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Benjamin C. Gutzler
Old Dominion University

Mark J. Butler IV
Old Dominion University, mbutler@odu.edu

Donald C. Behringer

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Casitas: a location-dependent ecological trap for juvenile Caribbean spiny lobsters, *Panulirus argus*

Benjamin C. Gutzler¹, Mark J. Butler, IV^{1*}, and Donald C. Behringer^{2,3}

¹Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA

²Fisheries and Aquatic Sciences Program, University of Florida, Gainesville, FL 32653, USA

³Emerging Pathogens Institute, University of Florida, Gainesville, FL 32611, USA

*Corresponding author: tel: +1 757 683 3609; fax: +1 757 683 5283; e-mail: mbutler@odu.edu

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Casitas are artificial shelters used by fishers to aggregate Caribbean spiny lobsters (*Panulirus argus*) for ease of capture. However, casitas may function as an ecological trap for juvenile lobsters if they are attracted to casitas and their growth or mortality is poorer compared with natural shelters. We hypothesized that juvenile lobsters may be at particular risk if attracted to casitas because they are less able than larger individuals to defend themselves, and do not forage far from shelter. We compared the nutritional condition, relative mortality, and activity of lobsters of various sizes in casitas and natural shelters in adult and juvenile lobster-dominated habitats in the Florida Keys (United States). We found that the ecological effects of casitas are complex and location-dependent. Lobsters collected from casitas and natural shelters did not differ in nutritional condition. However, juvenile lobsters in casitas experienced higher rates of mortality than did individuals in natural shelters; the mortality of large lobsters did not differ between casitas and natural shelters. Thus, casitas only function as ecological traps when deployed in nursery habitats where juvenile lobsters are lured by conspecifics to casitas where their risk of predation is higher. These results highlight the importance of accounting for animal size and location-dependent effects when considering the consequences of habitat modification for fisheries enhancement.

Keywords: aggregation device, casita, ecological trap, *Panulirus argus*, spiny lobster.

Introduction

Ecological traps, a subset of the broader concept of an evolutionary trap (Schlaepfer *et al.*, 2002; Robertson *et al.*, 2013), occur when a maladaptive and often novel habitat is chosen by an animal over more typical habitats where their fitness is greater (Robertson and Hutto, 2006). This is generally a result of anthropogenic change and occurs when the cues animals use to judge habitat suitability, are decoupled from habitat quality (Gilroy and Sutherland, 2007). Often the costs of ecological traps to animal fitness are associated with recruitment failures or decreased breeding success (Dwernychuk and Boag, 1972; Kriska *et al.*, 1998; Weldon and Haddad, 2005), decreased physical condition (Hallier and Gaertner, 2008; Semeniuk and Rothley, 2008), or increased mortality (Hawlena *et al.*, 2010; Ekroos *et al.*, 2012). Although the concept of an ecological trap was first described in the 1970s (Dwernychuk and Boag, 1972; Gates and

Gysel, 1978), few cases have been rigorously tested (Schlaepfer *et al.*, 2002; Pärt *et al.*, 2007) and most come from terrestrial systems. For example, passerine birds often prefer habitats with heterogeneous vegetation, and thus preferentially nest along human-created habitat edges where predators of nestlings are concentrated (Gates and Gysel, 1978; Weldon and Haddad, 2005). Mayflies lay their eggs on asphalt roads that reflect polarized light at a greater intensity than do the streams where eggs are normally laid (Kriska *et al.*, 1998). Only a few ecological traps are documented in marine environments. For example, tuna that are attracted to fish aggregation devices are in poorer nutritional condition than free-schooling tuna, and so are more vulnerable to exploitation (Hallier and Gaertner, 2008). Another potential marine ecological trap is one posed by casitas—artificial structures placed on the seabed to aggregate Caribbean spiny lobster (*Panulirus argus*) for ease of capture.

Casitas as possible ecological traps

Caribbean spiny lobsters support the most valuable fishery in the Caribbean (Chávez, 2009) where fishers use a variety of methods to capture them, including casitas (also known as pesqueros or condos) that mimic the natural crevice shelters used by lobsters. Casitas vary in size and construction, but are usually flat, rectangular structures $\sim 4 \text{ m}^2$ in area with at least two open sides $< 10 \text{ cm}$ in height. Lobsters aggregate in casitas, increasing their ease of capture by fishers. However, the potential effect of casitas on lobster population biology and productivity is contentious because of gaps in our understanding of their effects on lobsters of all sizes (Herrnkind and Cobb, 2007).

Generally, only a few lobsters share a natural den at a time, especially in nursery habitats (Childress and Herrnkind, 1997). However, casitas can contain dozens of individuals at concentrations far exceeding those found in most natural shelters (Mintz et al., 1994). When placed in environments with few natural shelters, casitas are very effective at aggregating lobsters, which are attracted to conspecifics via chemosensory cues (Zimmer-Faust et al., 1985; Ratchford and Eggleston, 1998). In nature, this behaviour aids them in finding scattered shelter and in group defence against predators (Ratchford and Eggleston, 2000; Childress and Herrnkind, 2001). Unlike larger lobsters, small juvenile lobsters are usually solitary and too small to deter predators, even when in groups, so they rely instead on camouflage for protection; thus, over-aggregation of small juvenile lobsters may be maladaptive (Anderson et al., 2013).

