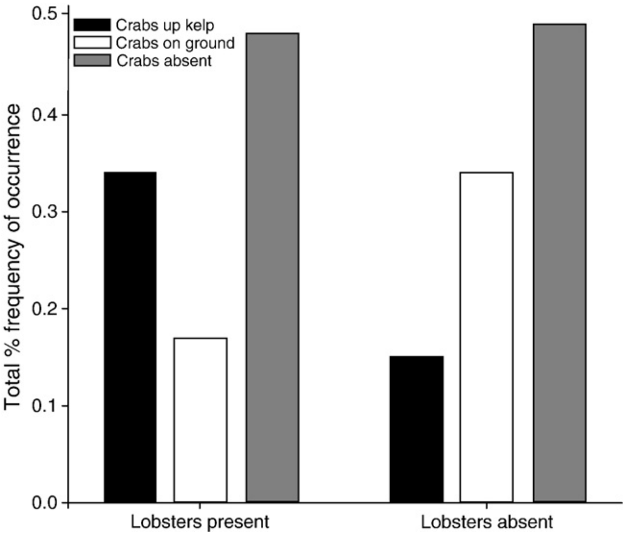

Fig. 2. Total percent frequency of occurrence of crabs up the kelp, on the ground, or absent from quadrats with respect to the presence or absence of lobsters from all field surveys combined.

(correlation coefficient = 0.219, $P = 0.092$), suggesting that there was not a particular size range of lobsters driving the observed patterns. In addition, no significant size correlation was found between the two species when simultaneously present on the ground (correlation coefficient = 0.077, $P = 0.665$).

3.2. Laboratory experiments

Laboratory experiments supported field observations (Fig. 3). Irrespective of the order in which lobsters were added into or removed from the tank, or the use of live versus artificial kelp, crabs were more frequently observed up the kelp when lobsters were present. In two of the six laboratory trials, the average percent number of crabs up the kelp exceeded 80% when lobsters were present, followed by a subsequent decrease (<40% up kelp) following lobster removal (Fig. 3). Results of both experimental trials using live kelp with only crabs on day 1 showed significant differences (trial 1: ANOVA, $P<0.001$; trial 2: ANOVA, $P<0.001$) (Fig. 3A). Specifically, post-hoc comparisons of both trials indicated the percent of crabs up the kelp was significantly less during day 1 (lobsters absent) versus days 2–4 (lobsters present) (all comparisons $P<0.05$); however, only during trial 2 did the removal of lobsters (day 5) have a significant effect on the percent of crabs up the kelp ($P<0.05$). Experimental trials using live kelp with both crabs and lobsters added to the tank on day 1, followed by lobster removal on day 5, showed a decrease in the percent of crabs up the kelp following lobster removal; however, a significant difference was only found for trial 2 (ANOVA, $P<0.001$) (Fig. 3B). Using artificial kelp, a significant effect was found during both trials regardless of the order in which lobsters and crabs were added or removed (trial 1: ANOVA, $P<0.001$; trial 2: ANOVA, $P<0.001$) (Fig. 3C). Post-hoc comparisons indicated that during trial 1, the percent of crabs up the kelp was significantly higher during days 3–4 when lobsters were present ($P<0.05$), but no difference was

