



Examining the ecological function of structure: species assemblages at casitas and coral heads in the Lower Florida Keys

Erica P. Ross^{1,*}, Jack Butler², Thomas R. Matthews¹

¹Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Marathon, Florida 33050, USA

²Florida International University, Miami, Florida 33199, USA

ABSTRACT: Casitas are artificial structures used widely in the Caribbean to facilitate the harvest of spiny lobsters by divers. Casitas are often used by many non-target species, and therefore have the potential to increase local species diversity and mitigate the loss of natural habitats. Their ecological impact, however, is largely unknown. We examined the distribution of benthic habitat and the abundance and diversity of fish and motile invertebrates at casitas (artificial structures), coral heads (natural habitat with vertical structure >15 cm high), and low-relief hardbottom (natural habitat with vertical structure <15 cm high). Casitas and coral heads exhibited similar habitat features and fish and invertebrate species assemblages. Low-relief hardbottom sites had significantly less abundant and diverse fish and invertebrate species assemblages than at either structure. The only significant difference observed between casitas and coral heads was the abundance of lobsters. Lobsters were found in significantly greater numbers at casitas than at either coral heads or on low-relief hardbottom. Determining how an increased concentration of lobsters at casitas affects the local ecology is complex, but our data suggest that the presence of lobsters in such large aggregations at casitas did not alter the surrounding flora and fauna. In regions with limited shelter, species composition and ecological function at casitas are similar to those at coral heads. This study shows that casitas may be efficient dual-purpose devices; that is, they function not only as lobster fishing gear, but also as the ecological equivalent of coral heads in shelterlimited habitat.

KEY WORDS: Casitas · Panulirus argus · Artificial reefs · Habitat impacts · Invertebrate communities

1. INTRODUCTION

Internationally, coral reefs are transitioning from complex coral-dominated landscapes to flat, algal, and soft coral communities (Hughes 1994, Hughes et al. 2003, McManus & Polsenberg 2004). This decline has been linked to disease, sedimentation, temperature extremes, and eutrophication, among other factors (Harborne et al. 2017, Hughes et al. 2017). Degraded coral reefs are unable to support the same biodiversity, abundance, and structural complexity of healthy reefs (McManus & Polsenberg 2004). To mitigate this loss, a modern restoration effort is underway. Artifi-

*Corresponding author: Erica.Ross@myFWC.com

cial structures have been deployed to mimic reef complexity and combat the loss of ecosystem services provided by healthy reefs (Bohnsack & Sutherland 1985, Fitzhardinge & Bailey-Brock 1989, Clark & Edwards 1999). Alteration of the marine habitat with artificial structures has been in use since as early as 3000 yr ago (Riggio et al. 2000). Historically, these structures were used to facilitate fishing, rather than as restoration tools (Fabi et al. 2011, Lee et al. 2018, Lima et al. 2019). However, as artificial fishing structures are often used by a many non-target species, they also have the potential to function as artificial reefs.

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Artificial structures deployed to increase the fishing efficiency of the Caribbean spiny lobster Panulirus argus have been in use in the Caribbean for more than 70 yr (Cruz & Phillips 2000, Briones-Fourzán & Lozano-Álvarez 2001, Spanier et al. 2011). These artificial shelters, called casitas (or 'pesqueros' in Cuba) are low-lying, table-like structures secured to the seafloor (Cruz & Phillips 2000). Casitas capitalize on the gregarious nature of P. argus by providing structure under which numerous lobsters may seek refuge from predators (Eggleston & Lipcius 1992, Arce et al. 1997). Casitas differ from traditional wooden-slat lobster traps in that they provide shelter while permitting animals to enter and exit freely. This unrestricted movement allows lobsters to perform important biological behaviors, such as foraging, escaping from predators, and reproducing, which are restricted in wooden-slat traps (Butler & Matthews 2018).

In the Bahamas, Mexico, and Cuba, casitas are the primary type of lobster fishing gear (Sosa-Cordero et al. 1998, Cruz & Adriano 2001, Gittens 2017). In Florida (USA), variations on this type of gear were used from the 1930s (Labisky et al. 1980, Little 1993, Hunt 1994) until 2003, when their use became illegal (Florida Administrative Code 2017, 68B-24.006). At present, commercial divers are permitted to collect lobsters only from natural shelters, such as those provided by sponges, coral heads, solution holes, and ledges. The commercial diving sector continues to advocate for the legalization of casitas as fishing gear, viewing them as an ecologically friendly alternative to traps because they have a lower discard mortality (Mintz et al. 1994, Matthews et al. 2001). With growing stakeholder interest in reincorporating casitas into the fishery, there is a pressing need to understand the ecological impact that casitas have on surrounding flora and fauna. Apart from lobsters, casitas are often also home to several nontarget fish and invertebrate species (Nizinski 2007), upon which the impact of casitas is unknown. Therefore, if casitas were to be reincorporated into the Florida lobster fishery, the potential for exploitation needs to be taken into consideration, as the use of artificial structures to increase fishing efficiency has previously led to overfishing (Bohnsack 1989, Brock 1994).

In addition to fishery concerns, the deposition of industrial materials on the seafloor is also controversial. Regulations that apply to the Florida Keys National Marine Sanctuary, which encompasses roughly 9933 km² around the Florida Keys, and the State of Florida forbid the deposition of materials into sanctuary and state waters without a permit (Florida Ad-

ministrative Code 2017). Opponents to the placement of such materials argue that use of casitas increases the amount of marine debris in the sanctuary and that, if not adequately secured, they can become dislodged from the seafloor, resulting in habitat damage. Proponents of casitas cite that the trap fishery damages benthic habitats and maintain that casitas, when properly constructed, directly impact a much smaller area of the benthos than traps (Nizinski 2007, Lewis et al. 2009, Uhrin et al. 2014). The ecological impacts of casitas as additional or alternative fishing gear for spiny lobsters are important considerations in working toward a sustainable lobster fishery.

