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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Competition with stone crabs drives juvenile spiny lobster abundance and distribution

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Abstract Interspecific competition is assumed to have a strong influence on the population dynamics of competing species, but is not easily demonstrated for mobile species in the wild. In the Florida Keys (USA), anecdotal observations have long pointed to an inverse relationship in abundance of two large decapod crustaceans found co-occurring in hard-bottom habitat, the stone crab *Menippe mercenaria* and the Caribbean spiny lobster *Panulirus argus*. We used them to explicitly test whether competition for a renewable resource (shelter) can drive the abundance and distribution of the inferior competitor. We first explored this relationship in shelter competition mesocosm experiments to determine the competitively dominant species. Results showed that stone crabs are clearly the dominant competitors regardless of the number of lobsters present, the presence of co-sheltering species such as the spider crab, *Damithrax spinosissimus*, or the order of introduction of competitors into the mesocosm. We also found that lobsters use chemical cues from stone crabs to detect and avoid them. We then tested the ramifications of this competitive dominance in the field by manipulating stone crab abundance and then tracking the abundance and distribution of spiny lobsters through time. Increased stone crab abundance immediately resulted in decreased lobster abundance and increased aggregation. The opposite occurred on sites where stone crabs were removed. When we stopped removing stone crabs from these sites, they soon returned and lobster abundance decreased. This study explicitly demonstrated that interspecific competition can drive population dynamics between these species, and ultimately, community composition in these shallow water habitats.

Keywords Competition · Community ecology · *Panulirus argus* · *Menippe mercenaria*

Introduction

Physiological tolerances (Spicer and Gaston 1999; Holt and Barfield 2011) and larval dispersal (Anderson et al. 2009) determine much of the potential geographic distribution of a species, but environmental factors seldom fully explain population abundance and spatial distribution (Pearson and Dawson 2003; Hampe 2004). Especially at small spatial scales, population dynamics can be driven by resource availability and selection (MacArthur and MacArthur 1961; Shulman 1984; Dunning et al. 1992), or competitive interactions (Fletcher 2007).

Competition typically results when multiple organisms simultaneously require the same limited resource and it can shape their populations (Connell 1961; Tilman 1994). It may manifest as interference to resource access (Case and Gilpin 1974; Berger and Gese 2007), exploitation that reduces resource availability (Park 1954), or as a hierarchy of resource use (Langkilde and Shine 2004). The consequence is often a change in behavior or habitat use (Kuefler et al. 2013; Liesenjohann et al. 2013), reduced fitness or recruitment (Gustafsson 1987; Martin and Martin 2001)

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or changes in abundance and spatial distribution (Connell 1961; Robertson 1996; Hobbs and Munday 2004).

For organisms that face intense predation, access to appropriately sized and abundant shelter is vital to survival and growth (Beck 1995). As with any resource, if shelter is limited, competition can be particularly intense. Shelter limitation can result from increases in number of shelter-dependent organisms, a decrease in shelter abundance, or barriers to the use of shelter (Beck 1997). Proximate consequences of shelter competition may include increased mortality from predation (Holbrook and Schmitt 2002; Behringer and Butler 2010), species displacement (Capelli and Munjal 1982; Usio et al. 2001), increased emigration (Butler et al. 1995), and partitioned habitat use (Langkilde and Shine 2004), especially for the inferior competitor.

Benthic macroinvertebrates are often well suited for studies of competition and behavior because they can be abundant, and densities are often easy to manipulate at small spatial scales. The Caribbean spiny lobster *Panulirus argus*, Latrielle 1804 is a large benthic crustacean found throughout the shallow waters of the wider Caribbean Sea and like most marine crustaceans, *P. argus* has a complex life history (Kanciruk and Herrnkind 1978; Mintz et al. 1994). Juvenile lobsters emerge at approximately 20 mm carapace length (CL) from the vegetation they settled in as post-larvae and seek crevice shelters occupied by conspecifics (Andree 1981; Marx and Herrnkind 1985). Juvenile spiny lobsters are particularly dependent upon shelter and exhibit behaviors that may minimize the effects of shelter limitation. They are attracted to healthy conspecifics, a behavior that may expedite the search for shelter (Childress and Herrnkind 2001) or facilitate group defense (Butler et al. 1999; Lavalli and Herrnkind 2009). Sheltering behavior is largely driven by chemoreception as lobsters are attracted to chemical cues emanating from shelters containing healthy conspecifics (Zimmer-faust et al. 1985; Horner et al. 2006), but avoid shelters with threatening chemical cues from diseased lobsters (Anderson and Behringer 2013) or octopus (Berger and Butler 2001).

In the Florida Keys (USA), much of the shelter for juvenile lobsters is provided by the abundant sponges, coral heads, and limestone solution holes found in shallow (<3 m) hard-bottom habitat. Spiny lobsters are commonly observed co-occupying shelters with spider crabs (*Damithrax spinosissimus*), and healthy conspecifics, but avoid *Octopus* spp. and diseased lobsters (Berger and Butler 2001; Behringer et al. 2006). They are also rarely found co-occupying shelter with the stone crab *Menippe mercenaria*, Say 1818 or the toadfish *Opsanus beta*, Goode and Bean 1880 (pers. obs.), suggesting competition for access to shelter.

Like lobsters, stone crabs in the post-settlement juvenile stage (≤10 mm carapace width) seek shelters similar to those used by lobsters. Their growth, recruitment, abundance, and size distribution are determined by shelter abundance and distribution (Lindberg et al. 1990; Beck 1995, 1997). Unlike lobsters, stone crabs are solitary shelter occupants, only sharing shelter while mating (Wilber 1988), and are rarely found co-occupying shelters with other crustaceans.

Here we tested for competition between juvenile Caribbean spiny lobsters and stone crabs using a renewable resource, shelter, and determined its effect on lobster abundance and distribution. We first established whether spiny lobsters and stone crabs would compete in a shelter-limited mesocosm environment, next determined if stone crab chemical cues mediated juvenile spiny lobster shelter choice, and finally, we determined the effect of stone crab abundance on juvenile spiny lobster abundance and distribution in the wild.

Methods

All animals were collected in the middle Florida Keys and maintained in isolated, aerated aquaria with ambient photoperiod (10:14 h) and water conditions (35 ± 1 ppt, 25 ± 1 °C) via a flow-through system for no more than 48 h until they were used in experiments. Aquaria were not equipped with shelter. To minimize the risk of pseudoreplication via recapture, all experimental lobsters were used only once before being released at least 2 km from any collection site.