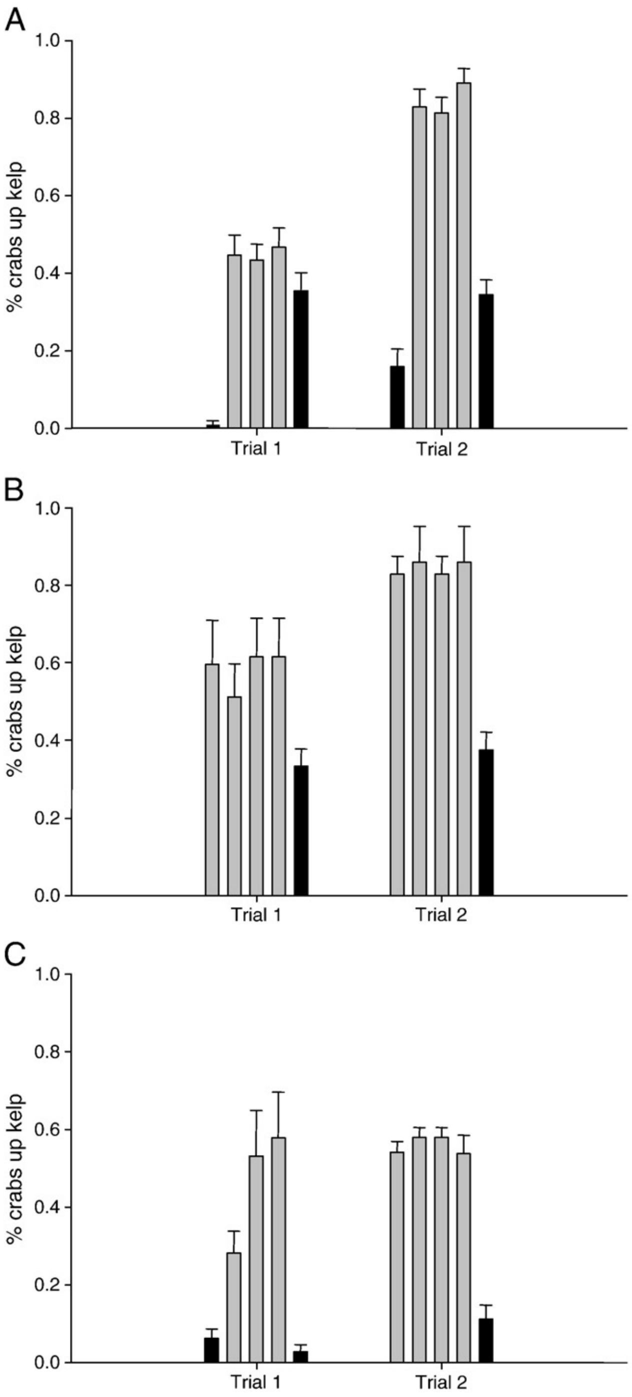

Fig. 3. Average percent number of crabs observed up the kelp with respect to the presence (gray bars) or absence (black bars) of lobsters. Each experimental trial lasted a 5-day period and each bar represents the average percent number of crabs observed up the kelp for one day (24 h period). Experiments included A) using live kelp: only crabs (day 1), both crabs and lobsters (days 2–4), only crabs (day 5); B) using live kelp: both crabs and lobsters (days 1–4), only crabs (day 5); C) using artificial kelp: one trial of both A (trial 1) and B (trial 2).

Table 2
Average size of lobsters (mm CL) and crabs (mm CW) from field surveys. Average size of both species is also shown when observed up the kelp and on the ground.

Species	Total number	Number up kelp	Number on ground	Average size (mm CW)	Average size up kelp	Average size on ground
American lobster (*H. americanus*)	185	2	183	53.65 (±1.42)	34.50 (±0.50)	53.86 (±1.43)
Rock crab (*C. irroratus*)	150	79	71	35.81 (±1.40)	33.90 (±1.38)	37.93 (±2.53)

detected during the first day of lobster addition (day 2) ($P>0.05$). In contrast, during both trials, the removal of lobsters (day 5) resulted in a significant decline in the percent of crabs found up the kelp ($P<0.05$).

4. Discussion

Results herein suggest that kelp may provide an alternative habitat for the smaller and subordinate rock crab when in the presence of the competitively dominant American lobster in Gulf of Maine subtidal kelp forests. Alternative habitat use by rock crabs may provide a mechanism by which both species can coexist in a given unit of area where highest population densities of lobsters have been reported (Steneck and Wilson, 2001). Studies have shown that lobsters and crabs preferentially occupy structural shelter over soft substrate; however, crabs are displaced by lobsters when availability of shelter is limiting (Fogarty, 1976; Wang, 1982). Several studies have found that in soft-bottom habitats, where lobsters occupied crevices or rocks, crabs burrowed in the sediment (Cobb, 1971; Aiken, 1980; Hudon, 1987). Further, Hudon and Lamarche (1989) found high densities of both lobsters and rock crabs over boulders colonized by macroalgae and suggested that this added complexity may have contributed to the high densities. Additionally, Richards and Cobb (1986) found that Jonah crabs occupy alternative habitats when in the presence of lobsters in order to avoid direct competition with lobsters over shelter. As such, subtidal kelp forests may favor the coexistence of lobsters and rock crabs by reducing or mediating interspecific competition via three-dimensional space occupancy.

