Inter-habitat variation in density and size composition of reef fishes from the Cuban Northwestern shelf

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Abstract: Movement and exchange of individuals among habitats is critical for the dynamics and success of reef fish populations. Size segregation among habitats could be taken as evidence for habitat connectivity, and this would be a first step to formulate hypotheses about ontogenetic inter-habitat migrations. The primary goal of our research was to find evidence of inter-habitat differences in size distributions and density of reef fish species that can be classified *a priori* as habitat-shifters in an extensive (~600km^2) Caribbean shelf area in NW Cuba. We sampled the fish assemblage of selected species using visual census (stationary and transect methods) in 20 stations (sites) located in mangrove roots, patch reefs, inner zone of the crest and fore reef (12-16m depth). In each site, we performed ten censuses for every habitat type in June and September 2009. A total of 11 507 individuals of 34 species were counted in a total of 400 censuses. We found significant differences in densities and size compositions among reef and mangrove habitats, supporting the species-specific use of coastal habitats. Adults were found in all habitats. Reef habitats, mainly patch reefs, seem to be most important for juvenile fish of most species. Mangroves were especially important for two species of snappers (*Lutjanus apodus* and *L. griseus*), providing habitat for juveniles. These species also displayed well defined gradients in length composition across the shelf. Rev. Biol. Trop. 62 (2): 589-602. Epub 2014 June 01.

Key words: reef fishes, Caribbean, habitat, size composition, Cuba, ontogenetic changes.

Movement and exchange of individuals among habitats is critical for the dynamics and success of reef fish populations. Many fish species move among different coastal habitats created by mangroves, seagrass beds, and coral reefs during their life cycles (Grol, Nagelkerken, Rypel & Layman, 2011). Consequently, conservation efforts to protect species and biodiversity are developing to provide protection of habitats including linking corridors for all life stages (Mumby et al., 2004; Sale et al., 2005). Recent research indicates that more consideration should be given to the ecological processes that occur along nursery-reef boundaries that connect neighboring ecosystems (Nagelkerken, Grol & Mumby, 2012).

In a recent review, Adams et al. (2006) classified coral reef fishes based on their

ontogenic migration patterns. The authors define three groups: Group A) habitat specialists that use the same habitat at all life stages, Group B) habitat generalists which are not site-attached and use a variety of habitats, and Group C) ontogenetic shifters. The latter species switch habitats during their life time, such as the transition from larval to juvenile to maturing adults. These species in particular depend on ontogenetic habitat change from the back-reef to the fore-reef (Adams & Ebersole, 2009).

The nursery function of back-reef habitats has been inferred by studying spatial and temporal patterns in the size distribution of juveniles and adults across such habitats (Mumby et al., 2004; Verweij, Nagelkerken, Wartenbergh, Pen & van der Velde, 2006; Dorenbosch, Verbeck, Nagelkerken & van der Velde, 2007). Size segregation among habitats could be taken as evidence for habitat connectivity and this would be a first step to formulate hypotheses about ontogenetic inter-habitat migrations.

Most research on reef fish habitat segregation in the Caribbean has been done at relative small spatial scales (<10km^2). Several studies are restricted to non-estuarine bays of small islands (Nagelkerken & van der Velde, 2002; Beets, Haught & Schmitges, 2003). In one case, the study area was a portion of the shelf less than 10km^2 (Aguilar-Perera & Appeldoorn, 2007). In other cases, several locations were sampled around a small island with a total surface of less than 200km^2 (Adams & Ebersole, 2002; Grober-Dunsmore, Frazer, Lindberg & Beets, 2007). Mumby et al. (2004) and Chittaro, Usseglio & Sale (2005) studied larger spatial scales (10-100km^2).

Fish assemblages of the NW Cuban shelf have been recently investigated and spatial variations of assemblage composition have been discussed at a region-wide scale (González-Sansón et al., 2009a; González-Sansón, Aguilar, Hernández, Cabrera & Curry, 2009b), and at smaller scales (Aguilar, González-Sansón, Munkittrick & MacLatchy, 2004; Aguilar, González-Sansón, Faloh & Curry, 2008; González-Sansón, Aguilar, Hernández & Cabrera, 2009c; González-Sansón & Aguilar, 2010).