In the Caribbean, casitas were initially introduced as artificial reefs for fishing enhancement, but the ability of casitas to act as modern artificial reefs, which restore the habitat complexity and ecosystem services provided by natural hardbottom communities, needs to be evaluated. In this study we aimed to assess casitas for their (1) effects on benthic habitat, (2) effects on surrounding fish and invertebrate communities, and (3) potential for performing ecological functions similar to those of the natural habitat in our study area. To evaluate the effects of casitas on benthic habitat and on the fish and invertebrate communities, we compared species assemblages at casitas to those in nearby low-relief hardbottom. To understand whether casitas can mimic the ecological function of natural structures (i.e. evaluate whether these artificial structures can function as artificial reefs and restoration tools), we first needed to determine the ecological value of natural structure. Therefore, we compared benthic habitat and the fish and invertebrate communities in natural habitat having highrelief structure (i.e. coral heads) to those in nearby natural habitat lacking structure (i.e. low-relief hardbottom). To evaluate whether casitas can fulfill the same ecological role as natural structures, we compared the benthic habitat distribution and composition of fish and invertebrate species assemblages at casitas with those at coral heads.

2. MATERIALS AND METHODS

2.1. Region of interest

We conducted field surveys in the Gulf of Mexico off the Lower Florida Keys at a depth of 7–14 m (Fig. 1). The lobster population in this region is made up of mostly legal-size, late-stage juveniles and subadults, with very few early juveniles or reproductively mature adults (Gregory et al. 1982). The benthic habitat is

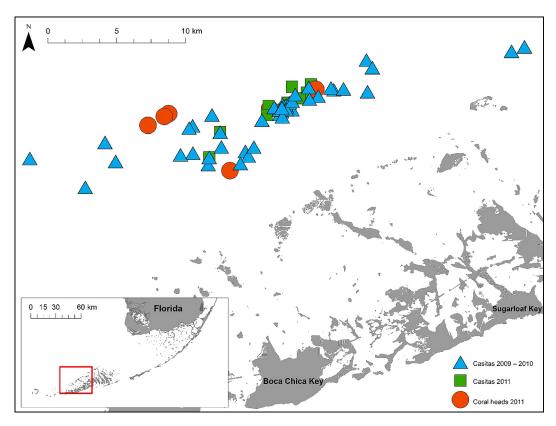


Fig. 1. Casita and coral locations in the Lower Florida Keys (USA)

characterized by macroalga-dominated hardbottom interspersed with seagrass patches and sand patches of different sizes (Hu et al. 2003, Bertelsen et al. 2009). Large (>1 m) coral heads are rare and spatially isolated. Most coral heads in our study area were dead and had been recolonized by an assemblage of sessile benthic species. Shelters suitable for larger juvenile and subadult lobsters are uncommon and generally restricted to small solution holes (<0.5 m²) or large coral heads. Casitas were also present in our study area (Herron 2005). Casitas were used in this region for years, prior to becoming illegal in 2003. This region therefore was a logical setting for this study, as it was a prominent location of the casitabased fishery and the large number of existing casitas ensured that the casita design in our study was relevant to those used earlier by commercial divers.

2.2. Field sampling

2.2.1. Site selection

We used side-scan sonar during May 2009 to August 2010 to identify 56 casitas (n = 39 in 2009; n = 17 in 2010) (Fig. 1). We also selected nearby low-relief

(<15 cm) hardbottom sites (n = 56) to serve as a representation of the natural benthic community in our study area. To select a low-relief hardbottom site (1 $\rm m^2$) near each casita, a direction 0° (i.e. north), 120°, or 240° was randomly selected, and a transect tape was run 25 m out from the center of the casita in that direction (Fig. 2A). The low-relief hardbottom site for that casita was located 25 m out in the selected direction.

In 2011, we identified high-relief (>15 cm) coral heads (n = 7). As live coral cover was sparse in our study area, the 7 coral heads we sampled were the skeletal remains of dead corals which had been recolonized by other sessile benthic species. We also identified nearby low-relief (<15 cm) hardbottom sites (n = 7) to serve as comparison for the effect of natural structure on biological communities. Low-relief hardbottom sites were selected in the same manner as the casita study, running the transects from the center of each coral head.

2.2.2. Benthic habitat percent cover surveys

To approximate benthic habitat and sessile invertebrate cover at each site type (casita, low-relief hardbottom, and coral head), we employed the planar point intercept method (Reed 1980, Lewis et al. 2009). A 1 $\rm m^2$ quadrat was constructed out of PVC and divided into a 10 \times 10 cm grid using nylon twine, creating 121 intersecting points (Fig. 2B). The type of benthic component (algae, bare substrate, scleractinian coral, fire coral, mollusks, octoorals, seagrass, sponges, tunicates, and other) observed below each point was recorded. To account for the canopy effect created by overlapping species, we allowed multiple habitat types at a point.

For sites having structure (i.e. casitas and coral heads), habitat was evaluated at the center of the structure and at several points from the center. To do so, we ran a transect tape out from the center of each structure in 3 directions, 0° (north), 120°, and 240° (Fig. 2A). Quadrats were centered on 5 points along each transect: atop the structure at its center (i.e. the origin of the transect); on the seafloor directly adjacent to the structure (i.e. edge of the quadrat flush with the structure); and, also on the seafloor, at 2, 4, and 6 m from the origin of the transect. For low-relief hardbottom sites, the benthic habitat was evaluated only once, using a quadrat centered directly at the 25 m mark on the selected transect, as described.

2.2.3. Fish and motile invertebrate community assemblages

Fish surveys were conducted using methods adapted from Bohnsack & Bannerot (1986). For each site type (casita, low-relief hardbottom, and coral head) a single-diver visual survey was conducted, centered over the site. All fish in a 7.5 m radius cylinder extending through the water column from seafloor to sea surface were identified to species and counted.

