Behavioral response to habitat loss in juvenile spiny lobsters

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ABSTRACT: Understanding behavioral changes is important when examining the impacts of rapid environmental change, particularly when critical resources such as protective shelters become locally limited during habitat loss events. In portions of Florida Bay (Florida, USA), cyanobacterial blooms have reduced the availability of large sponges, an important shelter for juvenile Caribbean spiny lobster *Panulirus argus*. We examined whether juvenile lobsters from regions with and without sponge shelters differed in: (1) aggressive and gregarious behaviors; (2) den use, den sharing, and den fidelity before and after shelter loss; and (3) dispersal from sites with and without artificial shelters. In laboratory experiments where individuals were paired with similar-size conspecifics, habitat type had no influence on aggression and gregariousness, but larger lobsters were more aggressive and shared dens less frequently than smaller lobsters. When these same individuals were placed into groups of 20 in a mesocosm and exposed to shelter loss, individuals from habitats with sponges showed a greater decrease in den use and den sharing than individuals from habitats without sponges. After shelter loss, large lobsters decreased their den use, den sharing, and den fidelity more than small lobsters. When individuals were released at their point of capture in Florida Bay, large individuals were resighted less often than small individuals. This study suggests that lobsters from habitats without sponges may respond differently to future shelter loss and that size plays an important role in determining whether juvenile spiny lobsters share shelters or disperse.

KEY WORDS: Caribbean spiny lobster · Social behavior · *Panulirus argus* · Aggression · Gregariousness · Sponge mortality

INTRODUCTION

Loss of habitat can alter the availability of important resources and can result in fragmented landscapes with populations experiencing increased mortality, movement towards habitat of better quality, or use of suboptimal habitat (Robertson & Hutto 2006, Gilroy & Sutherland 2007). Some animals are better than others at behavioral adjustments to these sudden losses of habitat, and variable responses to rapid environmental changes can greatly impact the ability of a species to deal with environmental change (Sih 2013). For example, the mountain brushtail possum increases sharing of hollow tree crevices when they are limited, whereas the agile antechinus does not (Banks et al. 2013). In reef damselfish, the loss of coral shelters results in higher intraspecific shelter competition and higher mortality among juveniles (Boström-Einarsson et al. 2013). Since behavioral responses to environmental changes can vary among

and within a species, it is important to understand how individuals are impacted by habitat loss.

Habitat loss is occurring world-wide, with shallow-water marine communities experiencing frequent and irregular losses of important habitats such as coral reefs, seagrass beds, and sponge assemblages (Fourqurean & Robblee 1999, Duarte et al. 2013). Shallow-water habitats are ecologically important and act as the primary nursery habitat for fishes, mollusks, echinoderms, and crustaceans (Ehrhardt & Legault 1999, Thayer et al. 1999), including the commercially important Caribbean spiny lobster *Panulirus argus* (Forcucci et al. 1994). In the past 20 yr, water quality in Florida Bay, Florida (USA) has declined, with localized mass sponge mortalities occurring after cyanobacterial (*Synechococcus* sp.) blooms (Butler et al. 1995, Phlips et al. 1999). Large sponges (>20 cm diameter) such as loggerhead (*Speciospongia vespara*) and vase (*Ircinia campana*) sponges provide shelter for juvenile spiny lobsters (Childress & Herrnkind 1997), and the loss of sponges from portions of Florida Bay has the potential to negatively impact this species (Herrnkind et al. 1997).

For juvenile Caribbean spiny lobsters, behavioral responses to habitat loss may be complex due to their gregarious nature and den sharing behavior (Berrill 1975). Juvenile Caribbean spiny lobsters begin using large sponges as shelters at approximately 15 to 25 mm carapace length (CL) (Andree 1981, Marx & Herrnkind 1985, Herrnkind & Butler 1986), when they first show attraction to conspecific odors (Childress & Herrnkind 1996). At this stage, juveniles are highly gregarious and exhibit den sharing behavior (Childress & Herrnkind 2001a). Den sharing occurs when one or more lobsters occupy the same crevice shelter, and the number of lobsters sharing a den can be highly variable (Eggleston & Lipcius 1992). At larger sizes, >35 mm CL, juvenile spiny lobsters develop a preference for coral and solution hole shelters over sponge shelters (Bertelsen et al. 2009). Since juvenile spiny lobsters rely on sponge crevice shelters as protection from predation (Smith & Herrnkind 1992, Childress & Herrnkind 1994, 2001a), loss of these natural shelters has the potential to influence their abundance and distribution (Herrnkind et al. 1997).

Gregarious behavior in spiny lobsters is mediated by attraction to conspecific odor cues released in the urine (Nevitt et al. 2000, Horner et al. 2008), and has the potential to benefit individuals in several important ways (Childress & Jury 2006). First, lobsters in high-density shelters have lower per capita risk of predation (Mintz et al. 1994, Butler et al. 1999), but this advantage is undetectable when juveniles are tethered under sponges in groups of 2 or 3 individuals (Childress & Herrnkind 2001a). Second, lobsters reduce their time of exposure to predation by 50% when searching for shelters with conspecific residents (Childress & Herrnkind 2001a). In addition, odor cues exuded by larger juveniles can be detected and followed by smaller individuals, acting as a guide during their habitat transition from macroalgae to natural crevice shelters (Childress & Herrnkind 2001a). Finally, postlarval Caribbean spiny lobster settlement is higher in sites where juvenile lobsters are abundant (Zito-Livingston & Childress 2009), potentially benefiting postlarvae through attraction to preferred sites. Despite the potential benefits derived from conspecific odor attraction and den sharing, nearly half of all juvenile lobsters in Florida Bay occupy natural crevice shelters alone (Davis & Dodrill 1989, Childress & Herrnkind 1997).