The goals of these studies were to identify natural and anthropogenic factors that may influence fish assemblage structure. All of these and other studies across the Caribbean (Nagelkerken & van der Velde, 2002; Beets et al., 2003; Aguilar-Perera & Appeldoorn, 2007) suggest a degree of habitat connectivity, but none was designed to specifically test the hypothesis of ontogenetic, habitat migrations, which probably occur across larger spatial scales of >100km^2.

The primary goal of our research was to find evidence for habitat-related differences in size composition of a group of selected fish species considered as habitat shifters at the NW Cuban shelf. The coast in this region has a variable shelf width but a general profile from mangrove, seagrass to coral reef is found, which makes it an ideal area to study ontogenetic habitat shifts of reef fishes. We hypothesized that ontogenetic migrations occur, and then tested the predictions that inter-habitat differences in size distribution and density of reef fish species would be apparent. The specific predictions were: (1) fish density and size composition for selected species among habitats have significant differences; and (2) a gradient in length composition across the island shelf from mangrove to fore reef is found.

MATERIALS AND METHODS

Study area: We included the spatial coverage assumed to be the normal range of reef fish species (e.g. Nemeth, Blondeau, Hezlieb & Kadison, 2007; Pina-Amargós et al., 2008), we studied an extensive area of the Caribbean shelf in Northwestern Cuba (Fig. 1). The shelf in the study area is broad with a distance from shore to the shelf-edge (200m isobath) ranging from 22 to 36km. Total surface of the study area was 584km^2. Mangroves were present along the shore occupying an almost continuous fringe of ~26km (excluding the coastal indentations). Red mangrove (*Rhizophora mangle*) was dominant and its roots provide a shallow (<1m deep) habitat for fishes. The width of the aquatic habitat associated with mangrove

roots was narrow (<5m) due to the small tidal range (<0.5m) in the area (Claro, Lindeman & Parenti, 2002). There is a bank-barrier reef near the edge of the shelf. Corals occupied an almost continuous and shallow (≤5m deep) reef crest 21km long and 2-5km wide. Dominant coral species were *Porites astreoides*, *Millepora complanata* and *Acropora palmata*. The fore-reef was narrow ranging from 500-900m from the crest to the 50m isobath. Coral diversity was relatively high for a Caribbean reef and dominant species were *Siderastrea* spp., *Porites astreoides*, *Montastrea* spp. and *Millepora alcicornis* (González-Díaz, González-Sansón, Alvarez & Perera, 2010). There is

a wide back-reef lagoon between the crest and the mangrove fringe. The depth of the lagoon varied from 6-8m near the crest and mangrove to 15-20m in the central portion. At this deeper zone, there were many patch reefs which rose from the bottom 14-18m and 6-9m from the surface. The remaining lagoons were covered by sand and extensive patches of turtle grass (*Thalassia testudinum*).