Mesocosm shelter competition experiment

To determine if interference shelter competition occurs between juvenile spiny lobsters and stone crabs in a shelter-limited environment, we video recorded mesocosm trials in which a single shelter was offered to a lobster and stone crab in one of several treatments. Trials were performed in 68 l plastic Rubbermaid Roughneck™ bins (61 cm × 40 cm × 42 cm deep). The bottom of each container was covered in Sakrete® concrete 4 cm deep with natural hard-bottom sediment lightly coating the top to resemble natural hard-bottom substrate. Shelter was provided using half of a terracotta pot placed abutting one end of the container. Preliminary trials, in which a single lobster or single stone crab was offered shelter in the absence of the other, showed that shelter size preference varied with lobster and crab size. This is consistent with results from the field showing that lobsters (Eggleston and Lipcius 1992) and stone crabs (Beck 1995) prefer shelter scaled to their body size. Therefore, in trials with two competitors, different shelter sizes were used according to the sizes of trial animals. Terracotta pots with 11.4 cm top diameter and 10.2 cm depth were offered

to lobsters <30 mm CL and stone crabs with <60 mm CW). Pots with 15.2 cm diameter and 14.0 cm depth were offered to lobsters ≥31 mm CL and stone crabs ≥61 mm CW. Hence, test animals in each trial were roughly matched by size such that stone crabs <60 mm CW were paired with lobsters <30 mm CL (or approximately 60 mm total length), and similarly for the larger size shelter (size ranges used are reported in results below). This was done to minimize bias in shelter suitability for one of the competitors and to ensure both competitors could occupy each shelter. Trials with three or four competitors required more volume and larger shelter sizes. Thus, these trials were conducted in 380 l Rubbermaid™ stock tanks (134.6 cm long × 78.7 cm wide × 63.5 cm deep) with one shelter (30.5 cm long × 10.2 cm high × 30.5 cm wide). For each trial, the experimental mesocosm was filled with ambient seawater (35 ± 1 ppt, 25 ± 1 °C). Aerated ambient seawater in a 120 l elevated head tank drained into the experimental container at a rate of 4.0 ml s^{-1}. In all experiments, animals were placed side-by-side in the container and confined to separate vertical 15 cm tall × 11.4 cm diameter polyvinyl chloride tubes until escape responses from handling subsided. The tubes were then removed and a video camera recorded the 2-h trial. Trials were conducted during the light photoperiod, as they would naturally be seeking shelter at this time. To remove any olfactory residue from prior trials, all equipment was rinsed with freshwater and allowed to dry for at least 10 h prior to reuse.

Prior to competition experiments, one stone crab ($n = 29$) or one lobster ($n = 29$) were tested alone to determine shelter use in the absence of competition. The shelter competition experiments consisted of four treatments. *Treatment 1* tested for competition between a single lobster and a single stone crab added simultaneously ($n = 33$). *Treatment 2* tested for competition between a single lobster and a single stone crab, but with the lobster introduced to the mesocosm 30 min prior to the stone crab ($n = 29$). This tested the hypothesis that initial shelter occupancy might give a lobster a competitive advantage over a stone crab. *Treatment 3* included three lobsters and a single stone crab ($n = 29$) to assess the hypothesis that the lobsters' gregarious nature might facilitate group shelter defense. *Treatment 4* tested the potential for the addition of a spider crab to facilitate group shelter defense and included a lobster, stone crab, and spider crab ($n = 29$). The spider crab *D. spinosissimus* is a common, herbivorous crab that often co-occupies shelters with lobsters. In each competition treatment, regardless of the number of crabs or lobsters present, the dependent variables were the time spent within the shelter by a pre-determined 'focal' lobster and the final shelter resident.

A *t* test was used to compare the sheltering time of a lobster with that of a stone crab when no competitor was present. A one-way ANOVA was used to compare treatment effects (lobster only and the four lobster-stone crab competition treatments) on the time each focal lobster spent in the shelter, followed by a post hoc Bonferroni pairwise comparisons test to determine which, if any, treatments differed. A 4 × 4 contingency table analysis was used on the four competition treatments only to test if final shelter occupant was independent of the four treatments and four possible outcomes: (1) the lobster was the final occupant, (2) the stone crab was the final occupant, (3) no occupant at end of trial, or (4) both stone crab and focal lobster in shelter at end of trial. The lobster only treatment could not be included in this analysis because without a stone crab all outcomes were not possible.

Chemosensory driven shelter selection

To test for the effect of stone crab chemical cues on lobster shelter selection we conducted chemosensory Y-maze experiments (Anderson and Behringer 2013). In Y-maze experiments, a lobster was placed in one end of a container and given the option of sheltering in one of two separated refuges at the other end of the container or occupying neither shelter. From each shelter a different chemical cue was emitted. A series of chemical cues known to attract (healthy conspecifics) and repel (diseased conspecifics) lobsters were compared with those of spider crabs and stone crabs, respectively. Juvenile Caribbean spiny lobsters are commonly infected with a pathogenic virus termed PaV1 (*Panulirus argus* Virus 1) and healthy lobsters have been shown to avoid infected lobsters using chemosensory cues (Behringer et al. 2006; Anderson and Behringer 2013). Heavily infected lobsters can be identified by gross observation of milky-white hemolymph, which is normally clear (Shields and Behringer 2004). From seasonal surveys, spider crabs were of similar size to stone crabs and reproductive adults were not uncommon where the species are sympatric. Treatments included a stone crab odor in one shelter and no odor (seawater only) in the other ($n = 45$), stone crab odor in one and diseased lobster odor in the other ($n = 37$), spider crab odor in one shelter and no odor (seawater only) in the other ($n = 32$), and spider crab odor in one shelter and healthy lobster odor in the other ($n = 30$). Four 80 l Y-mazes, with dimensions 94 cm long × 62 cm wide × 20 cm deep (Fig. 1), were constructed of epoxy-coated plywood and left with an open top for observation and placement of lobsters. A vertical partition (72 cm × 18 cm) bisected ¾ of the length of the container. This effectively separated the two shelters and their respective flows of water and chemical cues, while giving the lobster equal exposure and access to sense each cue. Unidirectional water flowed from each shelter to a drain at the opposite end of the Y-maze and was maintained at a rate
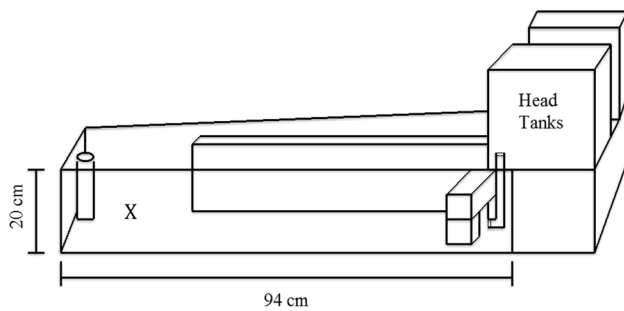
Fig. 1 Y-maze design used to test for the effect of chemical cues on lobster shelter choice. Chemical cues flowed from two head tanks through two separated shelters to a drain spout. A focal lobster was placed at the "X" at the beginning of each trial

of 1 cm s^{-1} by elevating the upstream end by 4° (Anderson and Behringer 2013). Each treatment animal was contained in one of two 120 l head tanks filled with seawater, which drained into the upstream end of one of the two sides of the Y-maze at a rate of 4.0 ml s^{-1}. Stimulus animals in head tanks were not visible to the lobsters in the Y-maze to ensure that visual cues did not affect lobster shelter choice. Water drained from each head tank into a shelter in the Y-maze 6.35 cm from the bottom of the head tank. Crevice shelters were comprised of one concrete brick leaning against another.