Den sharing may not be as egalitarian as it might seem, and aggression has the potential to influence den use. Juvenile lobsters will often push, jostle, or whip approaching conspecifics (Berrill 1975), using odor cues to evaluate the aggressiveness of potential den mates (Shabani et al. 2009). All lobsters do not share dens to the same extent, and aggregations have the potential to vary in size. The development of aggregations will thus be influenced by conspecific interactions with different levels of aggression and gregariousness altering the propensity to cohabitate. These observations raise an important question—Do some spiny lobsters share dens more than others, and, if so, which individuals do best when there is a loss of habitat?

A recent mass sponge mortality in the middle Florida Keys created an opportunity to study the impact of habitat loss on juvenile spiny lobsters inhabiting previously established research sites within the Florida Keys National Marine Sanctuary (Fig. 1). In the fall of 2007, a massive cyanobacterial bloom smothered and killed all large sponges bayside of Lower Matecumbe Key and the east end of Long Key (4 eastern stations), whereas sponges remained abundant bayside of Grassy Key and the west end of Long Key (4 western stations). We thus set out to: (1) determine the influence of habitat type, sex, size, molt, and injury on aggressive and gregarious behavior; (2) experimentally examine patterns of den use, den sharing, and den fidelity before and after a simulated shelter-loss event; and (3) track individually marked juveniles in the field to estimate retention in habitats with and without sponges and artificial shelters.
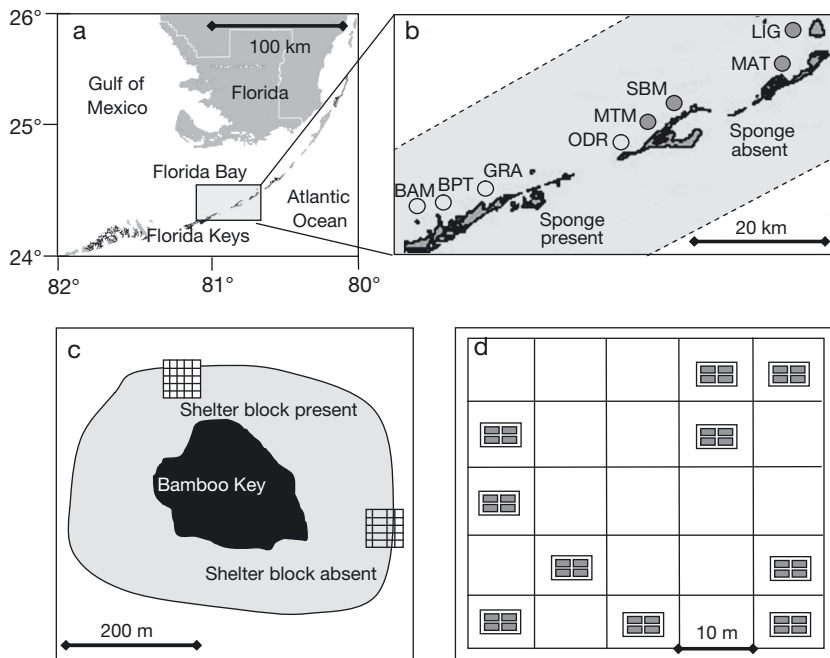
Fig. 1. Map of the study stations and sites in the middle Florida Keys. (a) South Florida and the Florida Keys. Our study sites were located in the middle Florida Keys (enclosed by a gray box). (b) The location of our 8 stations: 4 with sponges absent (LIG, MAT, SBM, MTM) and 4 with sponges present (ODR, GRA, BPT, BAM). All stations are within the boundaries of the Florida Keys National Marine Sanctuary (FKNMS) which is highlighted in gray with boundaries marked by a dashed line. (c) Each station had two 25 × 25 m sites separated by a minimum distance of 0.5 km. Each site had 10 artificial block shelters at the time of lobster collection. Before the lobsters were released, one site at each location had all artificial shelter blocks removed (shelter blocks absent), while the other site remained as before (shelter blocks present). (d) A representation of the 25 × 25 m grids placed on the shelter block present sites. Each shelter-block-present site contained 10 artificial shelter blocks. At shelter-block-absent sites, all artificial shelter blocks were removed after Expt 1 and before Expt 3

MATERIALS AND METHODS

Site description

Eight stations, each containing two 25 × 25 m sites (n = 16) were established bayside of the middle Florida Keys (Zito-Livingston & Childress 2009; our Fig. 1a,b). These sites were used in May 2005 for a study of juvenile recruitment and again for a monthly census of juvenile lobsters from May to October of 2006 through 2008. Ten artificial concrete shelter blocks were added to each site to supplement natural crevice shelters, and the locations of all natural and artificial shelters were mapped. In 2007, 4 of the 8 stations experienced a loss of natural sponge shelters (Childress pers. obs.). The 4 stations east of the Long Key landfill (MTM, SBM, MAT, LIG) lost all large sponges (>20 cm diameter) and were considered sponge-shelter-absent sites (Fig. 1b). The 4 stations west of the Long Key landfill (ODR, GRA, BPT, BAM) remained abundant in large sponges and were considered sponge-shelter-present sites (Fig. 1b).

All 16 sites were remapped during this study, and all known crevice shelters, natural and artificial, were censused by divers (Fig. 1c). After experimental lobsters were collected from each site, the artificial shelter blocks were removed from 1 of the 2 paired sites at each station. This resulted in 4 site types that differed in the presence or absence of sponge and artificial shelters for Expt 3 (sponges present with shelter blocks present, sponges present with shelter blocks absent, sponges absent with shelter blocks present, and sponges absent with shelter blocks absent). These site differences in shelter abundance provided us with replicate collections of lobsters experiencing similar shelter availability and allowed us to examine the influence of habitat type on aggression, gregariousness, denning behavior, and dispersal throughout our 3-phase experiment.

Collection and housing conditions

Twenty juvenile *Panulirus argus* (15 to 48 mm CL) were collected from May to November 2011 and May to July 2012 by hand net from each of the 16 sites for a total of 320 individuals. If 20 lobsters were not found within the field site, lobsters were collected from areas surrounding the site that had similar sponge abundances as the collection site. Lobsters were collected at least 1 d prior to experimentation, resulting in 16 sequential collections (8 each in 2011 and 2012).