Most research on casitas has focused on their effects on large, fishery-sized lobsters targeted by fishers (de la Torre and Miller, 1987; Sosa-Cordero et al., 1998; Nizinski, 2007). Other studies have examined the potentially beneficial effects of small shelters on juvenile lobster populations in nursery habitats where shelters may be scarce (Eggleston et al., 1992; Arce et al., 1997; Butler and Herrnkind, 1997; Briones-Fourzán et al., 2007) and post-settlement predation on juvenile lobsters is a major population bottleneck (Herrnkind and Butler, 1986; Butler and Herrnkind, 1997). Depending on the habitat where casitas are placed, they aggregate juvenile, adult, or both lobster stages. It is thus crucial to understand the effects of casitas on lobsters of all sizes (ages), especially because casitas are currently deployed throughout the Caribbean and their use is expanding.

Many predators of juvenile lobsters (e.g. grouper, Epinephelinae; snapper, Lutjanidae; triggerfish, Balistidae; nurse sharks, *Ginglymostoma cirratum*) also are attracted to casitas (Eggleston et al., 1992; Mintz et al., 1994). These gape-limited piscine predators pose little threat to legal-sized lobsters, but small juvenile lobsters that occupy casitas may not be able to avoid or fend off such predators. The concentration of lobsters and other animals attracted to casitas also depletes food resources in the area immediately surrounding the casita (Nizinski, 2007). Large lobsters are highly mobile and can forage beyond the prey-depleted zone near casitas, whereas less mobile juvenile lobsters are perhaps unable to reach prey-rich areas outside this zone (Butler and Herrnkind, 2000). Increased predation pressure near casitas may also indirectly limit the movement and foraging of small lobsters (Weiss et al., 2008).

Like other artificial structures deployed in the sea to attract fish and invertebrates for ease of capture (e.g. fish aggregating devices, artificial “reefs”), it remains unclear whether casitas enhance lobster populations (the “Production” hypothesis) or merely redistribute lobsters by concentrating them for easier exploitation (the “Attraction” hypothesis; Pickering and Whitmarsh, 1997; Wilson

et al., 2001; Granneman and Steele, 2014). Some contend that adding casitas to habitats where a lack of structure limits lobster abundance may reduce predator-induced mortality (Briones-Fourzán and Lozano-Álvarez, 2001) or permit lobsters to exploit underutilized areas, thus expanding their range, population size, and “production” (Sosa-Cordero et al., 1998). But the “population expansion” hypothesis assumes that *P. argus* populations are normally limited by density-dependent growth, for which evidence is currently lacking (Butler and Herrnkind, 1997; Behringer and Butler, 2006). Alternately, the “Attraction” hypothesis suggests that casitas simply change the spatial distribution of lobsters by aggregating them (Davis, 1985) without a commensurate increase in survival, growth, or reproduction. In addition, the unnatural aggregation of lobsters in casitas may subject them to more predators, pathogens, and perhaps greater intraspecific competition for food. We hypothesized that casitas act as an ecological trap by decreasing foraging success and increasing the risk of predation on small juvenile lobsters. Our study tested the potential effect of casitas on the Caribbean spiny lobster in two distinctly different habitats: shallow nursery areas and deeper adult lobster habitat.

Methods

Study area

Our study sites were located in the Florida Bay north of the Middle Florida Keys and in the Gulf of Mexico north of the Lower Florida Keys (FL, United States; Figure 1). The sites that we studied and the casitas we used in the Middle Keys were those originally deployed in 1990 by Mintz et al. (1994) near the Arsnicker Keys and Twin Keys within Everglades National Park. These sites were 2–3 m deep within mixed hardbottom and seagrass habitat typical of lobster nursery areas in the Florida Keys. Each site contained an array of 16 casitas made of concrete and PVC spaced $\sim 30 \text{ m}$ apart; most of them were still functional nearly 25 years after their initial deployment by Mintz et al. (1994). As described by Mintz et al. (1994), two types of casitas of slightly different dimensions were deployed at the two sites: eight “large” casitas ($177 \times 118 \times 6 \text{ cm}$) and eight

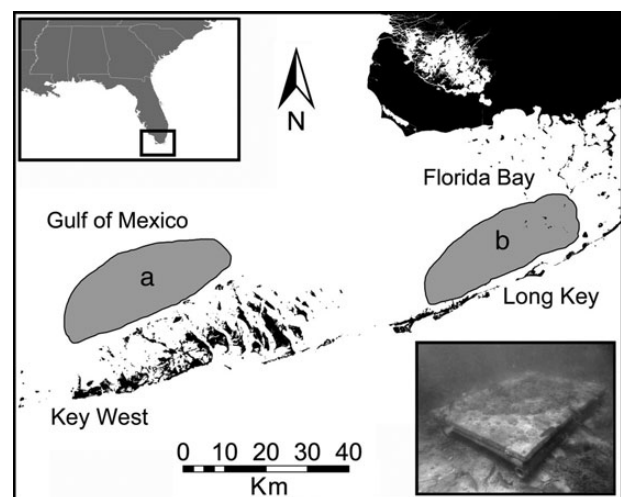


Figure 1. Study areas in the Florida Keys, FL, United States. (Top inset) Location of the Florida Keys at the southern terminus of the Florida peninsula. (Bottom inset) Photo of a casita. (a) Adult habitat study region in the Lower Florida Keys. (b) Nursery habitat study region in the Middle Keys.

“medium” casitas (157 × 105 × 4 cm). These casitas are roughly equivalent in size and shape to the casitas used in fisheries throughout the Caribbean, especially in the most important dimension of opening height, which is often 6–15 cm (Lozano-Álvarez *et al.*, 2003; Ley-Cooper *et al.*, 2013). However, the casitas used by fishers and those used in this study are much larger than the small, artificial structures employed in some experimental studies and referred to by various names (e.g. “small casitas”, *sensu* Eggleston *et al.*, 1990; “shelters” *sensu* Butler and Herrnkind 1997). At the Lower Keys sites, we used existing casitas deployed by fishers on sand habitat in ~10 m of water several km north of the islands. These casitas varied in size and construction, but were generally ~200 cm long × 150 cm wide × 6 cm tall with two open sides, and thus similar in size to those on our Middle Keys sites and those used Caribbean-wide by fishers.