Five hours prior to the start of each trial one treatment animal, or seawater only, was placed in one of the two aerated head tanks to allow accumulation of the chemical cue of interest, presumably urine. A coin toss was used to randomize placement of each treatment in the left and right side containers. As lobsters are nocturnal and seek shelter at dawn, trials started at 12:00 am and ended 1 h post-dawn. Each test lobster was placed in the open end of the Y-maze and kept in place using small hand nets as barriers until initial escape reactions from handling had ceased. Each Y-maze and head tank was rinsed with fresh water and left to dry for 10 h to avoid contamination of subsequent trials with chemical cues.

A binomial goodness of fit test was used to determine if the shelter chosen at the end of the experiment (1 h post-dawn) deviated from the predicted outcome. Lobsters do not co-occupy shelters with stone crabs in the wild, an observation that motivated this study. In contrast, lobsters shelter with spider crabs often. In treatments with a stone crab or spider crab cue compared to seawater, we expected the focal lobsters to select a shelter supplied with seawater when compared to one supplied with a stone crab cue, and select a shelter supplied with spider crab cue when compared with one supplied with only seawater (one-tailed tests). However, where we tested avoidance of stone crab and diseased lobster cues simultaneously, or attraction to spider crab and healthy lobster cues simultaneously, no

particular shelter choice was expected (two-tailed tests). Significance of tests was determined at $\alpha = 0.05$.

Hard-bottom shelter inhabitant surveys

Scuba surveys were conducted at nine hard-bottom sites in the Florida Keys to measure seasonal changes in shelter availability and use May–July 2012, April–March 2013, and June 2013. Sites were selected which were known from previous surveys to harbor stone crabs and lobsters and have similar abundance of crevice bearing structures.

Available shelter was defined as any sponge, coral, or solution hole ≥20 cm diameter that provided refuge in the form of holes, recesses, or crevices. Each survey consisted of two divers recording all shelter inhabitants found during a search resulting in a total survey time of 1 h. Divers haphazardly divided the search area in half to avoid multiple recordings of inhabitants. Animal processing time included recording of animal species, size [mm CL or carapace width (CW)], sex, injuries, shelter type occupied, distance to nearest neighbor, shelter size (< or ≥20 cm diameter), and whether the shelter provided refuge in the form of holes, recesses, or crevices. Processing time was not included in the 1 h survey time. Additionally, four nonoverlapping 25 × 2 m belt transects were haphazardly placed in the survey area and used to determine shelter abundance. This was done to ensure consistency in shelter abundance among sites used for the stone crab density manipulations described below. A scuba diver swam along each transect with a 2 m pole held perpendicular to a 25 m measuring tape and measured each shelter encountered. For each shelter, we recorded shelter type (sponge, coral, solution hole, or gorgonian), measured the shelter diameter, and determined whether the shelter provided refuge in the form of holes, recesses, or crevices.

Linear regression analyses were used on data from each season to determine if stone crab abundance could predict lobster abundance or number of lobsters co-occupying shelters. A mixed-effects ANOVA was used to determine if shelter abundance differed significantly among sites or survey periods.

Stone crab density manipulations

To test for the effect of stone crab presence on lobster abundance and distribution, we manipulated the densities of stone crabs on nine hard-bottom sites throughout the Florida Keys (Fig. 2). Seven of the nine sites from the seasonal surveys described above were used for stone crab density manipulation. A paucity of stone crabs required the establishment of two new sites previously un-surveyed. These additional sites were surveyed using the methods above and met our selection criteria. All had similar shelter
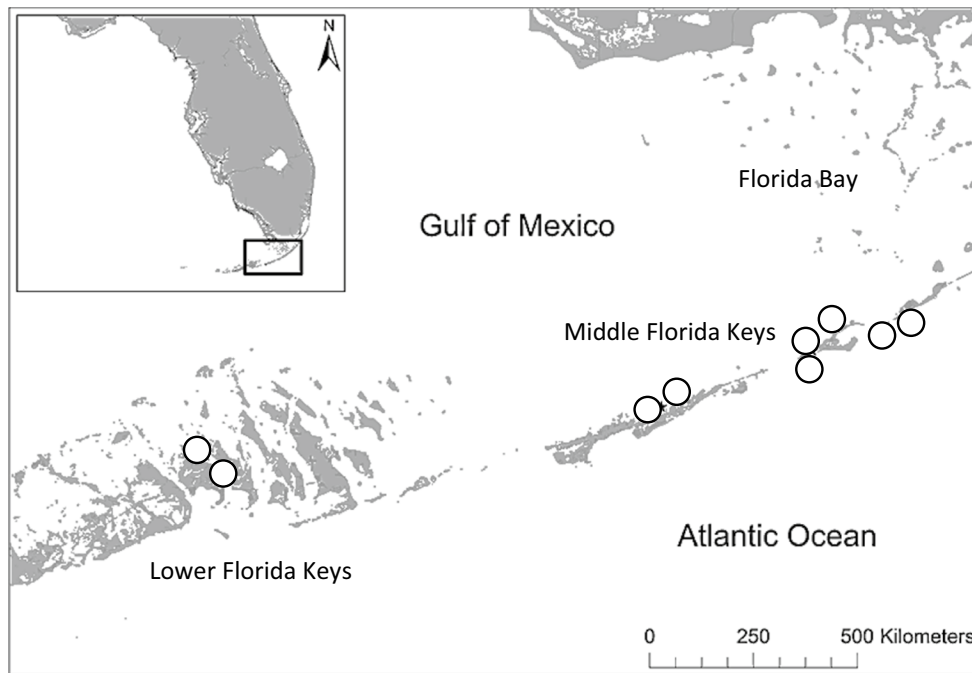
Fig. 2 Stone crab densities were manipulated at nine hard-bottom sites (*open circles*) in the middle and lower Florida Keys

abundance, past recordings of both lobsters and stone crabs, and were at least 2 km apart. The experimental study began immediately following the shelter inhabitant surveys.