During collection, lobsters were visually checked for PaV1, a pathogenic virus that is known to infect *P. argus*, and individuals that exhibited a chalky-white hemolymph were considered infected (Shield & Behringer 2004). Less than 1 % of lobsters were visibly infected, and these individuals were not used in this study. Replacement individuals were collected

immediately after diseased individuals were identified. None of the lobsters retained for experiments subsequently exhibited disease symptoms (chalky-white hemolymph) throughout the 3 wk they were observed.

Prior to experimentation, each lobster was photographed for identification (MacDiarmid et al. 2005), measured (nearest 0.1 mm CL), sexed (male, female), staged (premolt, intermolt, postmolt), and checked for injuries (missing legs, missing antennae, damaged telson) (see methods in Forcucci et al. 1994). For ease of identification, each individual also received a uniquely coded cable tie identification tag placed around the base of either the right or left antenna. This tag was shed during molting events, and all molting events were recorded while animals were in captivity, since post-molt behavior has previously been shown to differ from that of intermolt lobsters (Lipcius & Herrnkind 1982).

Molting was recorded as a binary measure (Y or N) based on whether the individual molted immediately prior to (characterized by soft-body during capture) or during the 2 wk in captivity, and was used to evaluate the impacts of molting on behavior. Hence, individuals that molted (~28%) were not excluded from any experiments. Individuals that had soft bodies during collection (postmolt) and soon after molted (premolt) and those that molted during the 2 wk in captivity were considered to have molted during experimentation. Intermolt lobsters were those that did not molt or have soft bodies during experimentation. After molting, lobsters were retagged by comparing distinctive rostral horn patterns between the molt and the individual (MacDiarmid et al. 2005), and their carapace length was remeasured.

We employed a 3-phase experiment using the facilities of the Keys Marine Laboratory in Long Key, Florida. All aquaria and the shallow pond mesocosm had continuously flowing filtered seawater from Florida Bay (salinity: 33 ± 3 ppt, temperature: 24 to 31°C) and were exposed to natural seasonal variation in photoperiod. Animals were initially housed in either a same-sex or mixed-sex pair since sheltering behavior of juvenile lobsters is not influenced by sex-specific shelter preferences (Zimmer-Faust et al. 1985). Lobsters were fed cut frozen shrimp and squid ad libitum each night after behavioral observations were completed to maintain normal nocturnal foraging rhythm. By tracking individually marked lobsters throughout each experiment, we were able to estimate individual differences in aggressive and gregarious behavior and determine if these traits predict denning behavior in captivity and dispersal in the field.

Expt 1: Measures of aggression and gregariousness

During Expt 1, 20 lobsters were observed in size-matched pairs for 1 wk to estimate levels of aggression and gregariousness. Pairs of similar-sized lobsters (maximum size difference: 3.2 mm CL) from the same site were housed in a 40 l aquarium. Each aquarium (n = 10) contained 1 concrete shelter block (40 × 10 × 20 cm) with 2 separate holes (15 × 5 × 20 cm) large enough for 4 juvenile lobsters.

We recorded the number of aggressive acts by each individual nightly between 20:00 and 24:00 h. Lobster pairs were observed simultaneously, with each aquarium being observed by 2 observers for 10 min under indirect red-light illumination (Martin & Bateson 1993). The time at which the single 10 min observation began was haphazardly determined. Aggressive acts included antenna whips (a rapid swipe of the antenna in the direction of the opponent), antenna pushes (a forward-facing push of an opponent with the base of the antennae), and body pushes (a lateral push of an opponent using the legs, tail, or body). The estimate of aggressiveness was the 7-night mean number of all aggressive acts initiated by the individual observed during the 10 min observation period.

To measure gregariousness, the frequency of lobsters co-occupying the artificial shelter was recorded twice a day (between 08:00 to 12:00 h and 20:00 to 24:00 h) at a single point in time for 7 d. When both individuals occupied the same shelter hole they were considered sharing a den; all other possible combinations (individuals both in separate shelter holes, outside of the shelter block, or one inside and one outside of the shelter block) were considered not sharing a den. Our estimate of gregariousness was expressed as the proportion of observations (out of 14) that an individual was observed sharing a shelter with a tank mate. We observed 16 sets of 20 lobsters; each set was collected from a different site in Florida Bay. Hence, Expt 1 was replicated 16 times, with each set of 20 lobsters observed sequentially.

Expt 2: Denning behavior and habitat loss

The 20 lobsters from Expt 1 were transferred to a large outdoor mesocosm pond with 10 artificial shelters where their denning behavior was observed before and after the removal of shelters. The removal of artificial shelters was presumed to simulate the sudden loss of sponge shelters in the field. Each set of 20 juvenile lobsters was placed in an oval concrete

outdoor pond or 'mesocosm' (30 × 15 × 1.3 m) that contained a center island. The mesocosm contained 3 mangrove snappers (*Lutjanus griseus*), approximately 40 cm standard length, as predators to stimulate the juvenile lobsters to adopt normal diurnal denning behavior and nocturnal foraging behavior. No evidence of predation occurred during the course of Expt 2, and snappers were fed frozen shrimp and squid ad libitum each day. Despite the lack of predation, lobsters displayed normal shelter defense behavior when snapper(s) swam close to the shelter blocks. We observed the 16 sets of lobsters that were used in Expt 1; each set was collected from a different site in Florida Bay. Hence, Expt 2 was replicated 16 times, with each set of 20 lobsters observed sequentially.