Motile benthic invertebrates were surveyed in a similar manner. A single-diver visually searched the seafloor within a 7.5 m radius circle centered at each site type. The species and number of individuals of each were recorded for all motile invertebrates >25 mm in length or diameter. Next, a maximum of 30 lobsters were collected at each site type for further data collection. Lobsters were measured for carapace length (CL), sexed, and inspected for signs of illness, injury, and reproductive activity (presence of eggs, spermatophores, or ovigerous setae). Immediately following data collection, each lobster was released on site. All surveys were conducted in the 6 wk period from mid-June to late July, just before the opening of the commercial lobster fishery (6 August to 31 March) to ensure that fishing did not interfere with lobster presence at each site type (FWC 2019).

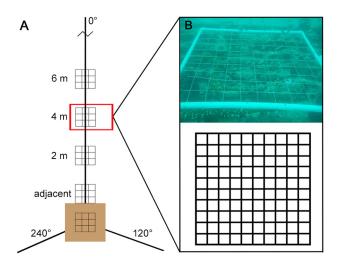


Fig. 2. Benthic habitat percent cover transects from each casita and coral head site. (A) Habitat quadrats were placed atop the coral head or casita, adjacent to the coral head or casita, and at 2, 4, and 6 m along each of 3 transects running 0° (north), 120°, and 240° from the coral head or casita. Quadrats are shown only on the 0° transect, and distance is not to scale. (B) Benthic habitat was evaluated at 121 intersecting points within a quadrat

2.2.4. Casitas as artificial reefs

To determine whether casitas can act as artificial reefs by fulfilling the same ecological role as coral heads, we resampled 9 randomly selected casitas alongside coral heads in 2011. Casitas were resampled to ensure we compared percent benthic habitat cover, fish, and motile invertebrate species assemblages between casitas and coral heads within the same year and season. Coral heads selected were of about the same width and length as casitas and provided information against which to compare the effect of structure on surrounding flora and fauna.

2.3. Data and statistical analysis

Statistical analyses were computed using R (version 3.6.3) and RStudio software (version 1.1.447, RStudio Team 2018) unless otherwise noted. Community assemblages were compared using the 'vegan' and 'pairwiseAdonis' packages in R (Arbizu 2019, Oksanen et al. 2019). PERMANOVA is robust to heterogeneity of variance for experiments with balanced designs (Anderson 2017). Homogeneity of site type dispersion was investigated with PERM-DISP for unbalanced comparisons (casita vs. coral head).

2.3.1. Dimensions of casitas and coral heads

We recorded the following general physical parameters associated with each casita and coral head: maximum length, maximum width, maximum height, maximum gap height (the height of any open space under a structure), and, for casitas, construction materials. Total volume of a casita was calculated by multiplying its height by its length and width. Sheltering volume (i.e. the space under a structure in which organisms might shelter) was calculated by multiplying casita gap height by its length and width.

Coral heads were irregularly shaped, so volume was calculated in 2 ways to best estimate their actual volume. In the first method, coral head volume was calculated using the formula for the volume of a hemisphere using the length measurement of the coral head as the diameter. In the second method, coral head volume was calculated using the formula for a rectangular cuboid by multiplying its height by its length and width. Likewise, sheltering volume of the coral head was also calculated in 2 ways. In the first method, sheltering volume was calculated using the formula for the volume of a cylinder using the gap height of the coral head as the height, and the length measurement of the coral as the diameter. In the second, it was calculated using the formula for the volume of a rectangular cuboid, by multiplying its gap height by its length and width.

2.3.2. Benthic habitat percent cover

The percent habitat cover around sites with structure (casita or coral head) was averaged across the 3 direction transects, yielding a mean percent habitat cover for each quadrat location (adjacent to and 2, 4, and 6 m from the center of the structure). Percent habitat cover atop each site type (casita, coral head, low-relief hardbottom) was measured only once. Benthic habitat communities for all quadrat locations (i.e. atop each site, adjacent to each structure, and 2, 4, and 6 m from each structure) were compared using a PERMANOVA (distance: Clark), and pairwise comparisons were used to evaluate differences in percent cover at each quadrat location; p-values for pairwise comparisons were Bonferroni-adjusted. Differences in percent habitat cover between casitas and coral heads were compared using the data from 2011 with a PERM-ANOVA (distance: Clark).

2.3.3. Fish and motile invertebrates

The effect of casita and coral dimensions (i.e. maximum length, maximum width, maximum height, maximum gap height, area, and volume) on fish and motile invertebrate abundance and diversity were investigated though log-likelihood tests of generalized linear models (GLMs). Fish and motile invertebrate abundance and diversity at casitas and at coral heads were compared to low-relief hardbottom sites. Community differences in abundance and diversity between the casitas, coral heads, and low-relief hardbottom sites were examined using a PERMANOVA (distance: Chao). Community differences between casitas, coral heads, and low-relief hardbottom sites were visualized using nonmetric multidimensional scaling (NMDS; distance: Chao). Differences between the fish and invertebrate communities observed at casita and coral heads in 2011 were compared using a PERMANOVA (distance: Chao) and visualized using NMDS (distance: Chao). Fish communities were compared at the family level. Invertebrate communities were compared at the species level.

2.3.4. Lobster abundance

We ran *t*-tests to compare the average abundance of lobsters in 2009–2010 at casitas vs. low-relief hardbottom, and in 2011 at coral heads vs. low-relief hardbottom and at casitas vs. coral heads; p-values were Bonferroni-adjusted.