A 25 × 25 m quadrat was placed haphazardly in each of the selected hard-bottom areas. Stone crabs added to sites were tethered to concrete bricks and placed within sheltering distance of haphazardly chosen but appropriately sized shelters. To tether the crabs, monofilament line was wrapped around the carapace to form a bridle and reinforced with cyanoacrylate glue. This allowed the crab uninhibited movement and use of limbs. A snap swivel was attached to the monofilament line on the dorsal carapace as a connection point for a 13.6 kg wire leader attached to the block. The tethers allowed stone crabs to use shelters within a 0.3 m radius of the brick. Each brick was 10.2 cm × 5.7 cm × 20. 3 cm and did not provide refuge for tethered crabs.

Surveys consisted of a single scuba diver recording pertinent data on each inhabitant within the quadrat. Three treatments were used in this experiment, including: (1) the removal of all stone crabs from three sites, (2) The doubling of the number of stone crabs at three sites, and (3) leaving three sites unmanipulated to serve as controls. Only stone crabs with 60–95 mm CW were used on addition sites as this was the size range available from collection areas. The stone crab addition treatment included doubling the densities of stone crabs within quadrants, but was never at an unrealistically high density not found in a past survey. Stone crabs removed from sites were transplanted to areas at least 5 km

away. A census of all inhabitants at each site was conducted at $t = 0$, $t = 24$ h, $t = 48$ h, $t = 1$ week, and $t = 2$ week. Treatments at each site were maintained by replacing missing stone crabs on addition sites and removing stone crabs from removal sites during each survey. Due to logistical constraints, crab removals stopped after $t = 48$ h, which allowed the system to return to pre-manipulation conditions.

A 2 × 2 repeated-measures MANOVA was used to determine if stone crab abundance (Factor 1, 3 levels) and time (Factor 2, 5 levels) affected lobster abundance and aggregation. Dependent variables were the density of lobsters within a site, percentage of lobsters found co-occupying shelter with conspecifics, and mean lobster aggregation size. Post hoc multiple comparison tests were used to determine which treatments differed. SPSS version 22 (SPSS IBM, New York, U.S.A.) was used to perform these analyses.

Results

Mesocosm shelter competition experiments

Mean lobster size was 30.6 ± 11.8 s.d. mm CL, mean stone crab size was 54.9 ± 14.1 s.d. mm CW and mean spider crab size was 60.1 ± 14.1 s.d. mm CW. A *t* test showed lobsters ($n = 29$) and stone crabs ($n = 29$) occupied shelter for similar amounts of time in the absence of a competitor ($t = 1.88$, *df* = 27, $P = 0.331$).

Sheltering time and final shelter occupant did not differ between small and large animals ($t = 5.49$, $df = 27$, $P = 0.742$). Therefore, these groups were combined for further analyses. The amount of time lobsters occupied shelter decreased significantly in the presence of a stone crab. A one-way ANOVA showed that the time a lobster spent sheltering was dependent on treatment ($F = 10.32$, $df = 30$, $P = 0.012$). ANOVA assumptions of normality, equal variances, and lack of outliers were met with raw data. Post hoc Bonferroni multiple comparisons analysis revealed the only significantly different treatment was the control in which a lobster had no competitor present (Table 1). When only a stone crab was present ($n = 33$), the focal lobster spent 141.8% less time in the shelter than when no stone crab competitor was present ($n = 29$). The outcome was similar with multiple lobsters in addition to the stone crab ($n = 30$, 125.6% less time in shelter), the presence of a spider crab ($n = 30$, 127.4% less time in the shelter), and initial occupancy of the shelter by the lobster ($n = 31$, 124.2% less time in the shelter). The presence of multiple lobsters, presence of a spider crab, and initial shelter occupancy by the lobster did not significantly differ in their effect on the time focal lobsters occupied the shelter (Fig. 3). Contingency table analysis of *only the competition treatments*

(Table 2) showed that the final shelter occupant at the end of each trial was the stone crab and this did not differ significantly among treatments ($\chi^2 = 16.92$, $df = 9$, $P = 0.4197$). The final shelter occupant was a stone crab in 67.2% of trials across all treatments, a lobster in 12.5% of trials, neither in 19.5%, of trials, and both in 0.8% of
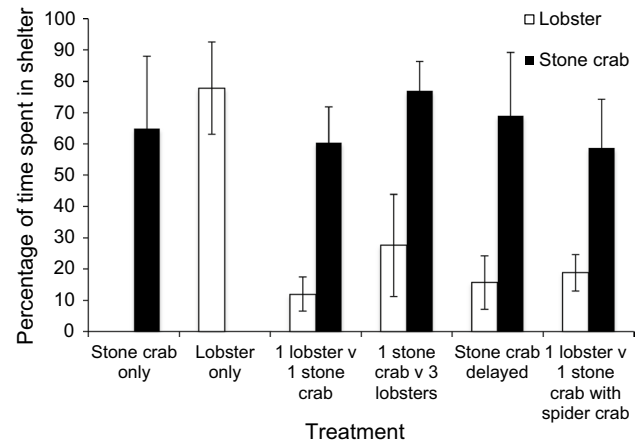

Fig. 3 Results of mesocosm shelter competition experiment. Presence of a stone crab significantly reduced lobster shelter time. *Error bars* represent 1 standard error

Table 1 Bonferroni multiple comparisons test showed shelter time of a lobster with no competitor differed from all other treatments in mesocosm experiments

Group i	Group j	Mean difference	SE	P	95% CI	
					Lower bound	Upper bound
Lobster only	Stone crab	3.501	0.748	**0.029**	3.04	3.96
	Multiple lobsters	3.359	0.634	**0.012**	2.174	5.323
	Spider crab	3.024	0.713	**0.035**	1.977	5.44
	Stone crab (D)	2.471	0.675	**0.017**	1.058	3.249
Stone crab	Lobster only	−3.501	0.748	**0.029**	−3.96	−3.04
	Multiple lobsters	−1.758	0.44	0.35	−2.615	−0.886
	Spider crab	−1.828	0.313	0.45	−3.12	−0.554
	Stone crab (D)	−1.19	0.287	0.66	−1.85	−0.521
Multiple lobsters	Lobster only	−3.359	0.634	**0.012**	−5.323	−2.174
	Stone crab	1.758	0.44	0.35	0.886	2.615
	Spider crab	−1.389	0.668	0.75	−2.75	1.098
	Stone crab (D)	1.955	0.531	0.082	−0.845	3.004
Spider crab	Lobster only	−3.024	0.713	**0.035**	−5.44	−1.977
	Stone crab	−1.828	0.313	0.45	0.554	3.12
	Multiple lobsters	1.389	0.688	0.75	−1.098	2.75
	Stone crab (D)	−1.577	0.092	0.092	−3.61	0.183
Stone crab (D)	Lobster only	−2.471	0.675	**0.017**	−3.249	−1.058
	Stone crab	1.19	0.287	0.66	0.521	1.85
	Multiple lobsters	−1.955	0.531	0.082	−3.004	0.845
	Spider crab	1.577	0.747	0.092	−0.183	3.61