Sampling methods: We sampled four habitat types: mangrove (MA), patch reefs (PR), inner zone of the crest (IC) and fore-reef (FR). We located five sampling stations within each habitat type (Fig. 1, Table 1). Stationary
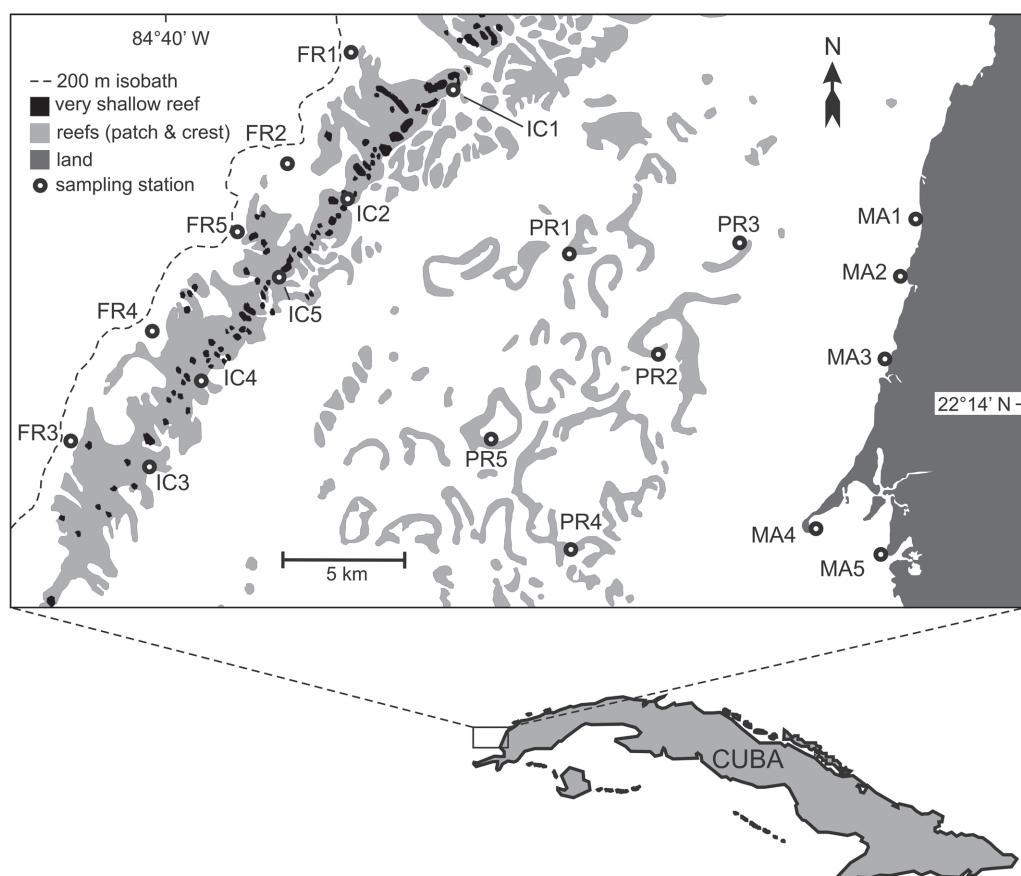
Fig. 1. Study area. Locations of sampling stations are black and white circles. MA: mangrove, PR: patch reefs, IC: inner crest, FR: Fore reef. Numbers indicate replicates within each habitat.

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visual censuses (Bohnsack & Bannerot, 1986) were conducted by two scuba divers at the PR, IC and FR habitats. Instead of 7m as recommended in the method, we used a radius of 5m (area of sampling unit ~79m^2) to address any potential visibility variability among sites. At mangrove roots, we used 40m long transects (measured with a rope) for visual censuses by two snorkelers. The average distance of observation within the root habitat was 2m from the edge of the mangrove roots towards land, for a total area of 80m^2, which was equivalent to that of the stationary visual censuses. Ten censuses (five per each diver) were done at each station for each habitat type. This sampling protocol was repeated twice over one week in June and September 2009.

For the census, we targeted *a priori* a selected group of reef fish species considered habitat-shifters (*sensu* Adams et al., 2006) by several authors (Cocheret de la Moriniere, Pollux, Nagelkerken & van der Velde, 2002; Dorenbosch et al., 2007). These species were from the families: Serranidae (genera *Cephalopholis*, *Epinephelus* and *Mycteroperca*), Lutjanidae, Haemulidae, Chaetodontidae, Scaridae and Acanthuridae, and *Lachnolaimus maximus* (Labridae) and *Sphyraena barracuda* (Sphyraenidae). The individuals of *Scarus iseri* and *S. taeniopterus* were usually indistinguishable in the field and we hereafter refer to them as *S. iseri/taeniopterus*. Following the approach of Nagelkerken, van der Velde, Gorissen, Meijer, van't Hof & den Hartog (2000), we used 5cm bins to estimate fish body length to reduce differences in size estimation between observers. We used the criteria of Nagelkerken & van der Velde (2002) to classify the sampled fishes as juvenile or adults.

For the inter-habitat comparisons in our study area, we did not transform the data to density in terms of number of individuals per unit area. Instead, we averaged the values of the ten censuses made at each station, and used this average as a density indicator expressed as the number of fish per 80m^2 (Bohnsack &

TABLE 1

Location, habitat type, and depth of stations sampled along the Northwestern coast of Cuba in 2009 (Figure 1)

