

The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico

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Abstract Several previous studies have attempted to correlate habitat complexity and reef fish species diversity. These studies have mostly examined natural reef systems, but results differed. To examine this relation, we built 1 m² habitats with 20 replicates of five complexity levels from July to August 2001 in the northeastern Gulf of Mexico ($n=100$). In June and July 2002, we built new habitats using the 2001 design, but also added a sixth complexity level ($n=120$). In order of increasing complexity these included: cage, shell, cage-shell, block-shell, cage-block-shell, and shell-block-pyramid habitats. Most fish in both years were juveniles and included species common to reef structures in the northeastern Gulf of Mexico. In 2001, we identified 26 fish species, and the dominant species was red snapper, *Lutjanus campechanus* (41%), followed by rock sea bass, *Centropristis philadelphica* (23%), and sand perch, *Diplectrum* spp. (14%). In 2002 we identified 36 species, and the dominant species was tomtate, *Haemulon aurolineatum* (36%), followed by *Diplectrum* spp. (19%), and *L. campechanus* (13%). In 2001, species diversity and

richness were significantly ($P < 0.05$) higher on more complex habitats ($H' = 1.7$, $S = 11-12$) compared to less complex habitats ($H' = 0.8-1.0$, $S = 4-9$). In 2002, patterns among diversity, richness and reef complexity were less apparent with only the least complex habitats shell and cage showing significantly lower values. In both years, multidimensional scaling grouped by complexity levels with cage and shell habitats showing the clearest separation from other habitat types. Also, with few exceptions (only 8%) analysis of similarities showed significant ($P < 0.05$) differences in fish communities across complexity levels. Although community composition varied between years, this study provided evidence to support the hypothesis that habitat complexity increased reef fish species diversity.

Keywords Habitat complexity · Multidimensional scaling · Species diversity

Introduction

The influence of habitat complexity on species diversity has been studied extensively by community ecologists. They have sought correlations among various components of habitat complexity and species diversity with most work based on terrestrial systems. These studies have suggested a positive correlation between habitat complexity and species diversity. Rozensweig and Winakur (1969) found that

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rodent species diversity could be accounted for by habitat complexity. Similar results were found for birds (MacArthur and MacArthur 1961; Roth 1976), insects (Murdoch et al. 1972), and lizards (Pianka 1967).

In recent years, increased concern over habitat and species loss in marine systems has prompted investigations into the relation between habitat and species diversity in marine systems. Habitat complexity was an important factor in settlement and habitat preferences for sponges, corals, and gastropods (Russ 1980; Carleton and Sammarco 1987; Beck 2000), but results differed when fish diversity and habitat complexity were compared. For example, several studies have shown a positive correlation between substrate complexity and fish diversity (Risk 1972; Roberts and Ormond 1987; McClanahan 1994; McCormick 1994; Szedlmayer and Able 1996; Gratwicke and Speight 2005a, b), while one study showed a positive correlation between habitat complexity and biomass, but not with species diversity (Carpenter et al. 1981). In contrast, other studies have shown no correlation (Bourget et al. 1994; Gray 1994; Caballero and Schmitter-Soto 2001) or conflicting results between study sites (Luckhurst and Luckhurst 1978; Ohman and Rajasuriya 1998).

Increased habitat complexity may reduce predation pressures by providing refuge and escape routes from predators. Rooker et al. (1998), suggested that habitat complexity was linked to survival of newly settled red drum, *Sciaenops ocellatus*, and Beukers and Jones (1997) found that habitat complexity modified predator impact on lemon damselfish, *Pomacentrus moluccensis*. Similar results were found for fish communities associated with seagrass meadows (Hindell et al. 2000). Complex habitats may also allow coexistence of competing species through reduction of territorial competition (Sale 1980).

Most previous studies investigating the correlation between habitat complexity and marine fish community structure have been descriptive and conducted on natural reef systems (McCormick 1994; Beukers and Jones 1997; Ohman and Rajasuriya 1998) with few controlled experimental studies (Talbot et al. 1978; Hixon and Beets 1989; Fujita et al. 1996). While these studies have contributed significantly to understanding reef fish communities, a persistent difficulty has been low replication. For example, Hixon and Beets (1989) used two replicates of four

treatments, Talbot et al. (1978) used four replicates of four treatments, and Fujita et al. (1996) used one replicate of three treatments.

Bonhsack and Sutherland (1985) stressed the need for controlled experimentation in marine ecological studies and suggested that artificial habitats could provide an ideal tool for testing habitat complexity hypotheses. They are easy to construct, manipulate, survey, and allow for controlled experimentation with replication (Gratwicke and Speight 2005a). Equally important for the practical aspects of ecological experimental design is that marine communities settle quickly, often within days of structure placement (Shulman 1984).