The mesocosm contained 10 double-stack concrete shelter blocks (40 × 20 × 20 cm) each with 4 sheltering holes (15 × 5 × 20 cm). The shelter blocks were arranged in a circle around the center island of the mesocosm approximately 3 m from the edge of the mesocosm and 4 m apart. Similar shelter blocks in the field have held as many as 16 juvenile lobsters (Zito-Livingston & Childress 2009). This is within the range of lobsters naturally found in sponge shelters in Florida Bay (Childress & Herrnkind 1997) and suggests that the maximum capacity of the 10 shelter blocks in the mesocosm is 160 lobsters. Therefore, we surmised that the 10 shelter blocks in the mesocosm had the capacity to shelter a set of 20 lobsters.

The naïve individually tagged lobsters were released into the mesocosm at night (between 20:00 and 23:00 h). Each day between 08:00 and 12:00 h, the locations of all 20 individuals were recorded by diver census (see methods in Childress & Herrnkind 1996). The lobsters were located for 4 d after introduction to the mesocosm. On Day 4, after recording the location of all individuals, 5 shelter blocks (every other block) were removed from the mesocosm such that the remaining 5 shelter blocks were still in a circle but were now 8 m apart. On Days 5 through 7, the locations of the 20 lobsters among the remaining 5 shelter blocks were recorded. Molted lobsters (those without identification antenna tags) were captured by hand net, identified using rostral horn patterns (MacDiarmid et al. 2005), measured, retagged, and returned to the shelter where they were captured.

We measured 3 aspects of denning behavior averaged for 4 d before shelter loss and 3 d after shelter loss (den use, den sharing, and den fidelity). Den use was defined as an individual residing within a shelter block with or without conspecifics and was averaged separately for all days before and after the shelter-loss event as a proportion of observations. Den sharing was defined as an individual residing within a shelter block along with one or more conspecifics regardless of whether they were sharing the same shelter hole or not and was averaged as described above for den use. Den fidelity was defined as the number of consecutive days an individual remained in the same shelter block even if it changed shelter holes and was averaged as described above for den use. For example, if an individual was using Shelter B after the shelter-loss event (on Day 5) and remained in Shelter B the next 2 d (on Days 6 and 7), it received a den fidelity score of 1.

Expt 3: Dispersal behavior and habitat loss

The 20 individually marked lobsters from Expts 1 and 2 were released back into the field at their original site of collection and were resighted by divers for 1 wk to examine dispersal. At the time of collection, all 16 sites contained 10 artificial shelter blocks, each with 4 sheltering holes. At half of the 16 sites (1 site from each station), all 10 artificial shelter blocks were removed after the lobsters were collected but prior to their release. At the other half of the 16 sites, all 10 artificial shelter blocks remained. The removal of shelter blocks allowed us to examine the influence of both habitat type (sponge shelter present and sponge shelter absent) and shelter treatment (shelter block absent and shelter block present) on dispersal behavior as a fully crossed factorial design. Expt 3 lasted 1 wk and was replicated 16 times, once for each collection of lobsters from a different site in Florida Bay.

Mark-resight methods (Arnason et al. 1991) were used to examine the relationship between resight probability, habitat type, shelter treatment (shelter block present or shelter block absent), and behavioral characteristics of individual lobsters. All 20 individually marked lobsters were haphazardly released into crevice shelters at the sites where they had been collected 2 wk earlier. On the same day, all resident juvenile lobsters at each site were captured by hand net and tagged with an antenna tag. These resident lobsters were resighted for comparison with those that had been held in captivity. Residents that arrived after the initial release were recorded as new residents but were not resighted. Four times, on Days 1, 5, 6, and 7 after initial release, the position of experimental and resident lobsters (<45 mm CL) was recorded by snorkelers via direct observation between 10:00 and 16:00 h. Search time was limited to 1 h. Any individuals that needed to be removed from

shelters to identify antenna tags or have tags added were released back into the shelter from which they were removed.

Statistical analyses

All statistical calculations were performed using JMP 10 software (SAS Institute). Aggression and gregariousness measures from Expt 1 were square-root-transformed to meet the assumptions of normality and were analyzed using ANOVA to determine the relative influences of habitat type, size, sex, injury, and molt history (see Appendix 1 for classifications). Pearson correlations were used to examine if aggression and gregariousness were related within individuals.

Den use, den sharing, and den fidelity measures from Expt 2 were analyzed using a mixed-model ANOVA, with individual as a random factor to determine the relative influences of shelter-loss treatment, habitat type, size, sex, injury, molt history, aggression, and gregariousness. Pearson correlations were used to examine if den use, den sharing, and den fidelity were related before and after shelter loss and were also used to examine if aggression and gregariousness were related to any measure of denning behavior.

All released individuals in Expt 3 were classified as either 'resighted' or 'not resighted'. 'Resighted' individuals were those that had been observed on at least 1 of the 4 days. Individuals classified as 'not resighted' were those that were not observed on any of the 4 d. We then analyzed this binary outcome by habitat type (sponge shelter absent vs. sponge shelter present) and shelter-block treatment (shelter block absent vs. shelter block present) using a logistic regression model with individual characteristics of size, sex, injury, molt history, aggression, and gregariousness as covariates. Pearson correlations were used to examine if aggression and gregariousness were related to resight probability.

RESULTS

Expt 1: Measures of aggression and gregariousness

Aggression and gregariousness were not correlated among individual juvenile lobsters ($r = 0.01$, $p = 0.91$) despite both being correlated with size in opposite directions (size–aggression: $r = 0.37$, $p < 0.001$, size–gregariousness: $r = -0.20$, $p < 0.001$).