3. RESULTS

3.1. Dimensions of casitas and coral heads

Casitas were constructed mainly of 3 materials, metal (n = 45), concrete (n = 10), and PVC pipe (n = 1). Roof or cover materials were mostly metal (68%). Steel I-beam (17.5%), PVC pipe (29.8%), and concrete blocks (28.1%) made up the majority of support materials. The mean \pm SD area of all casitas (3.02 \pm 2.15 m²) used in 2009–2010 was less than that of the casitas (3.83 \pm 0.54 m²) that were resampled in the 2011 coral head–casita comparison analysis (Table 1). Volume and gap height were similar between casitas and coral heads in 2011, but the casitas were approximately twice as large in area, and the coral heads were almost 5 times as tall (Table 1). Mean sheltering volume was twice as large in all casitas (2009–2011)

Habitat type	Depth (m)	Length (m)	Width (m)	Area (m²)	Gap height (m)	Height (m)	Volume (m³)	Sheltering volume (m³)
Casitas 2009–2010 (n = 56)	9.46 ± 1.07	2.34 ± 0.68	1.58 ± 0.38	3.02 ± 2.15	0.16 ± 0.03	0.51 ± 2.09	1.40 ± 0.88	0.409 ± 0.39
Casitas 2011 (n = 9)	9.58 ± 0.46	2.05 ± 0.211	1.87 ± 0.20	3.83 ± 0.54	0.13 ± 0.02	0.19 ± 0.049	0.74 ± 0.14	0.52 ± 0.06
Coral heads 2011 (n = 7)	9.05 ± 1.30	1.34 ± 0.34	1.28 ± 0.34	^a 1.61 ± 0.74 ^b 1.89 ± 0.86	0.16 ± 0.43		$^{\rm c}1.07 \pm 0.50$ $^{\rm d}2.02 \pm 1.50$	^e 0.24 ± 0.17 ^f 0.27 ± 0.19
^a Calculated as a circle; ^b calculated as a rectangle; ^c calculated as volume of a hemisphere; ^d calculated as volume of a cube;								

Table 1. Dimensions of casitas and coral heads (mean \pm SD)

^aCalculated as a circle; ^bcalculated as a rectangle; ^ccalculated as volume of a hemisphere; ^dcalculated as volume of a cube; ^ecalculated as volume of a cylinder; ^fcalculated as volume of a cube

as in coral heads (Table 1), but, functionally, corals heads had even less sheltering space (Fig. 3).

3.2. Benthic habitat percent cover

In the 2009–2010 casita surveys, the benthic communities at casitas, the quadrat locations around them (2, 4, and 6 m), and low-relief hardbottom were significantly different (PERMANOVA df = 1, F = 15.106, p < 0.001). Pairwise comparisons showed that habitat percent cover on top of the casita was significantly different from all quadrat locations, except the one that was immediately adjacent to the casita (on casita

vs. 2 m: df = 1, F = 9.515, p = 0.028; on casita vs. 4 m: df = 1, F = 12.828, p =0.028; on casita vs. 6 m: df = 1, F =12.129, p = 0.028; on casita vs. lowrelief hardbottom quadrat: df = 1, F =23.194, p = 0.028). All quadrat locations were dominated (>75%) by bare substrate and macroalgae. When compared with habitat on low-relief hardbottom, habitat on casitas included less coverage by algae (11.00 \pm 21.46% at casitas vs. $36.86 \pm 24.16\%$ at lowrelief hardbottom, df = 1, F = 32.178, p < 0.001) and a greater percentage of bare substrate (79.17 \pm 23.05% at casitas vs. $54.93 \pm 23.44\%$ at lowrelief hardbottom, df = 1, F = 27.685, p < 0.001; Fig. 4A). Percent cover by sponges was significantly greater on casitas than on low-relief hardbottom $(4.76 \pm 6.46\% \text{ at casitas vs. } 1.02 \pm$ 3.65% at low-relief hardbottom, df = 1, F = 6.113, p = 0.015). Percent cover by seagrass was significantly less at casitas than at low-relief hardbottom

sites (0.00% at casita vs. $5.28 \pm 18.41\%$ at low-relief hardbottom, df = 1, F = 4.874, p = 0.029).

In the 2011 surveys evaluating the effect of natural structure (coral heads vs. low-relief hardbottom) in our study area, the benthic communities at coral heads, the quadrat locations around them, and low-relief hardbottom were not significantly different (PERMANOVA df = 1, F = 1.526, p = 0.072). Pairwise comparisons, however, revealed that benthic habitat on the coral heads was significantly different from that at all other quadrat locations (on coral head vs. adjacent: df = 1, F = 8.301, p = 0.03; on coral head vs. 2 m: df = 1, F = 16.537, p = 0.03; on coral head vs. 4 m: df = 1, F = 12.762, p = 0.045; on coral head vs. 6 m:

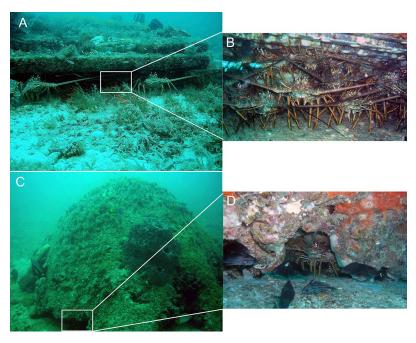


Fig. 3. Sheltering space under a casita and coral head. (A,B) Casitas have more sheltering space, since they have a single large, open cavern that is used for sheltering. (C,D) Coral heads provide less sheltering space, as the area underneath is generally made up of a complex series of small spaces

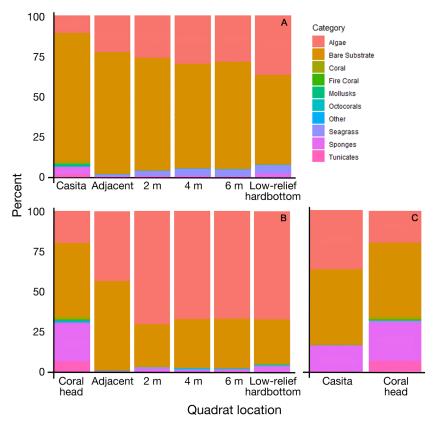


Fig. 4. Benthic habitat percent cover at all site types. (A) Benthic habitat percent cover at casitas, the quadrats around them, and low-relief hardbottom in 2009–2010. (B) Benthic habitat percent cover at coral heads, the quadrats around them and low-relief hardbottom in 2011. (C) Casita and coral head benthic habitat percent cover in 2011. Bare substrate and algae dominated all plots in all years. Benthic habitat percent cover was similar between casitas and coral heads in 2011

df = 1, F = 13.651, p = 0.03; on coral head vs. low-relief hardbottom: df = 1, F = 13.731, p = 0.03). Coral heads had significantly more sponges (21.85 ± 21.61% at corals vs. $3.23 \pm 2.09\%$ at low-relief hardbottom, df = 1, F = 6.464, p = 0.025) and tunicates (6.73 ± 7.27% at corals vs. 0.00% at low-relief hardbottom, df = 1, F = 5.33, p = 0.039) than did the nearby low-relief hardbottom (Fig. 4B). Low-relief hardbottom had significantly more algae than did coral head sites (67.18 ± 21.49% at low-relief hardbottom vs. 19.79 ± 6.18% at corals, df = 1, F = 5.04, p = 0.044).