In the Middle Keys, we compared the lobster populations from casitas to those from natural shelters (e.g. solution holes, coral heads, and large sponges) found in nearby hardbottom areas. At the study site in the Lower Keys, an eroded reef line between the Content Keys and Mud Keys as well as scattered coral heads are the dominant natural shelters used by lobsters in the area. Lobsters obtained from those shelters were therefore used for comparison to lobsters collected from casitas.

We handled and processed all lobsters humanely and in accord with applicable animal care regulations; in the United States, studies involving decapods are not subject to the same animal care regulations as vertebrates.

Effect of shelter type on nutritional condition

From May to August of 2012 and 2013, we compared the population structure and nutritional condition of lobsters captured by divers using hand nets and tail snares from a haphazard subset of casitas and natural shelters (e.g. coral heads, solution holes, and large sponges) at the two Middle Keys sites (Arsnicker Keys and Twin Keys) and in the Lower Keys. We also estimated the occupancy of casitas by surveying all lobsters present under 16 casitas ($n = 7$ in the Middle Keys and $n = 9$ in the Lower Keys), a subset of those that we visited during the entire study. After capture, we recorded the carapace length (CL), sex, injuries, and molt stage (based on microscopic analysis of pleopods; Lyle and MacDonald 1983) of each lobster ($n = 669$). We retained a subset of the lobsters for analyses of nutrition ($n = 325$), euthanizing them by rapid freezing and then dissecting out their hepatopancreas, which was then preserved in 95% ethanol. Later, the dry weight of each hepatopancreas was determined by drying at 60°C for 72 h and computing the dry weight index of the hepatopancreas (DWI; Bryars and Geddes, 2005). The DWI was superior to four other commonly used nutritional indices that we tested (Gutzler, 2014).

We analysed the data in a one-way ANCOVA with four levels to test the effects of casitas and natural shelters in the Middle Keys nursery habitat and Lower Keys adult habitat on DWI, using lobster CL as a covariate. We followed up by testing for differences between treatment group means using a difference contrast. We rank-transformed the data to avoid violating parametric assumptions.

Effect of shelter type on relative predation-induced mortality

We used tethering to assess differences in the relative mortality of large and small lobsters in casitas and natural shelters in the two Florida Keys study regions. Lobsters were tethered by tying

monofilament fishing line around their carapace between the second and third pereopods, and tying on a snap swivel on the dorsal side of the carapace before sealing the knots with cyanoacrylate superglue. The snap swivel was clipped to a brick with ~30 cm of monofilament for small (CL ≤ 35 mm) lobsters, or two bricks with ~50 cm of monofilament for large (CL ≥ 60 mm) lobsters. Tethered lobsters were placed by divers at the entrance of casitas or next to appropriately sized natural shelters such as solution holes, large sponges, and coral heads. In both cases, we used shelters already occupied by lobsters whenever possible. Each tethered lobster was thus able to freely move in and out of the shelter, and could retreat well within it. After 24 h, we returned and assessed mortality. Missing lobsters were considered killed if the tether was torn or there were remnants of carapace still attached to it; otherwise, we considered missing lobsters to have escaped and excluded them from the analyses. Less than 10% of the lobsters escaped their tethers. We tethered 184 lobsters at casitas and 147 lobsters at natural shelters during summer of 2012 and 2013. In the Middle Keys, where two distinct sizes of casita were used, we obtained usable data (excluding any potential escapes) from 58 lobsters at 13 different casitas of the “large” design and 25 lobsters under seven different casitas of the “medium” design.

Although the survival of tethered lobsters may be correlated with lobster density within casitas, it explains <10% of the variance in survival (Mintz *et al.*, 1994). Therefore, we did not determine lobster density within each casita before deploying tethered lobsters, so as to avoid disturbing the occupants. We never tethered lobsters in casitas that were unoccupied or sparsely occupied. We also did not quantify predator abundance around casitas for two reasons. First, measures of daytime predation only cover a fraction of the 24-h period, the very fraction when predation on lobsters is often low. Diver observations, especially daytime observations, also miss most of the transient predators that consume lobsters (Smith and Herrnkind 1992). Second, previous results revealed only a weak relationship between lobster survival and predator abundance near casitas (Mintz *et al.* 1994, Eggleston *et al.*, 1997).

We analysed the tethering data using a four-way log-linear contingency analysis to compare the effects of region, shelter type, and size on lobster survival. We followed up with both visual inspection of the data and subdivision of the contingency table to determine which comparisons between the sites, lobster size classes, and shelter types were responsible for differences between observed and expected frequencies.

Assessment of relative activity patterns between shelter types and size classes

We used accelerometry to test for differences in lobster activity between those dwelling in natural shelters vs. casitas, following protocols described in Gutzler and Butler (2014). We captured lobsters from casitas ($n = 7$) and natural shelters ($n = 13$) in the Middle Keys and affixed to them an electronic backpack that transmitted accelerometry data (AT-82 coded transmitter tag with a miniSUR receiver, Sonotronics, Inc.); lobsters were then immediately released back into their original shelter. After 24 h, we returned to the site and used a directional hydrophone (DH-4 Underwater Diver Receiver, Sonotronics, Inc.) to relocate and recapture the lobster. After recapture, we removed the backpack and released the lobster. The accelerometry data were processed in MATLAB®, then analysed using a split-plot ANOVA, with the fraction of data points spent active each hour as the factor of interest, shelter type as the whole-plot factor, hour of day as the subplot factor, and individual lobsters as

Table 1. Results of a one-way ANCOVA testing the effect of the four region × shelter combinations (Lower Keys natural habitat, Lower Keys casita, Middle Keys natural habitat, and Middle Keys casita) on the nutritional condition (hepatopancreas DWI) of lobsters, with CL as a covariate. Group means of DWI are shown below, with homogeneous subsets underlined as determined by a deviation contrast.