Treatments wherein the introduction of the stone crab was delayed 30 min are indicated with a (D). Significance was determined at $\alpha = 0.05$ and significant results are in bold

Table 2 Contingency table analysis of mesocosm experiments showed the final shelter occupant did not differ significantly among treatments

Treatments	Final shelter occupant				
	Lobster	Stone crab	Both	Neither	Total
1 stone crab	6 (4.25)	24 (22.84)	0 (0.27)	4 (6.64)	34
1 stone crab (delayed)	2 (3.75)	18 (20.16)	1 (0.23)	9 (5.86)	30
1 stone crab, 1 spider crab	4 (3.875)	23 (20.83)	0 (0.24)	4 (6.06)	31
1 stone crab, two lobsters	4 (4.12)	21 (22.17)	0 (0.26)	8 (6.45)	33
Total	16	86	1	25	128

Values in parentheses are expected values

trials. The lobster only treatment could not be included in the contingency table analysis because the possible outcomes of this treatment were not the same as the competition treatments.

Influence of chemical cues on shelter choice

Average size of the focal lobsters was 35.4 ± 7.7 s.d. mm CL, average stone crab size was 59.3 ± 7.7 s.d. mm CW, average spider crab size was 74.1 ± 11.3 s.d. mm CW, average healthy stimulus lobster size was 41.1 ± 9.4 s.d. mm CL, and average diseased stimulus lobster size was 28.5 ± 5.9 s.d. mm CL. As expected, a one-tailed binomial test showed focal lobsters chose seawater-only shelters

significantly more (66 versus 34%) in stone crab versus seawater-only treatments ($n = 41$, $P = 0.040$) suggesting an avoidance of stone crab chemical cues (Table 3; Fig. 4). Also as expected, focal lobsters selected shelters supplied with a spider crab chemical cue significantly more (68 versus 32%) than seawater only ($n = 32$, $P = 0.041$). Shelter choice in the stone crab versus diseased lobster treatments did not differ from random ($n = 32$, $P = 0.117$).

Hard-bottom shelter inhabitant surveys

Linear regressions for each season showed a significant positive relationship between stone crab abundance and number of small lobsters co-occupying shelters with conspecifics in Winter and Summer 2013, and number of large lobsters co-occupying shelters with conspecifics in Summer 2013 (Table 4). Small (<30 mm CL) and large (≥30 mm CL) lobsters occur in hard-bottom, but exhibit ontogenetic divergence in shelter use (Butler and Herrnkind 2000) and were therefore analyzed separately. Stone crab abundance and lobster abundance were only significantly related for large lobsters in Summer 2013. Mean lobster size was 37.1 ± 8.9 s.d. mm CL, and mean stone crab size was 57.3 ± 8.9 s.d. mm CW.

Juvenile lobsters were the most abundant shelter inhabitants in all surveys, followed by stone crabs, spider crabs, and other rare inhabitants (Fig. 5). Those other rare inhabitants included toad fish, swimming crabs (family Portunidae), and other small spider crabs (family Majidae).

Table 3 Chi square analyses of the binomial chemosensory experiments indicate a preference to shelter with seawater over stone crab chemical cues and a preference to shelter with spider crab chemical cues over seawater

Treatment	Trials	Number of times shelter was selected		Critical value	^{2}
Stone crab v seawater	41	14 (stone crab)	27 (seawater)	3.841	**4.122**
Stone crab v diseased	32	14 (stone crab)	18 (diseased lobster)	3.841	0.5
Spider crab v seawater	31	21 (spider crab)	10 (seawater)	3.841	**3.903**
Spider crab v healthy	33	12 (spider crab)	21 (healthy lobster)	3.841	2.45

Deviation from random shelter selection is denoted in bold. Significance was determined at $\alpha = 0.05$

Fig. 4 Results of chemosensory Y-maze experiments. *Bars* indicate the percentage of trials in which a focal lobster sheltered with chemical odor 1 or chemical odor 2 based on treatment. *Asterisks* indicate a significant departure from random (50% probability) shelter selection
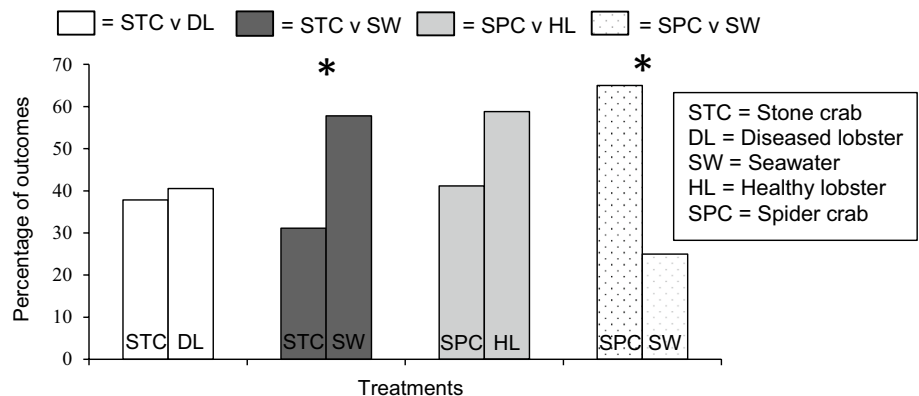
Ⓐ Springer

Table 4 Twelve linear regressions used to analyze percentage of lobsters co-occupying shelter and lobster abundance, with stone crab abundance as the predictor variable

Dependent variable	Survey period	Adjusted R^2	Mean square	df	F	P
Percent co-occupying shelter	Lobsters ≤30 mm CL					
	Summer 2012	0.02	326.198	1	1.161	0.32
	Winter 2013	0.651	2697.401	1	15.918	**0.005**
	Summer 2013	0.478	3702.534	1	8.326	**0.023**
	Lobsters ≥30 mm CL					
	Summer 2012	0.17	1418.055	1	2.633	0.15
	Winter 2013	0.104	1688.277	1	1.927	0.21
	Summer 2013	0.882	3163.265	1	60.979	**<0.001**
Lobster abundance	Lobsters ≤30 mm CL					
	Summer 2012	0.11	57.199	1	1.992	0.20
	Winter 2013	0.53	51.056	1	1.447	0.27
	Summer 2013	0.266	64.414	1	3.901	0.089
	Lobsters ≥30 mm CL					
	Summer 2012	0.197	26.612	1	2.96	0.13
	Winter 2013	0.201	667.042	1	3.011	0.13
	Summer 2013	0.412	155.866	1	6.612	**0.037**