Finally, in the 2011 surveys evaluating the ability of casitas to serve as artificial reefs by mimicking coral head communities, coral head and casitas had similar benthic habitat (Fig. 4C; PERMANOVA df = 1, F = 1.574, p = 0.081). The 3 dominant habitat types (bare substrate, algae, and sponges) did not differ significantly between coral heads and casitas.

3.3. Fish abundance and species diversity

Casita dimensions were not strongly correlated with fish abundance (n = 56, df = 55, length: p = 0.384, width: p =0.497, gap height: p = 0.356, max height: p = 0.754) or diversity (n = 56, df = 55, length: p = 0.326, width: p =0.521, gap height: p = 0.201, max height: p = 0.389). Fish abundance (n =112, df = 111, p < 0.001, Fig. 5A) and diversity (n = 112, df = 111, p < 0.001, Fig. 5A) were significantly higher at casitas than at low-relief hardbottom sites. Fisheries species, such as snappers and groupers, as well as species harvested for the aquarium trade, such as spotted drum, angelfish, butterflyfish, and parrotfish, were more common at casitas than at low-relief hardbottom. Community assemblages at casitas were significantly different from those at low-relief hardbottom sites (PERM-ANOVA df = 1, F = 39.141, p = 0.001), and NMDS ordination indicated 2 distinct community assemblages (stress = 0.19, Fig. 6A).

In the 2011 surveys, coral head dimensions were not strongly correlated with fish abundance (n = 7, df = 6, length: p = 0.617, width: p = 0.841, gap height: p = 0.656, max height: p = 0.542)

or diversity (n = 7, df = 6, length: p = 0.536, width: p = 0.821, gap height: p = 0.378, max height: p = 0.891). Fish species at coral heads were significantly more abundant (n = 14, df = 13, p < 0.001, Fig. 5B) and diverse (n = 14, df = 13, p < 0.001, Fig. 5B) than low-relief hardbottom sites. Community assemblages at the coral heads were significantly different from those at low-relief hardbottom sites (PERMANOVA df = 1, F = 3.974, p = 0.028); NMDS plots, however, did not show clear separation of fish family assemblages between these plot types (stress = 0.13, Fig. 6B).

From the 2011 surveys evaluating the ability of casitas to serve as artificial reefs, fish abundance and diversity were comparable between casitas and coral heads (Fig. 5C). Community assemblages at coral heads and casitas were not significantly different (PERMANOVA df = 1, F = 2.235, p = 0.242; PERMADISP df = 1, F = 1.83, p = 0.181), and NMDS ordination indicated that coral head and casita fish were similar (stress = 0.19, Fig. 6C).

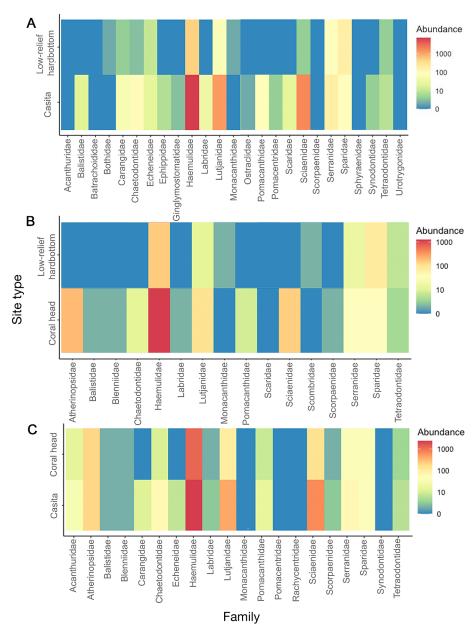


Fig. 5. Fish family assemblages at all site types. The abundance of various fish families (A) on casitas and low-relief hard-bottom sites, 2009–2010, (B) on coral heads and low-relief hard-bottom sites in 2011, and (C) on casitas and coral heads in 2011. Community assemblages differed between casitas and low-relief hardbottom and corals and low-relief hardbottom sites but not between casitas and coral heads. Differences were determined using PERMANOVAs

3.4. Abundance of motile invertebrates

Casita dimensions were not significantly correlated with invertebrate abundance (n = 56, df = 55, length: p = 0.558, width: p = 0.489, gap height: p = 0.394, max height: p = 0.095) or with diversity (n = 56, df = 55, length: p = 0.933, width: p = 0.479, gap height: p = 0.493, max height: p = 0.092). Panulirus argus was the most abundant motile invertebrate at casitas. Other large crustaceans such as the channel clinqing crab $Maquimithrax\ spinosissimus$ and the

Florida stone crab *Menippe mercenaria* were also more abundant at casitas than at low-relief hardbottom. Variegated sea urchins *Lytechinus variegatus* and sea biscuits *Clypeaster rosaceus* were more abundant at low-relief hardbottom sites than at casitas. Invertebrates at casitas were significantly more abundant (n = 112, df = 111, p < 0.001, Fig. 7A) and diverse (n = 112 df = 111, p < 0.001, Fig. 7A) than at low-relief hardbottom. Motile invertebrate species composition was significantly different between casitas and low-relief hardbottom sites (PERMANOVA)

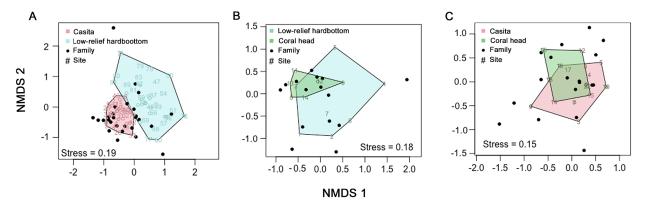


Fig. 6. Nonmetric multidimensional scaling (NMDS) of fish family assemblages on casitas, coral heads, and low-relief hard-bottom. (A) Casitas are clearly separated from low-relief hardbottom sites, while (B) coral head fish assemblages and low-relief hardbottom sites were slightly similar and (C) casita and coral head fish communities were slightly similar

df = 1, F = 60.085, p = 0.001), although NMDS plots did not indicate that (stress = 0.17, Fig. 8A).