Source	d.f.	MS	F	p
Carapace length (covariate)	1	252525.304	37.381	< 0.001
Shelter type + region	3	18422.838	2.727	0.044
Error	320	6755.488		
Total	325			
Group	Lower Keys casita	Lower Keys natural	Middle Keys casita	Middle Keys natural
Mean DWI	1.096	0.953	0.756	0.581

blocks. All data were rank-transformed because they violated parametric assumptions.

Results

Effect of shelter type on nutritional condition

Mean lobster size was 50.8 ± 22.2 mm CL (mean \pm 1 SD) in the Middle Keys ($n = 249$) and 84.0 ± 11.4 mm CL in the Lower Keys ($n = 76$). Sex ratios did not differ between regions or shelter types, and none of the lobsters collected appeared reproductively active. The lobsters captured in casitas were generally larger than those captured in natural shelters (mean size 66.0 ± 26.1 mm CL in casitas and 51.6 ± 21.1 mm CL in natural shelters, mean \pm 1 SD). We found a mean occupancy of 40.6 ± 27.1 lobsters (mean \pm 1 SD) per casita in the Middle Keys and 22.1 ± 14.9 (mean \pm 1 SD) in the Lower Keys. The fewest lobsters found under a casita were seven in the Lower Keys, whereas up to 83 lobsters were observed under a single casita in the Middle Keys.

Shelter type had no effect on lobster nutritional condition as measured by DWI (Table 1 and Figure 2). The covariate of lobster size (CL) explained the most variance in the data. Although the ANCOVA revealed significant differences between groups ($p = 0.044$), a deviation contrast (Middle Keys natural shelters as reference category) found no distinct homogeneous subsets. Most of the differences in the lobster nutritional condition were due to region, with lobsters in the Lower Keys having a higher DWI than those in the Middle Keys. The lobsters sampled for DWI were selected to ensure that the full size range of animals was sampled, and we did not include pre-molt or post-molt individuals, as these conditions can skew nutritional condition measurements (Oliver and MacDiarmid 2001, Behringer and Butler 2006).

Effect of shelter type on relative predation-induced mortality

There were no significant interactions between the effects of region, shelter type, and size on lobster survival (Chi-squared = 0.179, d.f. = 1, $p = 0.672$; Figure 3). Subdivision of the main contingency table and subsequent inspection of the data revealed that the only significant differences in survival occurred in small lobsters in the Middle Keys, where lobsters in casitas were killed at higher rates than those in natural shelters (Fisher’s exact test; $p = 0.023$). The small lobsters in Middle Keys casitas experienced the lowest overall survival after 24 h (57.9%), whereas large lobsters in casitas in the Lower Keys had the highest survival (97.4%). Small lobsters were subject to higher rates of mortality than large lobsters always.

A log-linear contingency table analysis examining the effects of lobster size and casita size (“large” vs. “medium”; *sensu* Mintz et al., 1994) on lobster survival after 24 h revealed no significant

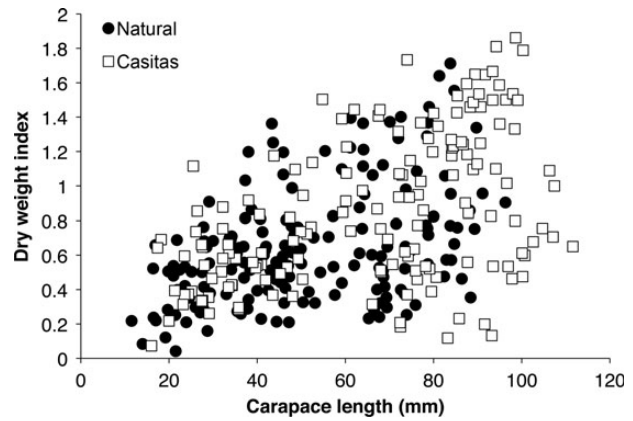


Figure 2. Nutritional condition (hepatopancreas DWI) of lobsters as a function of CL compared between natural shelters and casitas.

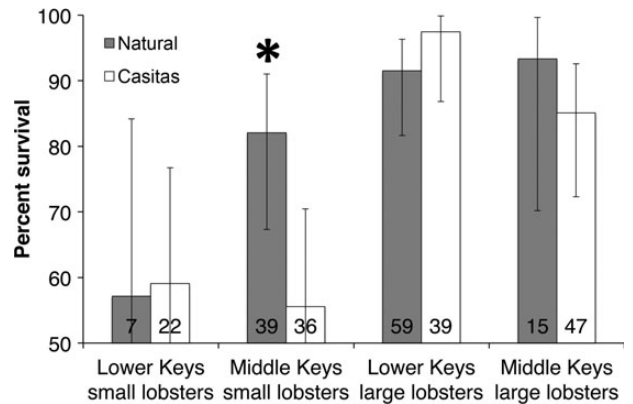


Figure 3. Percent of tethered lobsters of two size classes (small ≤ 35 mm CL; large ≥ 60 mm CL) surviving after 24 h in different shelter types and regions. Significant differences in survival between natural shelters and casitas are marked by an asterisk. Sample size is shown at the base of the bars. Error bars = 95% confidence intervals.

association (Chi-squared = 0.59, d.f. = 1, $p = 0.443$). A study conducted in the same area on the same casitas nearly 25 years before ours (Mintz et al., 1994) also found no significant difference in lobster survival between large- and medium-sized casitas, which is not surprising given that the two types of casitas are only ~20% different in area (2.0 vs. 1.6 m²) and the difference in the heights of their openings (2 cm) is likely too small to substantially change their value as shelters for lobsters in the broad size range we encountered (~25–75 mm CL).