In this study, we substantially increased replication ($n=20$ per treatment) by using artificial habitats. Specifically, we tested the null hypothesis that increased habitat complexity does not affect reef fish species diversity in the northeastern Gulf of Mexico.

Materials and methods

The study site was 21 km southeast of Dauphin Island, Alabama (Fig. 1). The area lacked natural reef

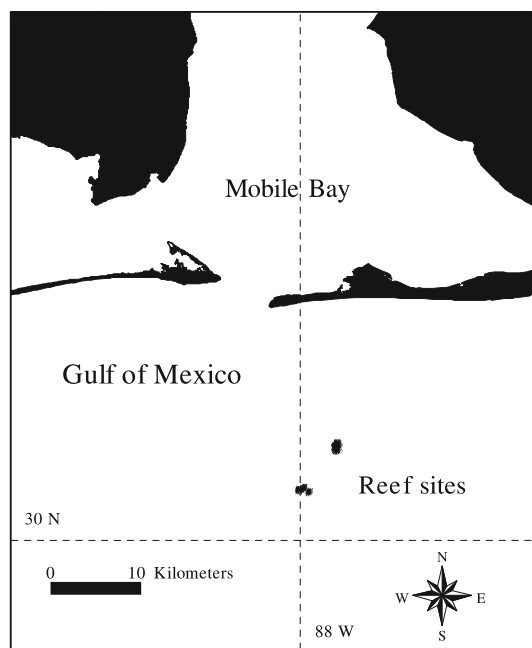


Fig. 1 Location of artificial habitats sites in the northeastern Gulf of Mexico

structure, was uniform in depth (20 m), and dominated by sand-mud substrates (Schroeder et al. 1995). From 24 July to 28 August 2001, we built 1 m² habitats with 20 replicates of five complexity levels ($n=100$). The following year we built new habitats from 12 June to 31 July using the 2001 design, but also added 20 replicates of a sixth complexity level ($n=120$). These 220 artificial habitats included: 40 cage (1×1×0.25 m) only habitats made of galvanized wire with 5×10 cm openings (cage), 40 oyster shell habitats (1×1×0.1 m, shell), 40 cage on shell habitats (cage-shell), 40 block on shell habitats (shell with four 20×20×40 cm concrete blocks, block-shell), 40 cage on block on shell habitats (cage-block-shell), and 20 habitats that each had 8 concrete blocks stacked in a pyramid shape on top of shell (pyramid-block-shell, Fig. 2). Complexity levels were based on the surface area that each different component added to each m² plot. Block surface area was calculated from simple linear measures (each block = 5129 cm²) while shell surface areas were measured using an image analyses system (total shell surface area for each habitat = 128,940 cm², Image-Pro Plus¹). Also, the wire cage added substantially to the habitat structure, but only added 162-cm² surface area. Thus, habitats were ranked in order of increasing complexity as: cage, shell, cage-shell, block-shell, cage-block-shell, and pyramid-block-shell. We built habitats in 200 m transects with each habitat 20 m apart, with alternating complexity levels. Two SCUBA divers constructed habitats by placing a 1 m² PVC square on the bottom and spreading oyster shells and concrete blocks within the square.

Fish populations were visually surveyed by SCUBA divers trained in reef fish species identification. Each habitat was surveyed completely and fish were identified to species. Species were also video taped for later verification. Transient schools of blue runner, *Caranx crysos*, crevalle jack, *Caranx hippos*, round scad, *Decapterus punctatus*, nurse shark, *Ginglymostoma cirratum*, greater amberjack, *Seriola dumerili*, *S. ocellatus*, and gulf flounder, *Paralichthys albigutta*, were not included in the reef fish analysis.

Mean abundances for each fish species were calculated for each habitat, and fish communities were compared with community measures: Shannon–