Small (<30 mm CL) and large (≥30 mm CL) lobsters were analyzed separately. *P* values in bold were significant at $\alpha = 0.05$
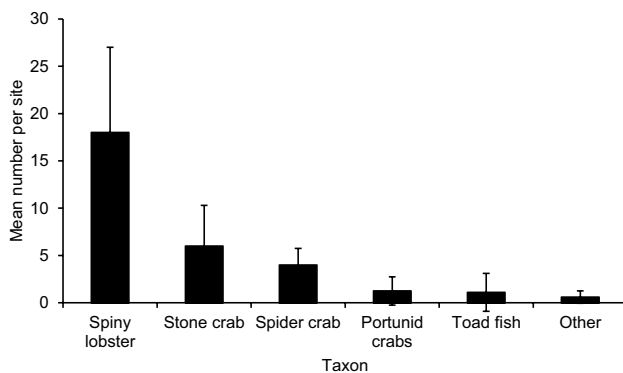

Fig. 5 Mean number of each taxon (±s.d.) per site across all hard-bottom habitat surveys

A mixed-effects ANOVA showed that shelter abundance did not vary among sites ($F_{(8,27)} = 1.991$, $P = 0.87$) or sampling period ($F_{(2,54)} = 1.166$, $P = 0.32$) and there was no significant interaction between site and sampling period ($F_{(16,54)} = 0.701$, $P = 0.78$). All assumptions of mixed-effects ANOVA were met with the raw data. Gorgonians were the most abundant structures on nearly all sites, but provide little refuge. No lobsters or crabs were recorded sheltering under gorgonians, so this group was omitted from analysis.

Stone crab density manipulations

Tethered stone crabs added to the three addition sites ranged from 53.1 to 99.4 mm CW with a mean of

71.8 ± 9.2 s.d. mm CW while those removed from sites ranged from 48.3 to 81.6 mm CW with a mean of 60 ± 12.7 s.d. mm CW. Lobster size across all surveys ranged from 18.4 to 67.8 mm CL with a mean of 35.6 ± 12.5 s.d. mm CL. All assumptions for a 2 × 2 repeated-measures MANOVA were met using the raw data. The interaction term, Time × Treatment, was not statistically significant and so the assumption of homogeneity among regression slopes was met. Assumption of equal variance of residuals was confirmed with Levene's test for lobster abundance. The multivariate tests showed a statistically significant between-subjects effect of treatment (Wilk's Lambda = 0.129, $F_{(12,76)} = 1.945$, $P = 0.024$) and a borderline significant within-subjects effect of time (Wilk's Lambda = 0.783, $F_{(26,44)} = 7.622$, $P = 0.048$). The between-subjects univariate tests showed a significant effect of treatment on lobster abundance ($F_{(2,6)} = 17.7$, $P = 0.033$), and the number of lobsters co-occupying shelters ($F_{(2,6)} = 21.2$, $P = 0.019$) (Table 5). Neither Time nor Time × Treatment interaction were significant. Post hoc pairwise multiple comparisons revealed that the addition of stone crabs to sites caused a decrease in lobster abundance relative to removal sites and control sites (Table 6). Conversely, the removal of stone crabs caused an increase in lobster abundance relative to the addition sites and control sites. However, the initial increase was followed by a decrease in lobster abundance after crab removals stopped at $t = 48$ h (Table 6; Fig. 6). The addition of stone crabs caused an increase in lobster co-occupancy relative to removal and control sites, removal of stone

Table 5 Repeated measures MANOVA testing effects of stone crab density manipulation on lobster abundance, shelter co-occupancy, and aggregation size

Effect	Source	Wilk's Lambda	F	Hyp. df	Error df	P
Within-subjects univariate tests						
Between-subjects	Intercept	0.429	1.835	12	58	0.063
	Treatment	0.129	1.945	12	76	**0.024**
Within-subjects	Time	0.783	7.622	26	44	**0.048**
	Time × Treatment	0.155	1.033	26	55	0.085

Source	Measure	df	Mean square	F	P
Within-subjects univariate tests					
Survey period	Abundance	4	18.333	4.406	**0.008**
	Co-occupancy	4	428.318	0.593	0.67
	Aggregation size	4	0.958	2.575	0.063
Survey period × Treatment	Abundance	8	25.1	6.032	0.081
	Co-occupancy	8	739.02	1.024	0.45
	Aggregation size	8	0.631	1.696	0.15
Error (survey period)	Abundance	2	4.161		
	Co-occupancy	2	721.849		
	Aggregation size	2	0.372		
Between-subjects tests					
Intercept	Abundance	1	2800.55	66.29	**0.008**
	Co-occupancy	1	98,656.9	43.38	0.052
	Aggregation size	1	163.211	282.56	0.14
Treatment	Abundance	2	7.489	17.7	**0.033**
	Co-occupancy	2	47.328	21.2	**0.019**
	Aggregation size	2	0.344	38.55	0.078
Error	Abundance	6	42.244		
	Co-occupancy	6	2274.584		
	Aggregation size	6	0.894		

P values in bold were significant at $\alpha = 0.05$

crabs caused a decrease in co-occupancy relative to addition sites, but not control sites (Table 6; Fig. 7). Mean lobster aggregation size (i.e., number of lobsters per shelter) did not change with Time or Treatment (Table 6; Fig. 8).

Discussion

This study presents empirical evidence for resource (shelter) competition between juvenile Caribbean spiny lobsters and stone crabs that results in significant shifts in population abundance and distribution. In mesocosm experiments, stone crabs excluded lobsters from shelter regardless of the number of lobsters present, the presence of another cohabitant (spider crab), or order of introduction to the mesocosm. Lobsters appear to avoid physical interactions with stone crabs by detecting and avoiding stone crab chemical cues. These laboratory results were mirrored on natural hard-bottom sites where stone crab abundance was positively

associated with increased aggregation of among lobsters, and in field experiments where increased stone crab density resulted in decreased lobster abundance and increased aggregation. The opposite occurred on stone crab removal sites. Exclusion of lobsters from shelters by stone crabs effectively reduces the shelter available to lobsters. Exclusion from shelter could in turn result in decreased survival, increased emigration, and altered spatial distribution that changes the composition of the benthic community.