Assessment of relative activity patterns across shelter types and size classes

Small lobsters showed very little diurnal activity, regardless of shelter type. However, we found a significant interaction between shelter type and time of day on lobster activity. Small lobsters sheltering in casitas were more active at night relative to those in natural shelters (Table 2 and Figure 4).

Discussion

The effects of casitas on lobster populations are complex and depend both on lobster size and the habitat within which casitas are deployed. Lobsters collected from casitas and natural shelters did not differ in nutritional condition. However, lobsters in the deeper adult habitats of the Lower Keys were in better nutritional condition than those in the Middle Keys nursery habitats, regardless of the shelter type from which they were collected. Small juvenile lobsters tethered in casitas in nursery habitats experienced significantly greater predation than those in natural shelters, whereas predation on large lobsters did not differ between shelter types or regions. These results indicate that casitas have minimal effects on large lobsters. However, if deployed in nursery habitats where small lobsters are abundant, casitas act as ecological traps for juvenile lobsters by aggregating them in inappropriately large structures where they suffer higher predation.

The casita – habitat interaction

Lobsters of all sizes are commonly found in shallow habitats, many of which are nursery areas. Casitas have become increasingly common throughout the Caribbean and are often used in shallow

nursery habitats where our results indicate that they have the most potential to cause harm. Fishers usually locate casitas in shallow (<5 m) areas that are close to shore and where they can harvest lobsters by free diving rather than scuba (de la Torre and Miller, 1987; Lozano-Álvarez and Briones-Fourzán, 1991; Ley-Cooper *et al.*, 2013). Yet, when casitas are deployed in nursery habitat, the increased rate of predation on small juvenile lobsters that are drawn to them by the odour of other lobsters within them produces an ecological trap acting on the very life stage considered to be the demographic bottleneck to the population (Butler and Herrkind, 1997).

Predator concentrations near casitas are often greater than those near the more widely dispersed natural shelters used by juvenile lobsters (Eggleston and Lipcius, 1992; Mintz *et al.*, 1994). Most of these piscine predators are gape-limited, and thus more of a threat to smaller juvenile lobsters. Indeed, predation on tethered small lobsters was high (40–45% killed in 24 h) whether in casitas or in natural shelters. The scaling of a shelter relative to the size of a lobster plays an important role in how effective it can be in providing refuge from predation (Eggleston *et al.*, 1990; Mintz *et al.*, 1994). Because casitas are sized to accommodate legal-sized lobsters for capture by fishers, they generally have a much wider opening than the shelters where small juvenile lobsters are normally found. In our study, we often observed predators of lobsters such as nurse sharks, red grouper, and loggerhead turtles (*Caretta caretta*) nearby or resting inside casitas, with lobsters either notably absent or occupying parts of the casita as far from the predator as possible. Thus, if predators can fit under the shelter, it is clearly not scaled appropriately for small lobsters and is unlikely to serve as a viable refuge.

In Florida, an illegal casita fishery is present in deeper water (~10 m). It is therefore one of the few areas in the Caribbean where it is possible to examine the effects of casitas in deeper habitats where subadult and adult lobsters are common. Our results suggest that casitas emplaced there have very different effects than those located in nursery habitats. Indeed, we found very few lobsters <50 mm CL at our Lower Keys site and most (76%) were larger than the minimum legal size limit of 76 mm CL. In this deeper region, large lobsters experienced no differences in mortality or nutrition between natural shelters and casitas. Thus, unlike casitas in nursery habitats where both small and large lobsters are present, casitas in deeper habitats have neutral effects on the lobster population.

Table 2. Results of a split-plot ANOVA testing the effect of shelter type and time of day (h) on the proportion of time small lobsters (CL ≤45 mm) spent active, as determined by accelerometry.

Source	d.f.	MS	F	p
Shelter type	1	40868.32	0.922	0.350
Individual (shelter type)	18	44340.04		
Hour	23	42337.03	4.067	<0.001
Shelter type × hour	23	19264.62	1.851	0.011
Error	351	10408.62		
Total	479			

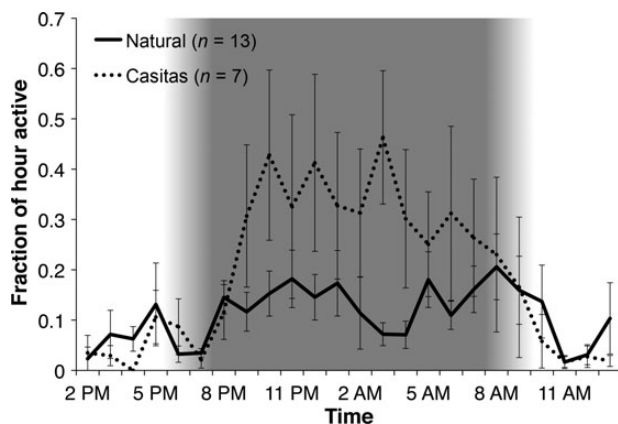


Figure 4. Activity patterns of small lobsters (CL ≤45 mm) in natural shelters and casitas as determined by accelerometry. The shaded area approximates hours of darkness. Error bars are ± 1 standard error.