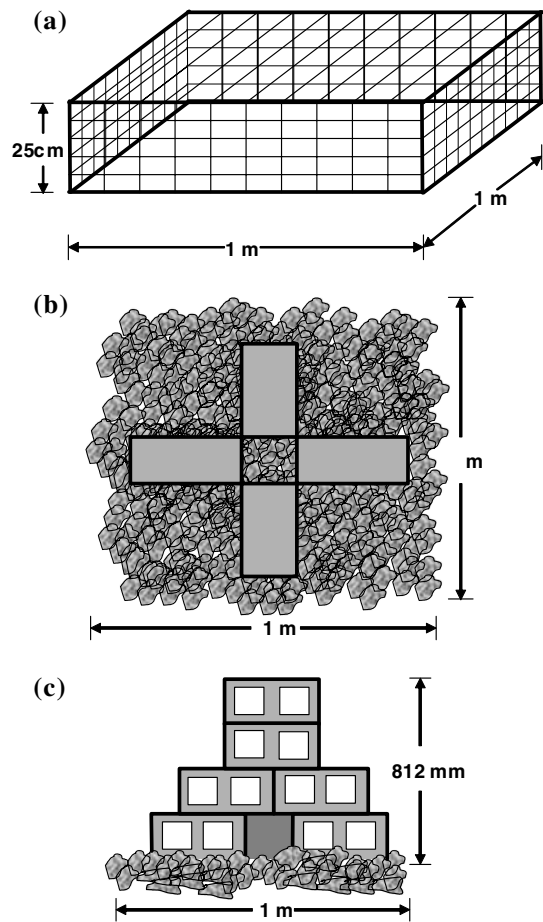


Fig. 2 Examples of three complexity levels and materials used: (a) cage, (b) block-shell, and (c) pyramid-block-shell habitats. Other habitat types were combinations of these components. All habitat types contained shell except cage

Wiener diversity index [$H' = -\sum p_i \ln(p_i)$], species richness (S), and evenness (J). For each year analysis of variance (ANOVA) was used to compare community measures among habitat types, and Tukey’s multiple comparison test was used to show specific differences. Abundance of the common species (>1% of the total) were compared among habitat types for each year using ANOVA, and Student-Neuman–Keuls multiple comparison test (Zar 1984). To show seasonal trends for 2001, mean abundances were compared across habitat types within each of five time periods (16–22 August, 29–30 August, 18–21 September, 24 October–8 November, 19 November), with ANOVA and Student-Neuman–Keuls multiple comparison test (Zar 1984). Surveys outside these time periods were not used in seasonal comparisons.

¹ MediaCybernetics, Silver Spring, MD 20910 USA

Reefs were only sampled once within each time period, but not all reefs were surveyed within each time period. However, nearly equal replicates of each reef type were sampled within each time period.

To compare the whole fish community among habitat types we calculated Bray–Curtis similarity coefficients among all habitats based on the root transformed abundance of each species for each year. We then used non-parametric Multidimensional Scaling (MDS) to plot the distances in two-dimensional space (Field et al. 1982). One-way analysis of similarities (ANOSIM) permutation tests were used for both global and pair-wise testing for significant differences among habitat types (Clarke and Green 1988). All statistical differences were considered significant at $P < 0.05$.

Results

All species identified during 2001 and 2002 surveys were reef fish common to the northeastern Gulf of Mexico (Hoesle and Moore 1977; McEachran and Feckhelm 1998, 2006). We completed 368 individual visual surveys from August to November 2001, and identified 26 fish species. Red snapper, *Lutjanus campechanus*, was the dominant species (41%), followed by rock sea bass, *Centropristis philadelphica* (23%), sand perch, *Diplectrum* spp. (14%), longspine porgy, *Stenotomus caprinus* (6%), and pigfish,

Orthopristis chrysoptera (5%, Table 1). These five species accounted for 88% of the fish surveyed. Most of the common species (>1% of the total abundance, 10 of 12) preferred the more complex habitats. Five species *L. campechanus*, *O. chrysoptera*, lane snapper, *Lutjanus synagris*, gray triggerfish, *Balistes caprisus*, and cubbyu, *Pareques umbrosus*, showed significantly increased abundance with increased complexity from cage or shell, to cage-shell, block-shell, and cage-block-shell (Table 1). Five other species, *C. philadelphica*, *S. caprinus*, bank sea bass, *Centropristis ocyurus*, pygmy filefish, *Monacanthus setifer*, and pinfish, *Lagodon rhomboides*, also showed significantly higher abundances on more complex habitats, but appeared to separate on only two levels, high complexity (cage-block-shell, block-shell, cage-shell) compared to low complexity (shell or cage). In 2001, only two species appeared to prefer less complex habitats, *Diplectrum* spp. and pygmy sea bass, *Serraniculus pumilio*, which showed significantly greater abundance on shell habitats compared to other habitats.