Stone crabs dominate shelter competition, emit chemical cues aversive to lobsters, and affect lobster abundance and distribution when shelter is limited. Nonetheless, stone crabs have not excluded lobsters from all hard-bottom habitats and lobsters can be the most abundant macroinvertebrates in some areas. Several processes may allow lobsters and stone crabs to coexist. For example, common predators or parasites may keep stone crab abundance below the level necessary to saturate shelter availability. Octopuses are common predators in hard-bottom and readily prey upon crustaceans such as stone crabs and lobsters (Berger and

Table 6 Pairwise comparisons of treatment means in stone crab density manipulation experiment

Measure	Treatment (i)	Treatment (j)	Mean difference	SE	P	Lower bound	Upper bound
Lobster abundance	Addition	Removal	−6.47	1.075	**<0.001**	−8.694	−4.247
		Control	−3.499	0.793	**<0.001**	−5.14	−1.858
	Removal	Addition	6.47	1.075	**<0.001**	4.247	8.694
		Control	2.971	0.884	**0.003**	1.141	4.801
	Control	Addition	3.499	0.793	**<0.001**	1.858	5.14
		Removal	−2.971	0.884	**0.003**	−4.801	−1.141
Co-occupancy	Addition	Removal	28.567	9.7	**0.007**	8.502	48.633
		Control	21.155	7.158	**0.007**	6.349	35.962
	Removal	Addition	−28.567	9.7	**0.007**	−48.633	−8.502
		Control	−7.412	7.981	0.363	−23.922	9.098
	Control	Addition	−7.158	21.15	**0.007**	−35.962	−6.349
		Removal	7.412	7.981	0.363	−9.098	23.922
Aggregation size	Addition	Removal	−2.769	4.554	0.092	−2.755	5.912
		Control	−1.902	9.052	0.665	−1.055	3.477
	Removal	Addition	−4.554	2.769	0.215	−5.912	2.755
		Control	13.836	11.411	0.093	−9.83	4.632
	Control	Addition	−9.052	1.902	0.086	−3.477	1.055
		Removal	−11.411	13.836	0.434	−4.632	9.83

P values in bold were significant at $\alpha = 0.05$

Fig. 6 Mean lobster abundance for each stone crab density manipulation treatment over time. Abundance is based on a 25 m × 25 m study site area. *Error bars* represent 95% confidence intervals
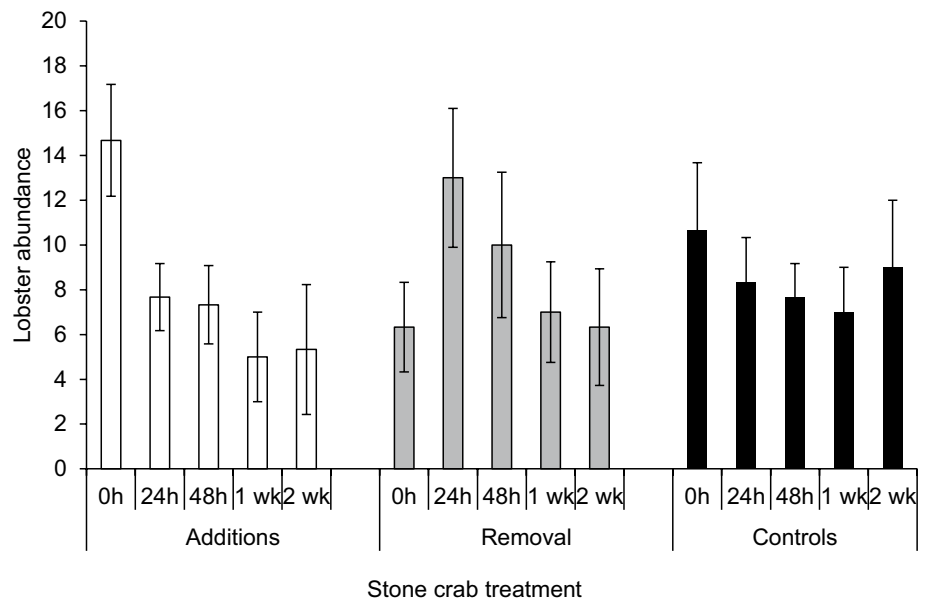
Butler 2001). Additionally, stone crabs are susceptible to the blood parasite, *Hematodinium* sp., which can reach a high prevalence in many crustacean populations (Stentiford and Shields 2005), and could keep stone crabs and lobsters from saturating shelter availability. Similarly, *P. argus* juveniles suffer high mortality from the pathogenic virus PaV1 that could keep their populations depressed (Shields and Behringer 2004; Moss et al. 2013). Co-existence could also be facilitated by inconsistent and unequal larval

recruitment. The 5- to 7-month planktonic larval duration of the Caribbean spiny lobster allows for transport of larvae throughout the Caribbean (Butler et al. 2011). Larvae that recruit to the Florida Keys are spawned throughout the Caribbean. The diversity of sources for spiny lobster larvae (Kough et al. 2013) may buffer poor recruitment from one area. In contrast, stone crab larvae have a planktonic larval duration of only 27–30 days (Porter 1960) which may preclude them from dispersing as far as spiny lobster larvae.