Coral head dimensions were not strongly correlated with invertebrate abundance (n = 7, df = 6, length: p = 0.116, width: p = 0.090, gap height: p =0.173, max height: p = 0.212) or diversity (n = 7, df = 6, length: p = 0.205, width: p = 0.347, gap height: p =0.401, max height: p = 0.206). Large crustaceans such as the channel clinging crab, the green channel clinging crab Mithraculus sculptus, the Florida stone crab, and hermit crabs (anomurans) were more abundant at coral heads than at low-relief hardbottom sites, whereas variegated urchins were more abundant at low-relief hardbottom sites than at coral heads. Invertebrates were significantly more abundant (n = 14, df = 13, p < 0.001, Fig. 7B) and diverse (n = 14, df = 13, p = 0.003, Fig. 7B) on coral heads than at low-relief hardbottom sites. Motile invertebrate species composition at coral heads was significantly different from that at low-relief hardbottom sites (PERMANOVA df = 1, F = 2.70, p = 0.042), and NMDS plots showed a partial separation of species assemblages between coral heads and low-relief hardbottom sites (stress = 0.14, Fig. 8B).

Motile invertebrate abundance was similar between casitas and coral heads with the exception of lobsters and *Cerithium* spp. (Fig. 7C). Invertebrate communities did not differ significantly between coral heads and casitas (PERMANOVA df = 1, F = 0.470, p = 0.623; PERMDISP df = 1, F = 3.322, p = 0.074). NMDS plots also showed that coral head and casita invertebrate communities were similar (stress = 0.16, Fig. 8C).

3.5. Lobster abundance and morphometrics

In the 2009–2010 casita surveys, lobsters were significantly more abundant at casitas than at low-relief

hardbottom sites. Few natural shelters of suitable size for lobsters were observed in the study area, and only 1 lobster was observed at our low-relief hardbottom sites from 2009–2010 (df = 1, F = 304.833, p < 0.0001). In 2011, 3 lobsters were observed at coral heads and none at low-relief hardbottom sites; this difference in abundance between these types of sites was not significant (df = 1, F = 2.076, p = 0.175). Lobsters were found in significantly greater numbers at casitas than at coral heads in 2011 (df = 1, F = 38.776, p < 0.001). All casitas sampled contained at least 6 lobsters. Of lobsters sampled from casitas, 80% percent were of legal size (>76.2 mm CL). The average size of lobsters that we sampled from casitas was $86.30 \pm 10.70 \text{ mm CL (Fig. 9)}$. Lobsters of >100 mm CL were predominantly male (4:1). No lobsters were observed with active reproduction characteristics (i.e. spermatophores, ovigerous setae, or eggs), severe injury (greater than 3 injuries), or Panulirus argus Virus 1. The overall male to female ratio was always approximately 1:1 (52% were female).

4. DISCUSSION

The use of casitas or any artificial structure to aggregate lobsters has been illegal in Florida since 2003 (Florida Administrative Code 2017, 68B-24.006). Commercial lobster divers still wish to use casitas, while other artificial materials, in the form of artificial reefs, are increasingly being used to enhance habitat. Little is known about the ecological effects casitas and other artificial materials have on the surrounding flora and fauna. Our results indicate that casitas have effects similar to those of naturally occurring coral heads. Casitas were shown to diversify benthic habitat and to increase the diversity and abundance of fish and motile inver-

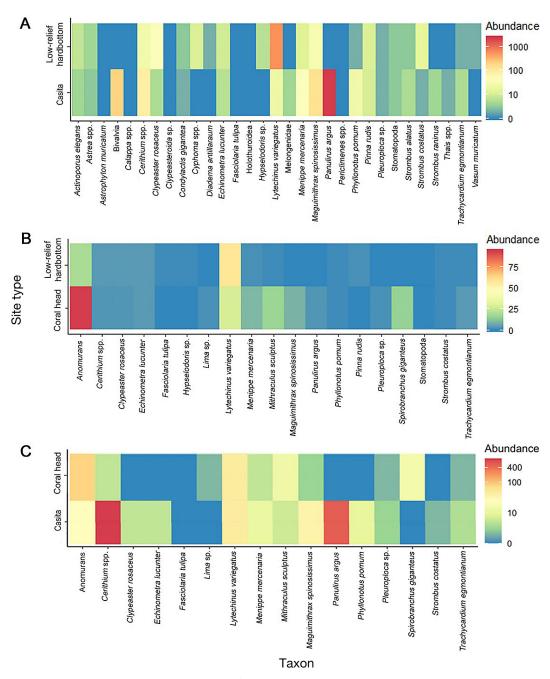


Fig. 7. Motile invertebrate species assemblages. (A) Community assemblages found in 2009–2010 on casitas were more diverse than those found at low-relief hardbottom sites. (B) Invertebrate communities found at coral heads were significantly more diverse than those found on low-relief hardbottom sites. (C) Communities were similar on the casita and coral heads in 2011. Differences were determined using PERMANOVAs

tebrate species over levels observed at low-relief hardbottom sites.