Laboratory experiments corroborated field surveys irrespective of the order in which crabs and lobsters were added into the tank or the use of live versus artificial kelp. It should be noted that laboratory experiments did not contain sand substratum which may have reduced any potential crab burial activities and consequently elevated the number of crabs observed up the kelp. Two specific conclusions can be reached from our laboratory experiments. First, the order in which decapods were added and removed from the experimental tank did not affect results. In all experimental trials, the addition of lobsters following crabs resulted in a significant movement of crabs up the kelp. However, in two of the six trials, the removal of lobsters on day 5 did not significantly impact the movement of crabs down the kelp. Behavioral differences among individuals may be responsible for the slower response time for crabs to move down the kelp following lobster removal and this may have been detected if experimental trials lasted longer (>1 day post-removal) as lobster scent may remain for longer periods of time post-removal. Second, results from experimental trials using artificial kelp showed similar patterns to those observed using live kelp, suggesting that crabs are likely not moving up the kelp for feeding purposes. We expected that if crabs were preying either upon organisms directly on the kelp fronds or in the water column, then crabs would have behaved differently. Given the lack of differences in the numbers of crabs up the kelp, irrespective of kelp species nor live versus artificial kelp, it appears that factors other than kelp type are driving observed patterns.

Movement of crabs up the kelp was likely due to interspecific competition, but difficult to ascertain whether predation by lobsters, limiting shelter or space, or a combination thereof was responsible. Lobster predation experiments by Jones and Shulman (2008) showed that rock crabs were the preferred prey of lobsters and suffered the highest predation rates among all decapods examined (rock crabs, Jonah crabs, green crabs *Carcinus maenas*). Further, Gendron et al. (2001) suggested that rock crabs provide lobsters with important proteins (particularly certain amino acids) necessary for growth and energy reserves. Several crabs were eaten during our experimental trials, thereby confirming direct predation of lobsters on rock crabs. The competitive dominance of lobsters over rock crabs for shelter and space observed in our study is consistent with Hudon and Lamarche (1989). Results suggest that the increased risk of predation on rock crabs by lobsters has forced rock crabs to use alternative substrate and food resources when coexisting with lobsters.

Movement of rock crabs up the kelp canopy appears to be size-specific. Size relationships between lobsters and rock crabs were negligible in our study; however, field surveys showed that rock crabs between 26 and 40 mm CW (25th and 75th percentile range) were the primary size range that occupied kelp canopies. One explanation for this size-selectivity is that large rock crabs (>40 mm CW) may be capable of competing directly with lobsters for space. Large rock crabs (37 to 125 mm CW) have been found to prey upon smaller lobsters and thus may not be subordinate at all sizes (Hudon and Lamarche, 1989). An alternative, but not mutually exclusive hypothesis may be that the kelp canopy cannot support the weight of large rock crabs. Of the four Jonah crabs found during field surveys in this study, one small individual was observed up the kelp (50 mm CW). Given the larger size of Jonah crabs relative to rock crabs, the latter species may be capable of utilizing the kelp environment because of its smaller size. If such size-selective patterns occur in kelp environments, rock crabs may only utilize the kelp for a portion of their lifespan. Alternatively, behavioral differences may explain why this resource partitioning appears to be species specific. Rock crabs typically respond to confrontation by fleeing and avoiding lobsters (Novak, 2004), in contrast to large Jonah crabs that display aggression (Richards, 1992), or crouch down to hold their position (Novak, 2004).

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