After reef deployment (13–55 days) we completed 119 (one reef was missed) individual visual surveys during August 2002, after which habitats were destroyed by tropical storms. We identified 35 fish species, and tomtate, *Haemulon aurolineatum*, was the dominant species (36%), followed by *Diplectrum* spp. (19%), *L. campechanus* (13%), *P. umbrosus* (5%), and *O. chrysoptera* (4%, Table 2). These five

Table 1 Mean abundance (mean) of fish per 1 m² and percent abundance (%) for species >1% of the total abundance on artificial habitats in the northeastern Gulf of Mexico for 2001

Species	Mean	Percent (%)	Habitat type				
			CBS	BS	CS	S	C
<i>L. campechanus</i>	16.2	41	28.5a	21.9b	17.2c	6.9d	4.7d
<i>C. philadelphica</i>	8.9	23	15.3a	10.9a	10.8a	5.0b	0.1c
<i>Diplectrum</i> spp.	5.6	14	4.8b	5.4b	7.4b	10.3a	1.1c
<i>S. caprinus</i>	2.5	6	3.7a	3.8a	2.6ab	1.5bc	0.1c
<i>O. chrysoptera</i>	1.9	5	6.0a	2.8b	2.8b	0.4c	0.1c
<i>C. ocyurus</i>	1.0	3	2.1a	1.6ab	1.2b	0.4c	0.0c
<i>L. synagris</i>	0.8	2	2.0a	1.1b	0.5c	0.2c	0.2c
<i>B. caprisus</i>	0.6	2	1.7a	0.9b	0.5c	0.2cd	0.0d
<i>P. umbrosus</i>	0.4	1	1.1a	0.6b	0.1c	0.1c	0.0c
<i>M. setifer</i>	0.3	1	0.6a	0.5a	0.4ab	0.2b	0.1b
<i>S. pumilio</i>	0.3	1	0.1b	0.1b	0.1b	1.4a	0.0b
<i>L. rhomboides</i>	0.2	1	0.4a	0.2ab	0.2ab	0.0b	0.1b

Habitat types: cage-block-shell = CBS, block-shell = BS, cage-shell = CS, shell = S, and cage = C. Significant differences ($P < 0.05$) in abundance for individual species among habitat types are shown by different letters

Table 2 Mean abundance (mean) of fish per 1 m² and percent abundance (%) for species >1% of the total abundance on artificial habitats in the northeastern Gulf of Mexico for 2002

Species	Mean	Percent (%)	Habitat type					
			PBS	CBS	BS	CS	S	C
<i>H. aurolineatum</i>	25.68	36	42.2a	53.1a	27.3ab	33.5ab	0.7b	0.0b
<i>Diplectrum</i> spp.	13.93	19	13.2	11.4	10.6	13.1	19.3	16.3
<i>L. campechanus</i>	9.57	13	10.7abc	14.4a	12.7ab	8.4bc	7.7c	3.8d
<i>P. umbrosus</i>	3.82	5	3.3bcd	8.7a	6.0b	3.7cb	1.3cd	0.2d
<i>O. chrysoptera</i>	3.02	4	7.0a	8.2a	2.1b	1.1b	0.0b	0.3b
<i>S. caprinus</i>	2.46	3	1.1	1.5	5.7	3.5	2.4	0.5
<i>C. philadelphia</i>	2.44	3	1.5b	3.4ab	2.9ab	4.9a	1.2b	1.0b
<i>B. capriscus</i>	2.04	3	4.1a	4.6a	2.5ab	1.0b	0.2b	0.1b
<i>S. pumilio</i>	1.68	2	1.3b	1.5b	2.2ab	2.0b	3.1a	0.1c
<i>Halichoeres</i> spp.	1.44	2	1.8ab	1.2ab	1.5ab	1.5ab	2.8a	0.0b
<i>M. setifer</i>	1.40	2	1.2	2.1	1.5	2.1	0.7	0.7
<i>C. ocyurus</i>	1.17	2	0.6	1.2	1.8	1.2	2.0	0.1
<i>P. variabilis</i>	0.96	1	1.7a	1.3ab	1.2ab	1.0ab	0.6cb	0.0c
<i>L. synagris</i>	0.81	1	2.6a	0.6b	0.4b	0.4b	0.9b	0.1b

Habitat types: pyramid-block-shell = PBS, cage-block-shell = CBS, block-shell = BS, cage-shell = CS, shell = S, and cage = C. Significant differences ($P < 0.05$) in abundance for individual species among habitat types are shown by different letters

species accounted for 77% of the fish surveyed. The additional level of complexity (pyramid) added only two new species to the 2002 species richness, blue runner, *Caranx crysos*, and cobia, *Rachycentron canadum*. Also, after excluding the fishes observed on pyramids, dominant species showed little change, *H. aurolineatum* (33%), *Diplectrum* spp. (21%), *L. campechanus* (14%), *P. umbrosus* (5%), and *O. chrysoptera* (3%). Similar patterns of fish abundance compared to habitat complexity were observed in 2002, but patterns were less distinct (not significant across all levels). Complexity levels tended to overlap, but still showed the general trend of increased abundance with increased complexity. Surprisingly, only one species *L. synagris*, showed significantly higher abundance on the pyramid-block-shell habitats (the most complex habitat).