Of the 4 indicators of community structure that we examined, 3 of them, namely benthic habitat percent cover, fish abundance, and invertebrate abundance, did not differ significantly between casitas and coral heads. Casitas and coral heads showed similar halo effects, areas surrounding a structure

with a decrease in algal cover and an increase in bare substrate, typically associated with invertebrate or fish grazing (Randall 1961, 1965). Casita and coral heads provided shelter to commercially important fish and aquarium species. Casitas and coral heads also provided shelter to invertebrate fishery species (Menippe merceneria and Panulirus argus) and prodigious grazers (Maguimithrax spinosissimus)

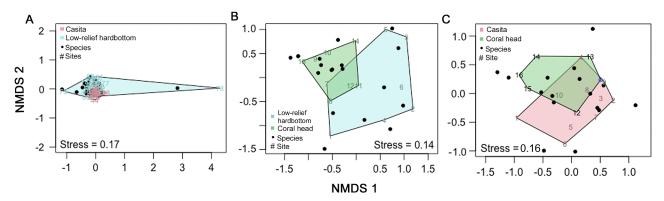


Fig. 8. NMDS of motile invertebrate species assemblages on casitas, coral heads, and nearby low-relief hardbottom sites. (A,B) Casita and low-relief hardbottom invertebrate communities were similar, while coral and low-relief hardbottom species assemblages were slightly different. (C) Coral and casita invertebrate species assemblages in 2011 were only slightly similar

(Spadaro 2019). The only significant difference observed between casitas and coral heads was that lobsters were more abundant at casitas. This difference likely reflects the different sheltering space that casitas provide, as the sheltering space under coral heads was a fraction of the sheltering space under casitas, leaving less room for larger invertebrates at coral heads.

Determining how an increased concentration of lobsters at casitas affects the local ecology is complex, but our data suggest that the presence of lobsters in such large aggregations at casitas did not alter the nearby flora and fauna, as there was no statistical difference in these communities between casitas, where lobsters were in high abundance, and coral heads, where there were few or no lobsters. Lobster aggregations, in our study, were almost exclusively found at casitas. Eggleston & Lipcius (1999) cautioned that long-term predation by large numbers of lobsters at casitas could have unknown effects on benthic prey populations. However, casitas had likely been present in our study area for years (Herron 2005), and our data show that benthic prey species in their vicinity were abundant. Lobster prey species, such as anomurans and Cerithium spp., were actually more abundant at casitas than at low-relief hardbottom sites, and Nizinski (2007) found similar results for casitas in the Upper Florida Keys. Briones-Fourzán & Lozano-Álvarez (2013), who summarized the results of casita studies across the Caribbean, also found no negative effect of lobster aggregations on surrounding prey species.

Other work in Florida has cautioned the placement of casitas in lobster nursery habitat, as a concentration of small lobsters may increase the abundance of large piscine predators (Gutzler et al. 2015). This was not an issue in our study, as this area has long been

dominated by large lobsters (Gregory et al. 1982) and the fish observed near casitas were mainly gapelimited juveniles unable to prey on the larger lobsters found inside the casitas (Mintz et al. 1994). Although these legal-size lobsters are less vulnerable to predation, they remain obligate crevice dwellers, as demonstrated by the lack of lobsters at low-relief hardbottom, which lacked structures suitable as daytime shelter. Further, in our study area the presence of lobster aggregations at casitas did not increase the abundance of piscine predators compared with that at nearby coral heads. It is possible that the methods we used to count fish did not capture the episodic presence of large predators. On few occasions, not captured by the fish surveys, large sharks, cobia, turtles, and dolphins were observed at casitas and at coral heads. However, studies conducted in the Caribbean indicate that these large predators are pre-

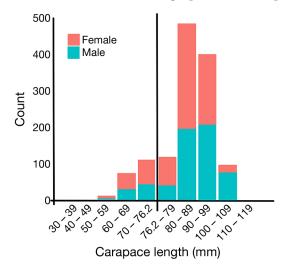


Fig. 9. Caribbean spiny lobster size-class frequency distribution on casitas in 2009–2011. A majority (>80%) of all lobsters captured on casitas were of legal size. Vertical line indicates the legal size

cluded from casitas due to their low gap height (Lozano-Álvarez & Spanier 1997).

Our sampling period (June-July) is typically associated with annual highs in macroalgal cover (Lirman & Biber 2000). The benthic communities of our study area are dominated by macroalgae with occasional small sponges and stony corals (Ruzicka et al. 2013). Large (2 m) but sparsely distributed coral heads and solution holes are the only sizeable natural structures in the region. This extreme lack of shelter in our study area may prevent reef-associated grazers from reaching densities great enough to reduce coverage by algae. Accordingly, with the increase in structure provided by casitas or coral heads, we found a feeding halo effect, or a significant decrease in algal cover near the casitas. Reduction in algal cover exposes settlement substrate for ecosystem engineers like corals and sponges, which is further supported by the increased presence of sponges and corals on top of casitas. The tops of casitas present a stable settlement habitat for sessile invertebrates. Akin to areas of old mortality on coral heads, the top of a casita is prime settlement habitat, because it is colonized by crustose coralline algae, a key settlement cue for corals, and, being above the sediment layer, poses less risk of burial or abrasion to recruiting coral larvae (Whalan et al. 2012, Tebben et al. 2015). Quadrats on top of casitas and adjacent to casitas in our study had a lower percent cover of seagrass than low-relief hardbottom. Work in the Upper Florida Keys has shown that casitas, and the halo they create, have negative effects on seagrass beds when placed in soft-bottom habitats (Eggleston & Lipcius 1999). In our study, however, the decreased cover of seagrass was likely due to the placement of casitas on hardbottom, which is not conducive to the growth of seagrass. Typically, strategic placement of casitas on hardbottom is necessary for proper anchoring, to prevent burial by sediment and excavation under the casita by groupers. However, casitas in the Bahamas are typically placed on soft sediments (Higgs 2016), and research in this area has found that even the placement of casitas on seagrass does not necessarily result in a seagrass die-off (van Tussenbroek et al. 2006).