Neither habitat type nor sex influenced juvenile lobster aggression (Table 1). Aggression increased significantly with body size, with larger individuals being more aggressive than smaller individuals ($F = 45.7$, $p < 0.001$; Fig. 2a, Table 1). Injury status also influenced mean aggressiveness, with injured lobsters showing significantly lower levels of aggression ($F = 16.4$, $p < 0.001$; Table 1). Likewise, lobsters that were classified as having molted showed signifi-

Table 1. *Panulirus argus*. ANOVA analyses for aggressive and gregarious behaviors. Aggression is the mean number of all aggressive acts per 10 min observation; gregariousness is the proportion of observations of den sharing with a conspecific. See Appendix 1 for a description of the main effects

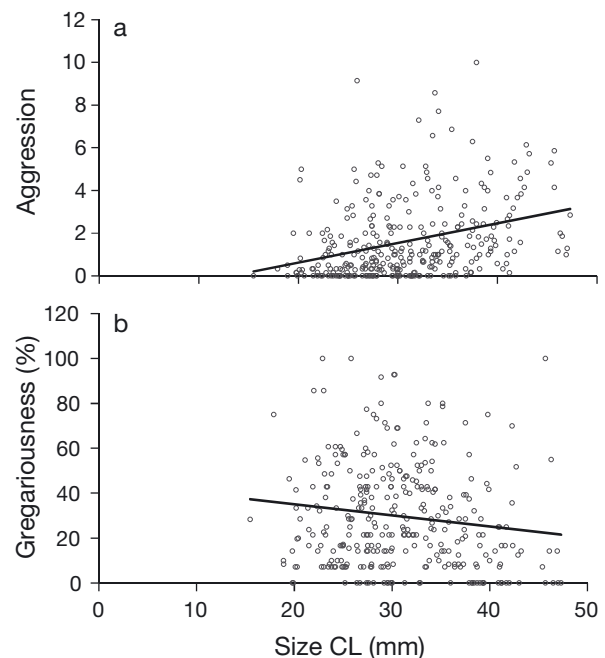| Behavior	Source	F-ratio	p-value
Aggression	Size	45.7	<0.001
	Habitat type (SP/SA)	0.1	0.76
	Sex (M/F)	2.3	0.13
	Injury (Y/N)	16.4	<0.001
	Molting (Y/N)	5.8	<0.05
Gregariousness	Size	8.3	<0.01
	Habitat type (SP/SA)	3.4	0.28
	Sex (M/F)	0.3	0.58
	Injury (Y/N)	1.2	0.28
	Molting (Y/N)	0.2	0.68

Fig. 2. *Panulirus argus*. Effect of size on aggressive and gregarious behavior: (a) mean aggression score and (b) percent gregariousness exhibited by size of juvenile spiny lobster. A best-fit line was added to show general trends. CL: carapace length

cantly lower levels of aggression ($F = 5.8$, p < 0.05; Table 1).

Neither habitat type nor sex influenced juvenile lobster gregariousness (Table 1). However, mean gregariousness decreased significantly with size ($F = 8.3$, p < 0.01; Fig. 2b, Table 1). Neither injury status nor molt status had any influence on mean gregariousness (Table 1).

Expt 2: Denning behavior and habitat loss

Den use was initially lower for lobsters from sponge-absent sites ($F = 11.4$, p < 0.001; Fig. 3a) and significantly decreased after shelter loss for lobsters from sponge-present sites ($F = 7.7$, p < 0.01; Fig. 3a).

There were also significant interactions between shelter loss, habitat type, and size (Table 2). The higher den use by lobsters from sponge-present sites
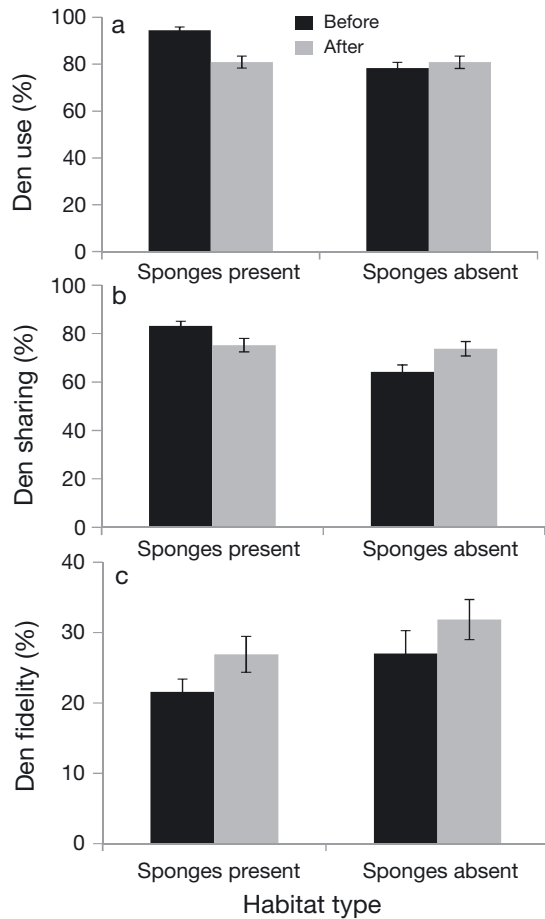

Fig. 3. *Panulirus argus*. Effect of habitat type on denning behavior before and after shelter loss. Mean percent: (a) den use, (b) den sharing, and (c) den fidelity before and after the shelter-loss event by habitat type (sponges present or sponges absent). Black bars represent data before the shelter-loss event; gray bars represent data after the shelter-loss event. Error bars are the standard error of the mean

Table 2. *Panulirus argus*. Mixed-model ANOVA for denning behavior. Den use is the proportion of days a lobster was found in a shelter block, den sharing is the proportion of days a lobster was found in a shelter block with one or more conspecifics, and den fidelity is the proportion of days a lobster was found in the same shelter block. The model includes interaction terms between the shelter-loss treatment condition (before [B] or after [A]) and the other main effects. See Appendix 1 for a description of the main effects