Fig. 7 Mean frequency of shelter co-occupancy among lobsters for each stone crab density treatment. *Error bars* represent 95% confidence intervals
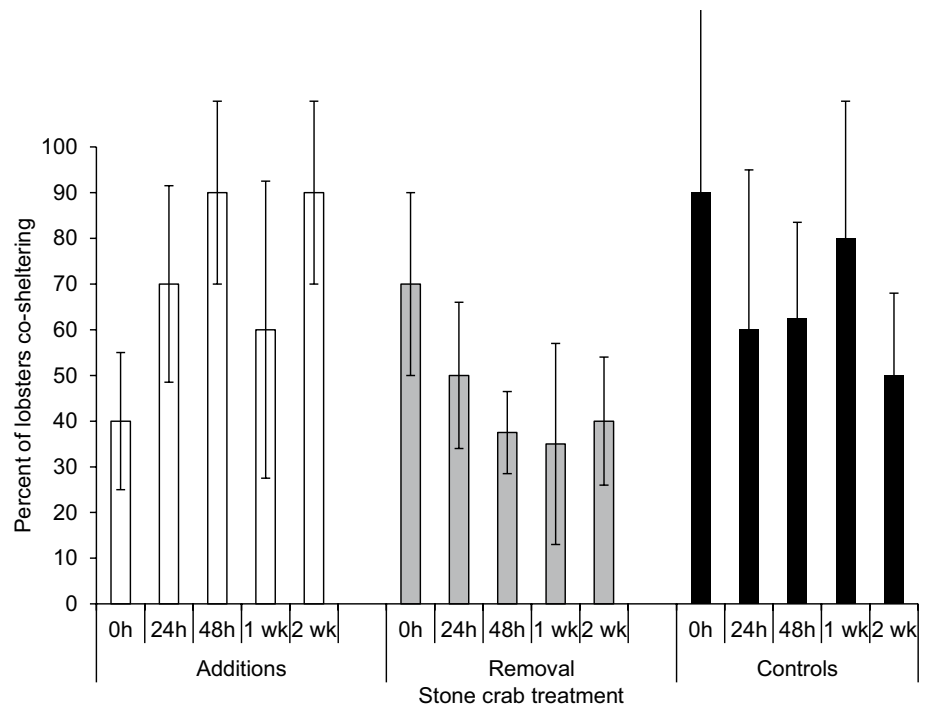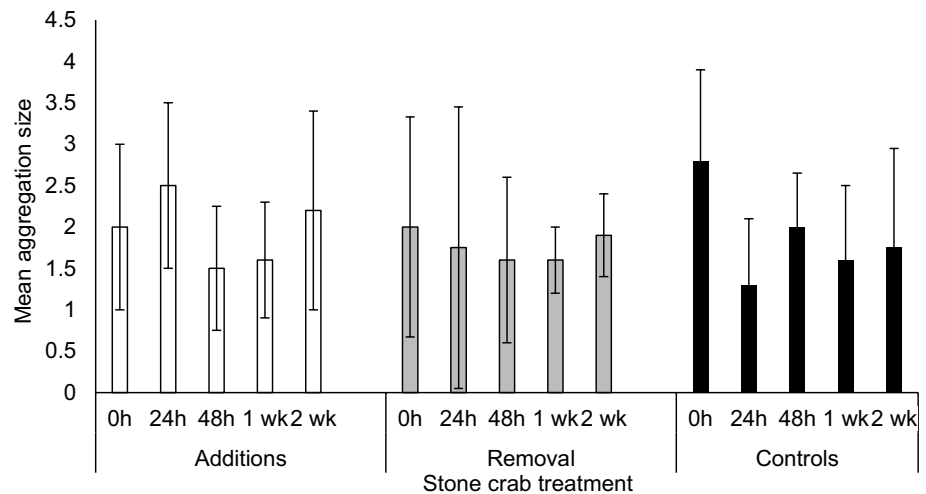

Fig. 8 Mean lobster aggregation size (number of lobsters per shelter) for each stone crab density treatment. *Error bars* represent 95% confidence intervals

Therefore, localized, unfavorable conditions for stone crab spawning or larval survival may significantly impact recruitment to juvenile stages.

Ontogenetic changes in resource requirements may also limit interspecific competition to only a part of species' life history. Wang (1975) found that shell competition between the hermit crabs *Pagurus pollicaris* and *Pagurus longicarpus* was limited to juvenile size ranges because as adult *P. pollicaris* grew larger than adult *P. longicarpus* they were eventually released from competition. In the Florida Keys, spatial overlap between spiny lobsters and stone crabs primarily occurs during their juvenile stage, but as they reach adulthood lobsters migrate to coral reefs where stone crabs are rarely found. Although this habitat shift may afford lobsters an

eventual ontogenetic release from competition, shelter competition may contribute to a bottleneck in recruitment to the adult population.

Our results showed that the addition of two lobsters or a spider crab did not improve the likelihood that a lobster would be successful in competing for a shelter, and thus did not support the group defense hypothesis (Codella and Raffa 1995; Lavalli and Herrnkind 2001), at least in the sense of defending a shelter against an aggressive competitor. However, we did not test the effect of multiple lobsters with prior residency of the shelter, and we recognize that even in trials where the introduction of a stone crab was delayed, this may not have been enough time to affect the outcome of a trial. Blank and Figler (1996) found that prior occupancy of

24 h gave the crayfish *Procambarus clarkii* an advantage over *Procambarus zonangulus* in shelter competition. In contrast, O'Neill and Cobb (1979) found that 24 h prior residency did not significantly affect the outcome of shelter competition between conspecific *Homarus americanus*.

Lobsters were consistently the most common shelter inhabitants in hard-bottom areas followed by stone crabs and spider crabs. Stone crabs and spider crabs comprised 24 and 18% of total shelter inhabitants, respectively. However, addition of stone crabs to hard-bottom sites resulted in significantly lower lobster abundance and increased shelter co-occupancy among those lobsters remaining within 24 h. In contrast, the removal of stone crabs from sites resulted in greater lobster abundance and decreased aggregation as lobsters dispersed to shelters previously occupied by stone crabs. Stone crab removal was only repeated during the initial daily surveys. Consequently, the extended periods between $t = 48$ h, $t = 1$ week, and $t = 2$ week allowed stone crabs to repopulate the sites. Stone crab densities on sites increased during intervals between these removals and this coincided with decreases in lobster abundance. This further supports our findings that increased stone crab abundance is related to decreased lobster abundance and suggests that if spiny lobsters and stone crabs co-occur in shelter-limited areas, lobsters will be excluded from those shelters.

Spiny lobsters are not notoriously aggressive animals. Hence, it is not surprising that they are ultimately excluded from shelters, and furthermore, that they have adapted a mechanism to avoid direct interactions with stone crabs. Our y-maze shelter selection experiments showed that lobsters avoid shelters occupied by stone crabs using only chemical cues, but can also decipher these from spider crab chemical cues to which they are attracted. In fact, lobsters were attracted to shelters emitting spider crab and healthy lobster chemical cues to a similar degree, which suggests their attraction to spider crab cues may facilitate a guide effect akin to that described for conspecific lobsters (Childress and Herrnkind 1997, 2001). Juvenile lobsters live in shallow, often well-lit environments in which vision can be useful, but sheltering behavior has been shown time and again to be strongly driven by chemoreception. Juvenile *P. argus* use chemoreception to avoid shelters containing diseased conspecifics (Anderson and Behringer 2013) or octopuses (Berger and Butler 2001), but use the chemical cues of healthy conspecifics to find shelter (Ratchford and Eggleston 1998). Interestingly, shelter choice between stone crab and diseased lobster odors was similar, suggesting that these chemical cues may represent a similar degree of threat. Furthermore, when given the option of sheltering with one of these two aversive chemical odors or going without shelter, many lobsters remained out of the shelters. Where stone crabs and diseased lobsters are abundant, lobsters may be left with few options other than emigration.

Conclusions

Early evidence of competitive exclusion was based on the assumption that communities existed in competitive equilibrium (Alley 1982). However, the dynamic nature of populations and environmental variability often preclude competitive exclusion. Our study shows that when the abundance of a competitor abruptly and continually reduces resource availability, an inferior competitor may eventually be excluded. However, low intensity competition is more likely to occur, resulting in changes in competitor behavior and redistribution with regard to resource use.

Author contribution statement DCB and JEH conceived and designed the study, JEH conducted the experiments, and DCB and JEH wrote the manuscript.

Compliance with ethical standards

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

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

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