Casitas and the “attraction vs. production” debate

Whether the aggregations of animals observed around artificial structures (e.g. artificial reefs, fish aggregation devices, and casitas) are the result of enhanced production of biomass or merely, the attraction of individuals from elsewhere has been debated for decades (e.g. Bohnsack, 1989; Pickering and Whitmarsh, 1997; Brickhill *et al.*, 2005). The attractive value of casitas for lobsters is undoubted, and accounts for the adoption of casitas as a fishing gear (Puga *et al.*, 1996). Yet, whether fishing devices like casitas increase the production of lobster biomass is uncertain. Lobsters are usually rare in areas such as seagrass where their prey is abundant, but structures suitable as shelter are scarce. Advocates of casitas argue that casitas deployed in these habitats can enhance lobster production by allowing exploitation of food resources that lobsters otherwise rarely access (Eggleston *et al.*, 1990; Lipcius *et al.*, 1998; Briones-Fourzán and Lozano-Álvarez, 2001). This ignores the possible ecological ramifications of increasing predatory pressure in seagrass communities. Moreover, for casitas to enhance lobster production, they must

increase lobster biomass in the population, whether by increased growth or decreased mortality (Bohnsack and Sutherland, 1985). However, other studies indicate that the growth of *P. argus* in the wild is not density-dependent and does not appear food limited (Behringer and Butler 2006, Nizinski 2007). Indeed, we found that the nutritional condition of both juvenile and adult lobsters were similar whether residing in natural shelters or casitas.

Accelerometry also gave us insights into the movement of small and large lobsters residing in casitas and natural shelters. We had hypothesized that the increased risk of predation for small lobsters sheltering in casitas would lead to a shift in their activity patterns, causing them to spend less time foraging away from casitas compared with larger lobsters or those in natural shelters (Weiss et al., 2008). Our results showed that small lobsters in casitas were more active overnight than lobsters in natural shelters, but we could not discern how far they moved. The greater activity of small lobsters near casitas could result from more intraspecific behavioural interactions near crowded casitas, or perhaps reflects greater foraging activity in the prey-depleted feeding halo that surrounds casitas (Nizinski, 2007).

Casitas as an ecological trap for lobsters

Our results indicate that casitas are an ecological trap for juvenile lobsters when deployed in the shallow nursery habitats like those in the Florida Keys. The trap is set when small juvenile lobsters follow their normally beneficial shelter-seeking instincts and are attracted to a casita by the odour of conspecifics (Nevitt et al., 2000). Large lobsters—whose size lies beyond the gape limit of most piscine predators, and who thus suffer no increase in mortality—are present in casitas in aggregations much denser than found in natural shelters (Mintz et al., 1994; Briones-Fourzán et al., 2007). Odours emanating from such dense lobster aggregations are very attractive to small, roaming lobsters (Childress and Herrnkind, 1997; Ratchford and Eggleston, 1998). However, the casita environment teems with predators of small lobsters, increasing the rate of mortality on this particularly vulnerable size class. An analogous situation occurs naturally. Large solution holes contain aggregations of large lobsters that are very attractive to small lobsters, whose abundance in the surrounding natural shelters is depleted by the presence of predatory groupers also living in the solution hole (Schratwieser, 1999).

The results of this research showing increased mortality of small lobsters in casitas contradict some previous studies, which concluded that casitas increase lobster production by enhancing survival (Briones-Fourzán and Lozano-Álvarez, 2013). However, of the studies purporting to demonstrate enhanced production of lobsters due to casitas, many did not directly test for differences in predation (Sosa-Cordero et al., 1998; Briones-Fourzán and Lozano-Álvarez, 2001; Briones-Fourzán et al., 2007). Those studies also often used smaller “mini-casitas” better scaled to suit juvenile lobsters, rather than the larger casitas used by fishers and which are at the centre of the attraction–production debate (Arce et al., 1997; Briones-Fourzán and Lozano-Álvarez, 2001; Briones-Fourzán et al., 2007; Lozano-Álvarez et al., 2009). Fishers use casitas with opening heights generally ranging from 6–8 cm (Lozano-Álvarez et al., 2003) to 15 cm or more (Ley-Cooper et al., 2013), although no uniform size or design exists. Some studies have cautioned against using casitas for fishing in nursery habitats and suggest only using smaller-scale shelters as enhancement devices (Sosa-Cordero et al., 1998). However, using the term “casita” or even “mini-casita” to describe smaller lobster aggregation devices designed for population enhancement is a risky

misnomer. Small, experimental structures that house small juvenile lobsters should not be called “casitas” because they do not function the same as the larger structures used by fishers. Smaller shelters properly scaled for juvenile lobsters enhance survival (Eggleston et al., 1990; Behringer and Butler, 2006), whereas larger casitas increase mortality on small juvenile lobsters. We therefore urge caution and the consideration of local habitat and lobster population features before implementing casita-based fisheries, so as to reduce the possibility of creating an ecological trap for juveniles.

Globally, marine fisheries are experiencing severe declines and collapses (Worm et al., 2009) from which the Caribbean spiny lobster is not exempt (Winterbottom et al., 2012). In the United States, fishery managers are legally obligated to identify and maintain essential habitats for preservation and conservation of fisheries resources (Rosenberg et al., 2000). Shallow nursery habitats are essential habitats because they harbour animals at their most vulnerable life stages (Lindeman et al., 2000). Casitas only operate as ecological traps in areas where small lobsters are present, so management that restricts their use in nursery habitats should be encouraged in the interest of preserving this valuable marine resource.