Significant differences in the community measures of species diversity and richness were detected among habitat types. In 2001, we detected a significant decrease in diversity and richness as complexity decreased from the more complex block-shell and cage-block-shell habitats ($H' = 1.7$, $S = 11.1-11.9$) to intermediate complexity shell and cage-shell habitats ($H' = 1.3-1.4$, $S = 7.5-8.5$) to the least complex cage habitat ($H' = 0.7$, $S = 3.6$). No significant differences were detected for evenness among habitat types (Fig. 3). Global and pair-wise ANOSIM tests detected significant differences among all habitat

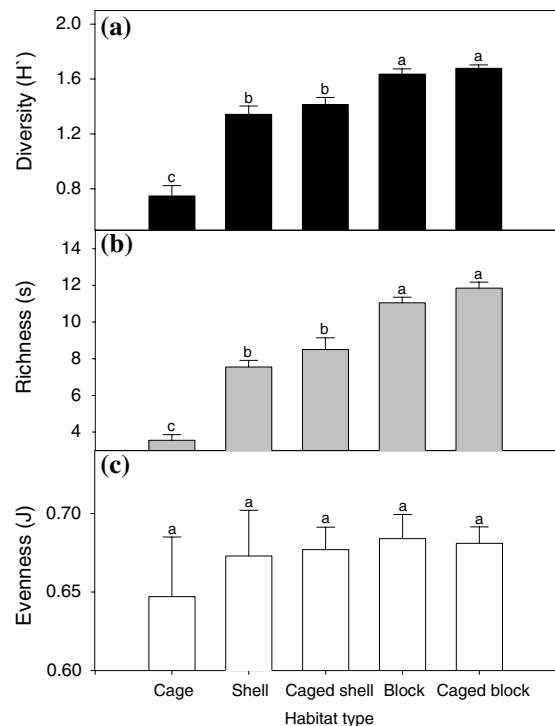
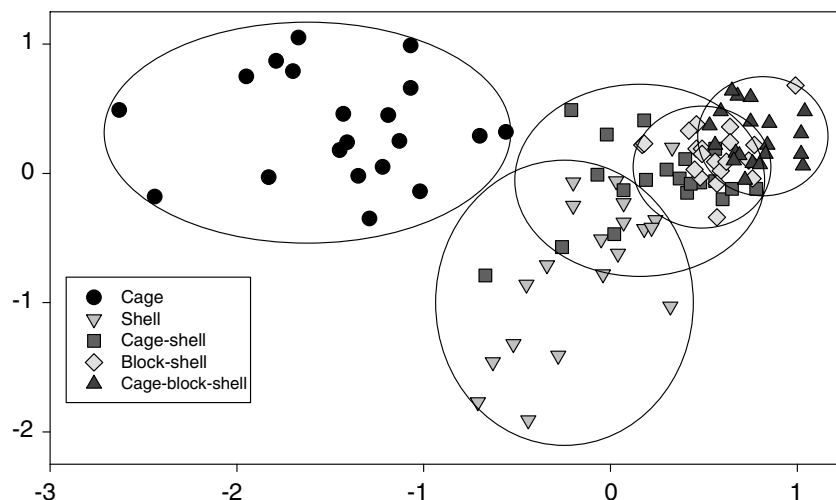


Fig. 3 Mean fish community measures by habitat type for 2001: (a) Shannon–Wiener diversity index + SE, (b) richness + SE, and (c) evenness + SE. Significant differences ($P < 0.05$) in community measures among habitat types are shown by different letters

Fig. 4 MDS plot, based on Bray–Curtis similarity coefficients among all habitats from root transformed abundance in 2001



types in 2001, and visual analysis of the MDS ordination plot of Bray–Curtis similarity coefficients showed a clear separation by habitat type (Fig. 4, Table 3).

Reef fish quickly recruited to the artificial reefs. At the end of August 2001, approximately 1 month after reef deployment, mean abundance peaked for most habitats (Fig. 5). Only cage habitats showed a later peak in mid-September. A general trend of greater abundance on higher complexity reefs was observed over all sample periods although significance varied. An exception was a consistent overlap in mean abundance between block and cage-shell reefs (Fig. 5). After the fish abundance peaked in the second sample period (29–30 August 2001) there was a subsequent decline in abundance on most reef types into the fall. Species richness and diversity showed later peaks in mid-September compared to abundance (Table 4). Patterns of individual species abundance showed similar peaks near the end of August for the two dominant species *L. campechanus* and *C. philadelphica* (Fig. 6).