Behavior	Source	*F*-ratio	p-value
Den use	Treatment (B/A)	7.7	<0.01
	Habitat type (SP/SA)	11.4	<0.001
	Size (CL, mm)	0.5	0.50
	Sex (M/F)	3.0	0.09
	Injury (Y/N)	2.8	0.10
	Molt (Y/N)	1.3	0.25
	Aggression	0.6	0.44
	Gregariousness	<0.1	0.88
	Habitat × Treatment	17.9	<0.001
	Size × Treatment	4.1	<0.05
	Sex × Treatment	0.5	0.48
	Injury × Treatment	0.7	0.39
	Molt × Treatment	0.4	0.50
	Aggression × Treatment	4.5	0.02
	Gregarious × Treatment	0.1	0.72
Den sharing	Treatment (B/A)	0.4	0.51
	Habitat type (SP/SA)	16.5	<0.001
	Size (CL, mm)	0.1	0.77
	Sex (M/F)	0.9	0.35
	Injury (Y/N)	5.2	0.02
	Molt (Y/N)	2.7	0.11
	Aggression	<0.1	0.90
	Gregariousness	<0.1	0.95
	Habitat × Treatment	14.9	<0.001
	Size × Treatment	4.6	<0.05
	Sex × Treatment	<0.1	0.92
	Injury × Treatment	<0.1	0.91
	Molt × Treatment	2.0	0.16
	Aggression × Treatment	1.4	0.24
	Gregarious × Treatment	<0.1	0.91
Den fidelity	Treatment (B/A)	1.4	0.23
	Habitat type (SP/SA)	4.1	<0.05
	Size (CL, mm)	15.0	<0.001
	Sex (M/F)	1.2	0.27
	Injury (Y/N)	0.2	0.63
	Molt (Y/N)	3.8	0.05
	Aggression	0.1	0.81
	Gregariousness	0.4	0.54
	Habitat × Treatment	1.0	0.31
	Size × Treatment	5.2	<0.05
	Sex × Treatment	0.0	0.91
	Injury × Treatment	3.4	0.07
	Molt × Treatment	<0.1	0.85
	Aggression × Treatment	1.3	0.25
	Gregarious × Treatment	0.8	0.37

over lobsters from sponge-absent sites disappeared after shelter loss ($F = 17.9$, $p < 0.001$; Fig. 3a). In contrast, the decrease in den use by large lobsters was observed only after shelter loss ($F = 4.1$, $p < 0.05$; Fig. 4a). Den use was not significantly related to sex, injury status, molt status, or gregariousness of individuals (Table 2).

Den sharing was significantly higher for lobsters from sponge-present sites than for those from sponge-absent sites ($F = 16.5$, $p < 0.001$; Fig. 3b), but it was not influenced by the sudden loss of shelters (Fig. 3b) or lobster size (Fig. 4b). There were, however, significant interactions such that den sharing differences in lobsters from sponge-present versus sponge-absent sites prior to shelter loss disappeared after shelter loss ($F = 14.9$, $p < 0.001$; Fig. 3b) and the

decrease of shelter sharing by large lobsters was observed only after shelter loss ($F = 4.6$, $p < 0.05$; Fig. 4b). Den sharing was not significantly related to sex, molt status, aggression, or gregariousness of individuals (Table 2).

Den fidelity was significantly lower for lobsters from sponge-present sites than for those from sponge-absent sites ($F = 4.1$, $p < 0.05$; Fig. 3c) and decreased with increasing size ($F = 15.0$, $p < 0.001$; Fig. 4c), but it was not influenced by shelter loss (Table 2). There was also a significant interaction between size and shelter loss, with larger lobsters showing even less den fidelity after shelter loss ($F = 5.2$, $p < 0.05$; Fig. 4c). Den fidelity was not significantly related to sex, injury status, molt status, or gregariousness of individuals (Table 2).

Only after shelter loss was aggression negatively correlated with den use ($r = -0.135$, $p < 0.05$) and den fidelity ($r = -0.16$, $p < 0.05$), but not with den sharing ($r = -0.06$, $p = 0.38$). Gregariousness was unrelated to all sheltering measures both before and after shelter loss.

Expt 3: Dispersal behavior and habitat loss

Overall, 73 of the 261 tagged lobsters (28%) were resighted at least once during the week after their release. Two factors emerged as the best predictors of lobster resight (Table 3). First, fewer lobsters were resighted in sponge-absent and shelter-block-absent sites ($\chi^2 = 5.2$, $p < 0.05$; Fig. 5a). Second, smaller lobsters were resighted more frequently than larger lobsters ($\chi^2 = 47.9$, $p < 0.001$; Fig. 5b). Aggression was negatively correlated with resight probability ($r = -0.13$, $p < 0.05$), but gregariousness was unrelated to resight probability ($r = 0.01$, $p = 0.85$).