At the time of this study, casitas were viewed negatively because their use undermined the goals of reducing fishing effort in the lobster fishery (Hunt 1994). The efficiency of lobster harvest off of casitas also led to other unconventional materials being deployed as artificial shelters. These improvised 'casitas' were commonly made of discarded and unsecured household remnants or appliances that led to habi-

tat damage. Therefore, in the Florida Keys casitas have been associated with a history of marine debris. The casitas surveyed during this research, however, were well anchored in hardbottom habitat. As lobster-fishing gear, casitas appear to have fewer detrimental impacts than the trap fishery. Traps move a considerable amount during strong but typical seasonal winds. During strong wind events, a trap can scour 1-4 m² of habitat, reducing coverage by sessile invertebrates as much as 50% (Lewis et al. 2009). Traps can become lost and continue to catch and kill lobsters and bycatch by ghost fishing, resulting in losses to other fisheries (Uhrin et al. 2014, Butler & Matthews 2015). The commercial trap fishery also causes additional mortality of lobsters that are used as live bait in traps (Butler & Matthews 2015, 2018). Finally, trap line and buoys pose an entanglement risk to several species of marine fauna, such as dolphins and turtles (Adimey et al. 2014). Our study showed that casitas have minimal negative effects on the natural habitat within the study area; on the contrary, they enhanced structure in the relatively lowrelief hardbottom landscape and diversified the benthic habitat of our study area. Further, since casitas do not restrict lobster movement, they have far lower associated mortality and fewer detrimental health effects than traps (Briones-Fourzán & Lozano-Álvarez 2013). Nevertheless, care is needed in their placement to ensure proper installation on the seafloor.

Casitas are the dominant lobster fishing gear across the Caribbean (Sosa-Cordero et al. 1998, Cruz & Adriano 2001, Gittens & Butler 2018), but their effect on lobster populations varies by region and with lobster size. In the Bahamas, casitas do not increase mortality or predation of lobsters of any size class (Gittens & Butler 2018). These findings are consistent with the results of our study. However, both areas are dominated by large lobsters (>50 mm CL), so the effects of casitas on juveniles are difficult to determine from these studies. In the Upper Florida Keys, where juveniles are abundant, smaller size class lobsters experience increased predation and mortality at casitas (Gutzler et al. 2015). In Mexico, survival of juveniles was increased under casitas at locations where habitat was limiting (Briones-Fourzán et al. 2007). Regional differences in predation levels are common, and juvenile abundance and survival at casitas is also mediated by local factors such as adequate postlarval supply, settlement substrate, food resources, and the scaling of the shelter (casita) to lobster size (Eggleston et al. 1990). Therefore, fishery managers should exercise caution when estimating the effect of casitas on the lobster population in different regions, as the interactions between casitas and the environment will likely vary from one location to the next.

Research from across the globe continues to examine if any artificial structure can fulfill the ecosystem services of natural reefs (Carr & Hixon 1997, Grossman et al. 1997, Pickering & Whitmarsh 1997, Perkol-Finkel et al. 2006, Ruzicka et al. 2013). Studies have shown that although artificial reefs can harbor high fish densities, their species composition is often distinctly different from that of natural reefs (Fowler & Booth 2012, Burt et al. 2013, Simon et al. 2013, Mills et al. 2017, Komyakova et al. 2019). Even studies within different regions of the Florida Keys (Noonan et al. 2021) have diverging results regarding the impact of artificial structure on fish communities. The ability of casitas and artificial reefs to restore lost ecological roles is also called into question by the attraction vs. production debate (Bohnsack 1989, Pickering & Whitmarsh 1997, Briones-Fourzán et al. 2007, Gutzler et al. 2015). Understanding where casitas lie on this spectrum of attracting nearby individuals vs. enhancing biomass and production is critical to preventing overfishing. Therefore, both location and design of casitas should be explored further, as these are important determinates for successful restoration and management of sustainable fisheries (Pickering & Whitmarsh 1997, Komyakova et al. 2019).

Hundreds of artificial reefs have been deployed throughout the Caribbean since their introduction in the 1960s (Hylkema et al. 2021). Unfortunately, comprehensive monitoring of these artificial reefs and comparisons with natural reef ecosystems are rare (Hylkema et al. 2021). As casitas originated as artificial structures for fisheries enhancement, rather than as artificial reefs for restoration, their ability to enhance species abundance and diversity, beyond lobsters, has seldom been directly investigated. Our study was conducted in only one region, with extremely limited natural shelter. To determine whether casitas can serve as true artificial reefs, this experiment needs to be replicated in areas with continuous or semi-continuous natural reef rather than the isolated coral heads used in our study. Still, the stark differences observed in flora and fauna species assemblages between casita and coral head sites and their respective low-relief hardbottom sites demonstrate the importance of structure and habitat complexity to the communities in our study area and show that in regions with few shelters, casitas appear to harbor flora and fauna communities similar to those communities found on the few remaining natural boulder corals.

5. CONCLUSION

North of the Lower Florida Keys, casitas appear to function in an ecologically similar way to natural habitat structures. Casitas and their associated halos mirrored those seen around coral heads. Casitas diversified benthic habitat by providing settlement substrate for sessile invertebrates. Casitas function as refugia in shelter-limited habitats, as both fish and invertebrate species assemblages were enhanced at casitas when compared to nearby low-relief hardbottom. Casitas remain a controversial type of fishing gear among lobster-trap fishers and their use is contrary to the policies of the Florida Keys National Marine Sanctuary. Nevertheless, the casitas evaluated in this study appeared well anchored and durable, reducing their probability of damaging sensitive habitats while at the same time providing ecological benefits. An assessment of casita designs, materials, and anchoring alternatives could further assuage concerns about casitas and contribute to their reincorporation as a safe and viable component of Florida's lobster fishery. This study has shown that casitas have positive ecological effects in shelterlimited habitats and so may be efficient structures that not only function as lobster-fishing gear but also replicate and enhance natural habitat.

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