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References

- Anderson, J. R., Spadaro, A. J., Baeza, J. A., and Behringer, D. C. 2013. Ontogenetic shifts in resource allocation: colour change and allometric growth of defensive and reproductive structures in the Caribbean spiny lobster *Panulirus argus*. *Biological Journal of the Linnean Society*, 108: 87–98.
- Arce, A. M., Aguilar-Dávila, W., Sosa-Cordero, E., and Caddy, J. F. 1997. Artificial shelters (casitas) as habitats for juvenile spiny lobsters *Panulirus argus* in the Mexican Caribbean. *Marine Ecology Progress Series*, 158: 217–224.
- Behringer, D. C., and Butler, M. J. 2006. Density-dependent population dynamics in juvenile *Panulirus argus* (Latreille): The impact of artificial density enhancement. *Journal of Experimental Marine Biology and Ecology*, 334: 84–95.
- Bohnsack, J. A. 1989. Are high densities of fish at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science*, 44: 631–645.
- Bohnsack, J. A., and Sutherland, D. L. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science*, 37: 11–39.
- Brickhill, M. J., Lee, S. Y., and Connolly, R. M. 2005. Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *Journal of Fish Biology*, 67: 53–71.
- Briones-Fourzán, P., and Lozano-Álvarez, E. 2001. Effects of artificial shelters (casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. *Marine Ecology Progress Series*, 221: 221–232.
- Briones-Fourzán, P., and Lozano-Álvarez, E. 2013. Essential habitats for *Panulirus* spiny lobsters. In *Lobsters: Biology, Management, Aquaculture and Fisheries*, 2nd edn, pp. 186–220. Ed. by B. F. Phillips. Wiley-Blackwell, Chichester. 474 pp.
- Briones-Fourzán, P., Lozano-Álvarez, E., Negrete-Soto, F., and Barradas-Ortiz, C. 2007. Enhancement of juvenile Caribbean spiny lobsters: an evaluation of changes in multiple response variables with the addition of large artificial shelters. *Oecologia*, 151: 401–416.

- Bryars, S. R., and Geddes, M. C. 2005. Effects of diet on the growth, survival, and condition of sea-caged adult southern rock lobster, *Jasus edwardsii*. *New Zealand Journal of Marine and Freshwater Research*, 39: 251–262.
- Butler, M. J., and Herrnkind, W. F. 1997. A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 452–463.
- Butler, M. J., and Herrnkind, W. F. 2000. Puerulus and juvenile ecology. In *Spiny Lobsters: Fisheries and Culture*, 2nd edn, pp. 276–301. Ed. by B. F. Phillips, and J. Kittaka. Fishing News Books, Oxford. 679 pp.
- Chávez, E. 2009. Potential production of the Caribbean spiny lobster (Decapoda, Palinura) fisheries. *Crustaceana*, 82: 1393–1412.
- Childress, M. J., and Herrnkind, W. F. 1997. Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? *Marine and Freshwater Research*, 48: 751–758.
- Childress, M. J., and Herrnkind, W. F. 2001. The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behaviour*, 62: 465–472.
- Davis, G. E. 1985. Artificial structures to mitigate marine construction impacts on spiny lobster, *Panulirus argus*. *Bulletin of Marine Science*, 37: 151–156.
- de la Torre, R., and Miller, D. L. 1987. Update on the Mexican Caribbean's artificial habitat-based spiny lobster (*Panulirus argus*) fishery: the evaluation of design, material and placement optimums. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 38: 582–589.
- Dwernychuk, L. W., and Boag, D. A. 1972. Ducks nesting in association with gulls: an ecological trap? *Canadian Journal of Zoology*, 50: 559–563.
- Eggleston, D. B., and Lipcius, R. N. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology*, 73: 992–1011.
- Eggleston, D. B., Lipcius, R. N., and Grover, J. J. 1997. Predator and shelter-size effects on coral reef fish and spiny lobster prey. *Marine Ecology Progress Series*, 149: 43–59.
- Eggleston, D. B., Lipcius, R. N., and Miller, D. L. 1992. Artificial shelters and survival of juvenile Caribbean spiny lobster *Panulirus argus*: spatial, habitat and lobster size effects. *Fishery Bulletin*, 90: 691–702.
- Eggleston, D. B., Lipcius, R. N., Miller, D. L., and Coba-Cetina, L. 1990. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. *Marine Ecology Progress Series*, 62: 79–88.
- Ekroos, J., Öst, M., Karell, P., Jaatinen, K., and Kilpi, M. 2012. Philopatric predisposition to predation-induced ecological traps: habitat-dependent mortality of breeding eiders. *Oecologia*, 170: 979–986.
- Gates, J. E., and Gysel, L. W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, 59: 871–883.
- Gilroy, J. J., and Sutherland, W. J. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology and Evolution*, 22: 351–356.
- Granneman, J. E., and Steele, M. A. 2014. Fish growth, reproduction, and tissue production on artificial reefs relative to natural reefs. *ICES Journal of Marine Science*, 71: 2494–2504.
- Gutzler, B. 2014. The ecological impact of casitas on Caribbean spiny lobster (*Panulirus argus*) populations in the Florida Keys, FL (USA). MS thesis, Old Dominion University, Norfolk, VA, USA.
- Gutzler, B. C., and Butler, M. J. 2014. Accelerometry as a tool for studying lobster behavior: preliminary results from the Florida Keys, FL (USA). *Lobster Newsletter*, 27: 8–9.
- Hallier, J.-P., and Gaertner, D. 2008. Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 353: 255–264.
- Hawlena, D., Saltz, D., Abramsky, Z., and Bouskila, A. 2010. Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology*, 24: 803–809.
- Herrnkind, W. F., and Butler, M. J. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series*, 34: 23–30.
- Herrnkind, W. F., and Cobb, J. S. 2007. Artificial shelters for clawed and spiny lobsters: a critical review of enhancement efforts. *American Fisheries Society Symposium*, 49: 925–932.
- Kriska, G., Horváth, G., and Andrikovics, S. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *Journal of Experimental Biology*, 201: 2273–2286.
- Ley-Cooper, K., De Lestang, S., Phillips, B. F., and Lozano-Álvarez, E. 2013. Estimates of exploitation rates of the spiny lobster fishery for *Panulirus argus* from tagging within the Bahía Espíritu Santo “Sian Ka’an” Biosphere Reserve, Mexican Caribbean. *Marine Biology Research*, 9: 88–96.
- Lindeman, K. C., Pugliese, R., Waugh, G. T., and Ault, J. S. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of Marine Science*, 66: 929–956.
- Lipcius, R. N., Eggleston, D. B., Miller, D. L., and Luhrs, T. C. 1998. The habitat-survival function for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. *Marine and Freshwater Research*, 49: 807–816.
- Lozano-Álvarez, E., and Briones-Fourzán, P. 1991. Fishery characteristics, growth, and movements of the spiny lobster *Panulirus argus* in Bahía de la Ascension, Mexico. *Fishery Bulletin*, 89: 79–89.
- Lozano-Álvarez, E., Briones-Fourzán, P., and Ramos-Aguilar, M. E. 2003. Distribution, shelter fidelity, and movements of subadult spiny lobsters (*Panulirus argus*) in areas with artificial shelters (casitas). *Journal of Shellfish Research*, 22: 533–540.
- Lozano-Álvarez, E., Meiners, C., and Briones-Fourzán, P. 2009. Ontogenetic habitat shifts affect performance of artificial shelters for Caribbean spiny lobsters. *Marine Ecology Progress Series*, 396: 85–97.
- Lyle, W. G., and MacDonald, C. D. 1983. Molt stage determination in the Hawaiian spiny lobster *Panulirus marginatus*. *Journal of Crustacean Biology*, 3: 208–216.
- Mintz, J. D., Lipcius, R. N., Eggleston, D. B., and Seebo, M. S. 1994. Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecific abundance. *Marine Ecology Progress Series*, 112: 255–266.
- Nevitt, G., Pentcheff, N. D., Lohmann, K. J., and Zimmer, R. K. 2000. Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecific odors in the field. *Marine Ecology Progress Series*, 203: 225–231.
- Nizinski, M. S. 2007. Predation in subtropical soft-bottom systems: spiny lobster and molluscs in Florida Bay. *Marine Ecology Progress Series*, 345: 185–197.
- Oliver, M. D., and MacDiarmid, A. B. 2001. Blood refractive index and ratio of weight to carapace length as indices of nutritional condition in juvenile rock lobsters (*Jasus edwardsii*). *Marine and Freshwater Research*, 52: 1395–1400.
- Pärt, T., Arlt, D., and Villard, M.-A. 2007. Empirical evidence for ecological traps: a two-step model focusing on individual decisions. *Journal of Ornithology*, 148: S327–S332.
- Pickering, H., and Whitmarsh, D. 1997. Artificial reefs and fisheries exploitation: a review of the “attraction versus production” debate, the influence of design and its significance for policy. *Fisheries Research*, 31: 39–59.
- Puga, R., Estela de Leon, M., and Cruz, R. 1996. Catchability for the main fishing methods in the Cuban fishery of the spiny lobster *Panulirus argus* (Latreille, 1804), and implications for management (Decapoda, Palinuridae). *Crustaceana*, 69: 703–718.