DISCUSSION

In this study, we examined individual variation in aggressive, gregarious, and denning behavior (den use, den sharing, and den fidelity) in relation to various characteristics (including size, sex, injury, and molt history) before and after a simulated shelter-loss event. Large, uninjured
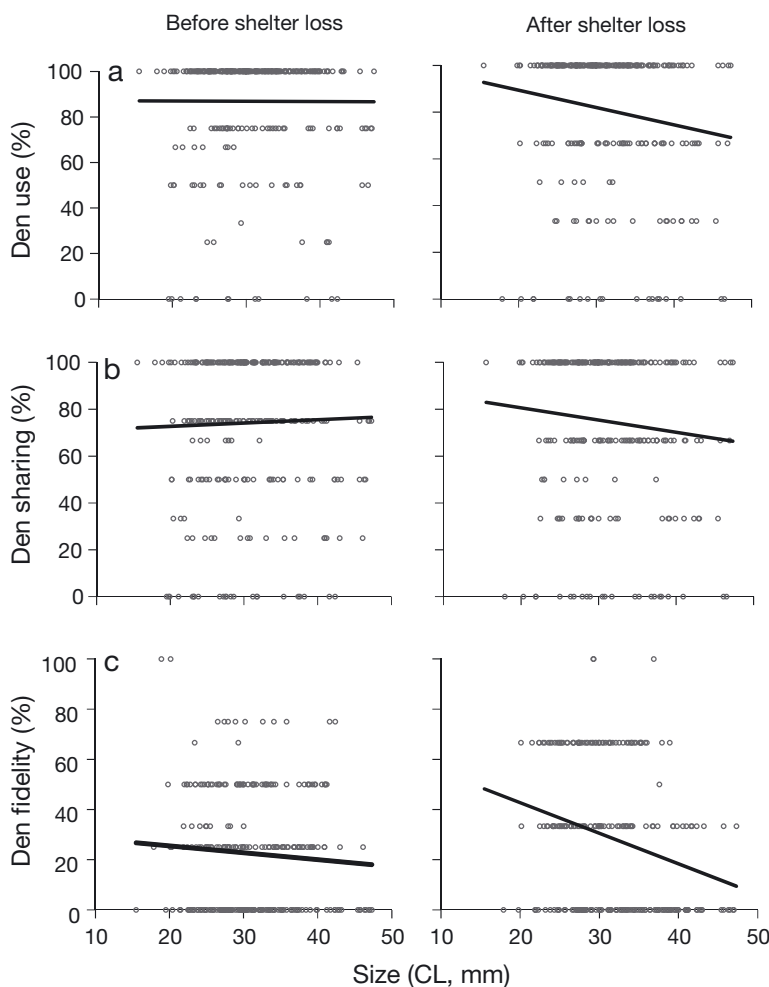
Fig. 4. *Panulirus argus*. Effect of size on denning behavior before and after shelter loss. Mean percent: (a) den use, (b) den sharing, and (c) den fidelity before and after shelter loss analyzed by lobster size. Left column: before shelter loss; right column: after shelter loss. Black linear best-fit lines reflect trends before and after shelter loss. CL: carapace length

Table 3. *Panulirus argus*. Logistic regression model for resight status (resighted vs. not resighted). Model includes interaction terms between the shelter-block treatment condition (blocks present [BP] or blocks absent [BA]) and the other main effects. See Appendix 1 for a description of the main effects

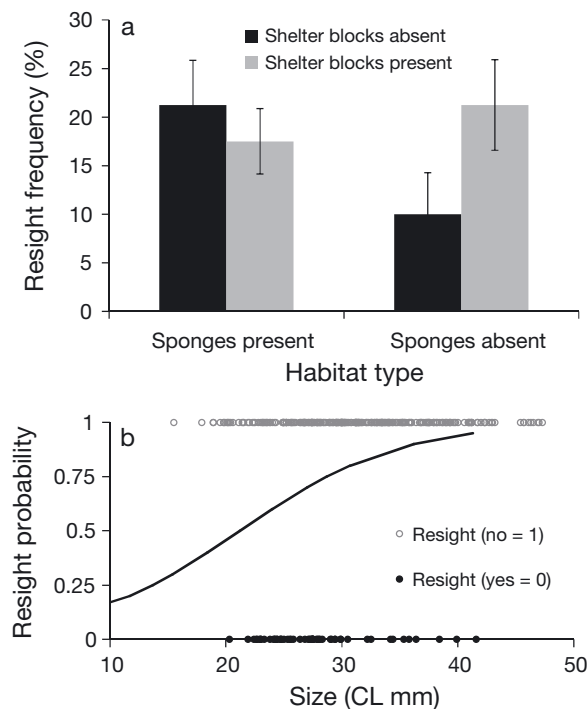| Source	χ^2	p-value
Treatment (BP/BA)	<0.1	0.98
Habitat type (SP/SA)	0.7	0.42
Size (CL, mm)	47.9	<0.001
Sex (M/F)	0.6	0.46
Injury (Y/N)	0.5	0.48
Molt (Y/N)	0.2	0.66
Aggression	1.2	0.27
Gregariousness	1.8	0.19
Habitat × Treatment	5.2	<0.05
Size × Treatment	2.8	0.10
Sex × Treatment	0.1	0.79
Injury × Treatment	0.3	0.61
Molt × Treatment	2.3	0.13
Aggression × Treatment	3.4	0.07
Gregariousness × Treatment	4.3	0.04

Fig. 5. *Panulirus argus*. Effect of habitat type, artificial shelter presence, and size on dispersal. (a) Mean percent resight frequency of juvenile spiny lobsters over 4 d by habitat type (sponge present, sponge absent, shelter block present, and shelter block absent). Error bars are the standard error of the mean. (b) The probability of resighting an individual of a particular size. Probability curve was based on data collected during Expt 3, with some individuals being resighted at least once (black) and other individuals never being resighted (gray)

individuals were the most aggressive, and small individuals were the most gregarious. The influence of body size on aggression has been well studied in other crustaceans, including clawed lobsters (Atema & Steinbach 2007), crayfish (Moore 2007, Martin & Moore 2008), and crabs (Pedetta et al. 2010). In a review of palinurid lobsters (Atema & Cobb 1980), size was the best predictor of aggression levels in *Jasus lalandii* (Fielder 1965) and *Panulirus interruptus* (Roth 1972). Although aggressive behavior has been described for spiny lobsters, few studies have clearly demonstrated how these behaviors impact competition for resources.

The patterns of den use, den sharing, and den fidelity after shelter loss did not match our expectation that large, aggressive individuals would exclude smaller individuals from entering and sharing dens. While some large, aggressive individuals occupied shelter blocks by themselves, many did not occupy shelter blocks at all. Instead, smaller, less aggressive individuals occupied the shelter blocks. As a consequence, smaller lobsters exhibited increased den use, den sharing, and den fidelity after shelter loss. In addition, smaller lobsters were resighted more often than larger lobsters during the mark-resight study. These results suggest that, although aggression may play a role in intraspecific interactions, competition for dens may not be as intense as predicted, even when shelter is limited. Rather than den competition, vulnerability may be a more important factor in determining sheltering behavior with respect to size and aggression. We hypothesize that larger juvenile lobsters, with their greater ability to disperse, decrease their predation risk by dispersing when shelters are limited. This hypothesis is supported by tethering experiments that have shown greater predation of smaller tethered juveniles than of larger tethered juveniles (Andree 1981, Eggleston & Lipcius 1992, Smith & Herrnkind 1992) and should be further examined by evaluating dispersal of juveniles using acoustic telemetry.