Significant differences in species diversity and richness were again detected among habitats in 2002. Cage habitats had significantly lower diversity ($H'=0.7$) compared to all other habitats ($H'=1.5$ – 1.7). Significantly lower richness values were detected for cage ($S=3.2$) and shell ($S=7.5$) compared to all other habitats ($S=9.3$ – 10.5). Only cage ($J=0.6$) and shell ($J=0.8$) habitats differed in evenness (Fig. 7). In 2002, the MDS analysis again showed separation by

habitat type, with cage and shell showing separate groups compared to the higher complexity levels (Fig. 8). The higher complexity levels (pyramid-block-shell, cage-block-shell, block-shell, and cage-shell) tended to show more overlap compared to the 2001 MDS plots. However, global and pair-wise ANOSIM tests again detected significant ($P < 0.05$) differences among most (86%) habitat type pair-wise comparisons in 2002 (Table 3).

Table 3 One-way global and pair-wise analysis of similarities test among reef types

Pair-wise comparisons	<i>R</i> statistic 2001	<i>R</i> statistic 2002
Block, Caged block	0.155	0.015 ns
Block, Cage	0.934	0.685
Block, Shell	0.579	0.335
Block, Caged Shell	0.180	0.011 ns
Caged block, Cage	0.970	0.782
Caged block, Shell	0.763	0.581
Caged block, Caged shell	0.446	0.082
Cage, Shell	0.804	0.387
Cage, Caged shell	0.863	0.559
Shell, Caged shell	0.304	0.236
Block, Pyramid		0.124
Caged block, Pyramid		0.085
Cage, Pyramid		0.735
Caged shell, Pyramid		0.153

Global test among habitat types for 2001, Global $R=0.545$, and for 2002, Global $R=0.357$. Both Global R 's and the following pair-wise tests showed significant differences ($P < 0.05$) between all pairs except those labeled ns

Fig. 5 Total mean number \pm SE per m^2 for all fishes by habitat type and sample period from artificial reefs in the northeastern Gulf of Mexico. Significant differences ($P < 0.05$) in mean abundance among habitat types are shown by different letters within each time period

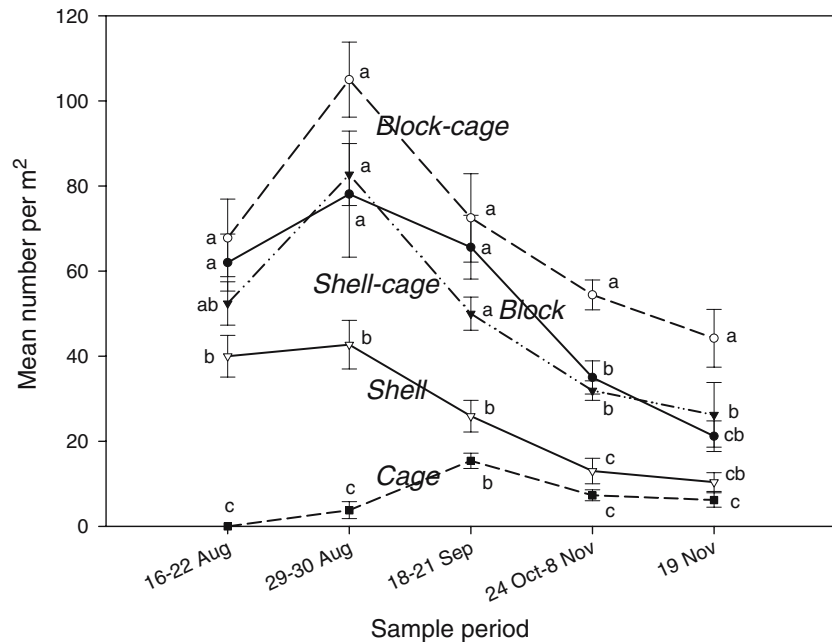


Table 4 Species richness and diversity (H') by habitat type and sample period in the northeastern Gulf of Mexico for 2001

Sample period	n	Species richness habitat type					Diversity= H' habitat type				
		CBS	BS	CS	Shell	Cage	CBS	BS	CS	Shell	Cage
16–22 Aug.	49	6.2	6.0	5.4	4.6*	0*	1.3	1.4	1.4	1.3	–
29–30 Aug.	48	6.8*	5.4	4.8	4.5	1.2*	1.2	1.2	1.1	1.2	0.4*
18–21 Sep.	50	7.6	8.0	6.1	5.0*	3.3*	1.5	1.5	1.4	1.3	0.8*
24 Oct.–8 Nov.	44	7.1*	4.7	4.9	4.0	1.9*	1.5*	1.1	1.2	1.1	0.4*
19 Nov.	29	6.8	5.4	4.0*	4.4	1.7*	1.3	1.3	1.0	1.3	0.4*