- Ratchford, S. G., and Eggleston, D. B. 1998. Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. *Animal Behaviour*, 56: 1027–1034.
- Ratchford, S. G., and Eggleston, D. B. 2000. Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. *Animal Behaviour*, 59: 793–799.
- Robertson, B. A., and Hutto, R. L. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87: 1075–1085.
- Robertson, B. A., Rehage, J. S., and Sih, A. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution*, 28: 552–560.
- Rosenberg, A., Bigford, T. E., Leathery, S., Hill, R. L., and Bickers, K. 2000. Ecosystem approaches to fishery management through essential fish habitat. *Bulletin of Marine Science*, 66: 535–542.
- Schlaepfer, M. A., Runge, M. C., and Sherman, P. W. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution*, 17: 474–480.
- Schratwieser, J. 1999. The impact of resident and transient predators on the population dynamics of juvenile Caribbean spiny lobster in Florida. MS thesis, Old Dominion University, Norfolk, VA, USA.
- Semeniuk, C. A. D., and Rothley, K. D. 2008. Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays *Dasyatis americana*. *Marine Ecology Progress Series*, 357: 271–282.
- Smith, K. N., and Herrnkind, W. F. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology*, 157: 3–18.
- Sosa-Cordero, E., Arce, A. M., Aguilar-Dávila, W., and Ramírez-González, A. 1998. Artificial shelters for spiny lobster *Panulirus argus* (Latreille): an evaluation of occupancy in different benthic habitats. *Journal of Experimental Marine Biology and Ecology*, 229: 1–18.
- Weiss, H. M., Lozano-Álvarez, E., and Briones-Fourzán, P. 2008. Circadian shelter occupancy patterns and predator-prey interactions of juvenile Caribbean spiny lobsters in a reef lagoon. *Marine Biology*, 153: 953–963.
- Weldon, A. J., and Haddad, N. M. 2005. The effects of patch shape on indigo buntings: evidence for an ecological trap. *Ecology*, 86: 1422–1431.
- Wilson, J. A., Osenberg, C. W., St Mary, C. M., Watson, C. A., and Lindberg, W. J. 2001. Artificial reefs, the attraction-production issue, and density dependence in marine ornamental fishes. *Aquarium Sciences and Conservation*, 3: 95–105.
- Winterbottom, M., Haughton, M., Mutrie, E., and Grieve, K. 2012. Management of the spiny lobster fishery in CARICOM countries: status and recommendations for conservation. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 64: 456–462.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., et al. 2009. Rebuilding global fisheries. *Science*, 325: 578–585.
- Zimmer-Faust, R., Tyre, J. E., and Case, J. F. 1985. Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin*, 169: 106–118.

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