In field experiments, 28% of released lobsters were resighted, with habitat type (specifically sponge-absent and shelter-block-present sites) and size influencing dispersal. Smaller individuals were less likely to disperse and therefore more likely to be resighted, supporting prior conclusions based on their vulnerability to predation when outside of shelters (Andree 1981, Eggleston & Lipcius 1992, Smith & Herrnkind 1992). Another explanation for the difference in dispersal between small and large juveniles is that larger juveniles have greater home ranges and are expected to disperse more widely over a matter

of days (Herrnkind 1980). Providing shelter blocks on sponge-shelter-absent sites resulted in a similar percentage of resighted juveniles (18%) as sponge-shelter-present sites (17%) and sponge-shelter-present sites with shelter blocks (15%). Since juveniles had a lower percent of resightings on sponge-shelter-absent sites without added shelter blocks (9%), providing artificial shelters may be one method of mitigating habitat loss.

Variation in Caribbean spiny lobster aggression, gregariousness, and denning behavior may provide a mechanism for dealing with habitat loss. Caribbean spiny lobsters exhibit ontogenetic shifts in habitat with corresponding changes in behavior. Specifically, smaller juveniles (15 to 20 mm CL) have recently migrated from algal beds and have experienced shifts in behavior from an asocial to a social lifestyle (Andree 1981, Marx & Herrnkind 1985, Childress & Herrnkind 1996, 2001b). In contrast, larger, subadult individuals (>45 mm CL) begin to exhibit migrations and use coral reef habitats (Kanciruk & Herrnkind 1972, Kanciruk 1980, Herrnkind et al. 1997, Bertelsen & Hornbeck 2009, Bertelsen 2013). Maintaining behavioral differences may be important for ontogenetic niche shifts (Childress & Herrnkind 2001a), and, since Caribbean spiny lobsters exhibit distinct shifts in habitat use, flexibility in behavior may be helpful for surviving habitat transitions and coping with altered conspecific interactions.

The abundance of resources in an area may influence shelter competition between conspecifics. For example, post-pueruli of *Panulirus longipes* that have recently settled are more aggressive when competing for limited shelter or food (Berrill 1976). In our mesocosm experiments, habitat type influenced den use and den sharing, with individuals from sponge-absent sites exhibiting lower den use and den sharing than individuals from sponge-present sites. In sponge-absent sites, the decrease in den use and den sharing was driven primarily by lobster size rather than whether a lobster previously lived in a sponge-present or sponge-absent site. Although aggressive encounters were seen, gregarious behavior was still exhibited, suggesting that the relationship between aggression, gregariousness, and denning behavior is complex.

For juvenile spiny lobsters, sharing a shelter requires cooperation between 2 or more individuals and is influenced by habitat type and the size distribution of juveniles in the group. In our mesocosm study, juvenile spiny lobsters from sponge-absent sites did not change their level of den use with the sudden loss of shelter, suggesting behavioral adaptation to shelter-limited environments. These individuals shared shelters less even when shelters were abundant, suggesting that juvenile lobsters from sponge-absent habitats had previously experienced shelter competition and were less willing to share shelters with conspecifics.

By determining how animals behaviorally respond to habitat loss, we can better predict the impacts of future environmental change. As a commercially important species, understanding potential influences of habitat loss on spiny lobster abundance and distribution is important for effective management of this fishery. Here, we show that, although larger individuals exhibited higher levels of aggression, aggression did not predict denning behavior. We expected that shelter loss would increase competition for shelter. Instead, large, aggressive individuals were less likely to use dens, share dens, and remain in dens for consecutive days than smaller, less aggressive individuals. For this gregarious species, these results suggest that individuals are plastic in their behavior and that there is a cost associated with den sharing for larger individuals when shelter is limited. Understanding the role of habitat selection can improve monitoring, management, and conservation of animals and their habitat (Jonzén 2008). This study is a step forward in evaluating the role of individual behavioral variation in influencing den competition and the behavioral mitigation of habitat loss.

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Appendix 1. Description of behaviors and main effects used in ANOVA analyses

Variable	Abbreviation	Description
Shelter-loss treatment	B: before A: after	During Expt 2, shelter loss was created by removing 50% of the shelter blocks from the mesocosm. Measurements were taken before and after shelter-block removal.
Shelter-block treatment	BP: shelter block present BA: shelter block absent	Binary measure of the presence or absence of artificial shelter blocks on field sites in Expt 3.
Habitat type	SP: sponge present SA: sponge absent	Binary measure of the presence or absence of large sponges (>20 cm diameter).
Size	n/a	Continuous measure of carapace length (mm) at time of collection.
Sex	M: male F: female	Binary measure determined at time of collection.
Injury	N: no injury Y: yes or +1 injuries	The number of injuries an individual had at time of collection.
Molt history	N: no Y: yes	Binary measure with intermolt lobsters not having molted (N) and postmolt, premolt, and molted lobsters having molted (Y).
Aggression	n/a	Continuous measurement determined in Expt 1 and defined as the number of aggressive acts initiated by an individual.
Gregariousness	n/a	Continuous measurement determined in Expt 1 and defined as 2 individuals occupying the same hole within a shelter block.
Den use	n/a	Continuous measurement determined in Expt 2 and defined as an individual residing within a shelter block with or without conspecifics.
Den sharing	n/a	Continuous measurement determined in Expt 2 and defined as an individual residing within an shelter block with 1 or more individuals.
Den fidelity	n/a	Continuous measurement determined in Expt 2 and defined as the number of consecutive days an individual remained in the same shelter block.
Resight	n/a	Binary measure of individuals being resighted or not resighted. Resighted individuals were those that had been sighted on at least 1 of the 4 d.