Habitat types: cage-block-shell = CBS, block-shell = BS, cage-shell = CS. n = number of individual reef surveys. *Significant differences ($P < 0.05$)

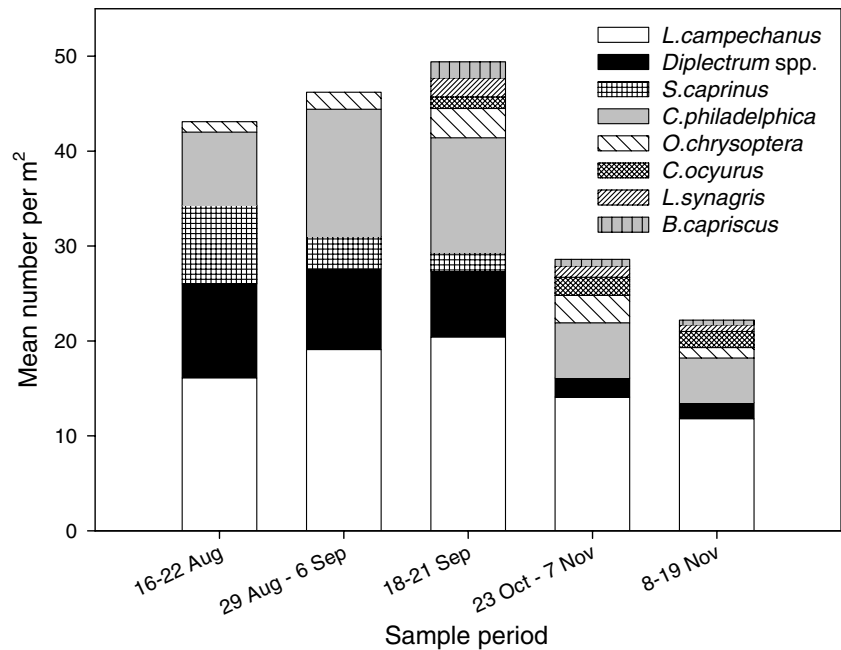
Discussion

The habitat complexity and reef fish diversity patterns in the present study were similar to patterns observed in several other marine studies (Risk 1972; Roberts and Ormand 1987; Etter and Grassle 1992; McCormick 1994; McClanahan 1994; Beck 2000), as well as the classical studies in terrestrial systems (MacArthur and MacArthur 1961; Pianka 1967; Rozensweig and Winakur 1969; Murdoch et al. 1972; Roth 1976). Colonization of artificial habitats by juvenile reef fish occurred rapidly. The ten most abundant species by habitat type were observed within 3–4 weeks of habitat placement. Talbot et al. (1978) and Shulman (1984) also observed rapid recruitment of juveniles to newly constructed

artificial habitats. Apparent preferential selection of habitat type was noted for several species. For example: *L. campechanus*, *O. chrysoptera*, *L. synagris*, *B. caprisicus*, and *P. umbrosus*, all showed significantly increased abundance at each level of complexity (Table 1). An interesting observation was the increased abundance of *S. caprinus* with increased complexity on two levels, high complexity (cage-block-shell, block-shell, cage-shell) vs. low complexity (shell or cage). This species is usually considered an open water habitat species, yet still showed significant attraction to more complex habitats.

Shulman (1984) suggested that reef fish prefer habitats with hole sizes near their own body size and the present study supported this relation. Larger reef fish, *L. campechanus*, *O. chrysoptera*, *L. synagris*,

Fig. 6 Mean number per m^2 for dominant fish species by sample period from artificial reefs in the northeastern Gulf of Mexico



B. capriscus, and *P. umbrosus*, were significantly more abundant on habitats that offered larger hole sizes (i.e., blocks). Also, newly settled *H. aurolineatum*, and *L. campechanus* were found on all habitat types where oyster shell rubble provided hole sizes that matched their body sizes. We suggest that the main function of increased complexity was increased predation refuge, for example mesh size of cages was small enough to exclude large predators, but large enough to allow easy access to habitat by small fish common to shelf habitat in the northeastern Gulf of Mexico. Previous studies have predicted similar predation effects on juvenile reef fish (Jones 1991; Carr and Hixon 1995; Connell 1997).

During this study there were several major storm events that destroyed habitats. In 2001, a series of winter storms destroyed habitats after four surveys were completed. Then in 2002, tropical storm Hanna destroyed habitats after one complete survey. Previous studies have concluded that full recruitment may take several months (Bonhsack and Talbot 1980), and we suggest that the less distinct patterns in 2002 compared to 2001, were due to less time allowed for reef fish recruitment. A difficult pattern to explain is the increased number of species (35) observed in 2002 compared to 2001 (26 species), even though we had fewer samples and less time for fish recruitment

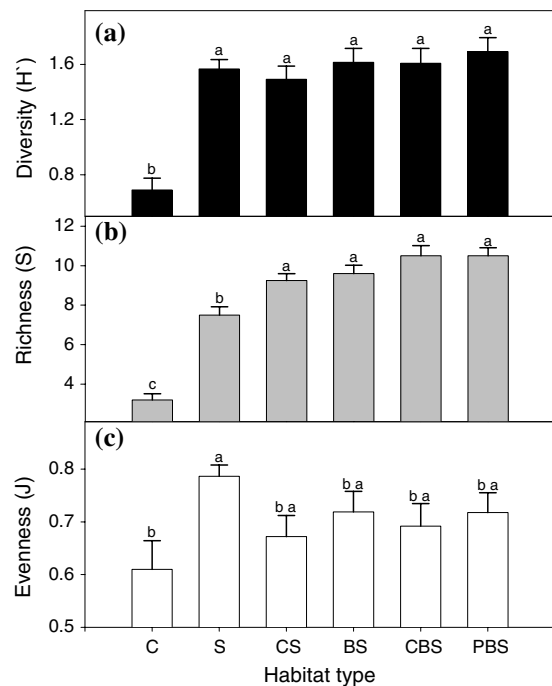
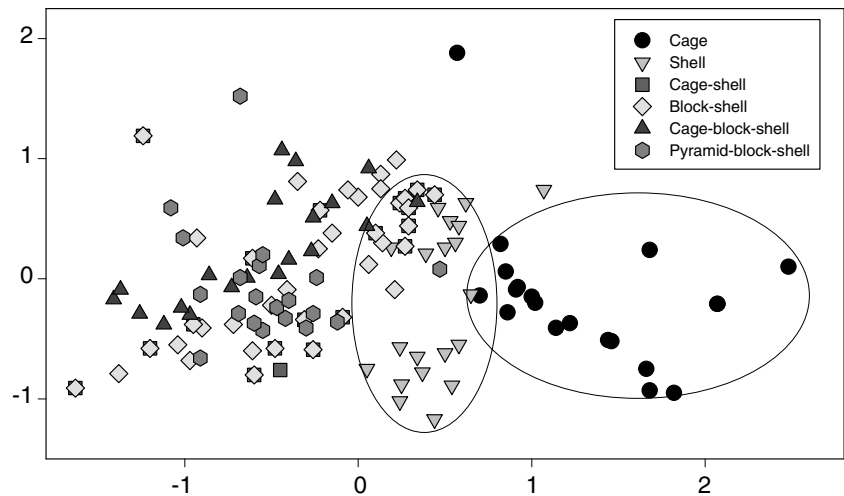


Fig. 7 Fish community measures by habitat type for 2002: (a) Shannon–Wiener diversity index + SE, (b) richness + SE, and (c) evenness + SE. Cage = C, shell = S, cage-shell = CS, block-shell = BS, cage-block-shell = CBS, and pyramid-block-shell = PBS habitats. Significant differences ($P < 0.05$) in community measures among habitat types are shown by different letters

Fig. 8 MDS plot, based on Bray–Curtis similarity coefficients among all habitats from root transformed abundance in 2002



in 2002 compared to 2001. It is well recognized that fish recruitment is highly variable from year to year which may account for the different species in these 2 years, but the fact that diversity and complexity patterns were persistent between these two different years further validates this relation.

Artificial habitats provided an ideal tool for comparisons of community structure across different levels of habitat complexity. They allowed for replication, were easily manipulated and of known age and type. Previous studies have incorporated various levels of complexity, but few replicates (Talbot et al. 1978; Hixon and Beets 1989). We used 20 replicates each of five complexity levels in 2001, and added 20 replicates of a sixth complexity level in 2002. Greater replication allowed increased power in testing the effects of habitat complexity on fish species composition. Habitat complexity appears to play an important role in reef fish community structure. In 2001 there was a clear relation between habitat complexity and fish diversity. We also detected a significant complexity effect on fish diversity in 2002 even though we were only able to complete one survey. One possible caveat with the present study was that as habitat complexity increases, food resources may also increase. In contrast, Russ (1980) showed that increased complexity reduced fish feeding efficiency on marine epifaunal communities, which suggest that increased prey shown with increased complexity may be negated by decreased foraging ability on the part of predatory fishes. Thus, the relations of fish diversity to increased food resources and habitat

complexity is not clear. Future research should attempt to separate these components of prey availability from complexity and shelter effects.

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