Site	Latitude	Longitude	Habitat	Depth (m)
FR1	22° 21.902′ N	84° 37.612′ W	Fore reef	14
FR2	22° 19.441′ N	84° 39.196′ W	”	12
FR3	22° 13.238′ N	84° 44.368′ W	”	15
FR4	22° 15.718′ N	84° 42.420′ W	”	16
FR5	22° 17.906′ N	84° 40.330′ W	”	16
IC1	22° 21.150′ N	84° 35.243′ W	Inner crest	5
IC2	22° 18.672′ N	84° 37.726′ W	”	4
IC3	22° 12.712′ N	84° 42.473′ W	”	4
IC4	22° 14.600′ N	84° 41.240′ W	”	5
IC5	22° 16.899′ N	84° 39.375′ W	”	4
PR1	22° 17.478′ N	84° 32.386′ W	Patch reef	6
PR2	22° 15.253′ N	84° 30.289′ W	”	7
PR3	22° 17.584′ N	84° 28.239′ W	”	8
PR4	22° 10.857′ N	84° 32.377′ W	”	9
PR5	22° 13.275′ N	84° 34.290′ W	”	8
MA1	22° 18.203′ N	84° 23.937′ W	Mangrove roots	<1
MA2	22° 16.896′ N	84° 24.537′ W	”	<1
MA3	22° 15.093′ N	84° 24.812′ W	”	<1
MA4	22° 11.295′ N	84° 26.636′ W	”	<1
MA5	22° 10.793′ N	84° 24.785′ W	”	<1

Bannerot, 1986). It is a relative estimate of abundance that allowed for comparisons within this study.

A hierarchical agglomerative cluster analysis was performed using the Bray-Curtis index as the similarity measure and clustering based on group average (UPGMA). SIMPROF test (Clarke, Somerfield & Gorley, 2008) was used for identifying significant clusters. Non-parametric multidimensional scaling (MDS) was employed for ordination of samples based in the same distance matrix as the cluster analysis. The combination of clustering and ordination analyses has been described by Clarke & Gorley (2006) as the most effective way to check the adequacy and mutual consistency of both representations. Contribution of each species to total dissimilarity between pairs of habitats was calculated using the SIMPER routine. Only species adding to at least 90% dissimilarity were retained for comparative analyses. A two-way crossed ANOSIM based on *a priori* classification of samples (habitats x date) using sites inside habitats as replicates was performed on Bray-Curtis dissimilarities calculated between pairs of species. All analyses were performed on log-transformed number of individuals per count using PRIMER 6.0 (Clarke & Gorley, 2006).

A two-way fixed effects factorial design ANOVA, using date of sampling and habitat as factors, was performed on the average number/80m^2 (fourth-root transformed) for each of the most abundant species separately. A Student-Newman-Keuls post-hoc test was used for the pairwise comparisons of averages. Correlation between sampling dates for the percentage of juvenile fish was tested using the Spearman's rank correlation coefficient. Significant correlation indicates that date of sampling had no effect on juvenile abundance. A Kruskal-Wallis test was used to test the significance of observed differences among habitats for the median juvenile percentage. A Post-hoc pairwise test using z-transformation was applied to discriminate differences between pairs of habitats. All tests were performed with a level of significance equal to 0.05 using STATISTICA 7.0 (Statsoft, 2006).

RESULTS

A total of 11 507 individuals of 34 species were counted in 400 censuses (Table 2). The ten most abundant species were *Haemulon aurolineatum*, *S. iseri/taeniopterus*, *L. griseus*, *Ocyurus chrysurus*, *Sparisoma aurofrenatum*, *Haemulon plumieri*, *Sparisoma viride*, *L. apodus*, *Acanthurus coeruleus*, and *A. bahianus*. These species accounted for >90% of individuals per census. Nine species occurred in at least two habitats (with averages >1/80m^2). *H. aurolineatum* was present in large numbers at a few sites of the PR habitat resulting in a high aggregation (61.5±29.5). The remaining species had lower densities and thus we could not perform reliable single-species quantitative analyses. We used the total assemblage data for exploratory multivariate analyses and analyses by species restricted to the nine species present in at least two habitats.

The assemblage composition varied notably among habitats (ANOSIM´s global R=0.752, p<0.001, 999 permutations), but was similar among sampling periods per habitat (global R=0.08, p=0.148, 999 permutations). All pairwise comparisons between habitats were also significant (p<0.005). The numerical classification and multidimensional scaling yielded diagrams those were highly consistent with ANOSIM results. Samples formed two well separated groups (SIMPROF Pi=16.36, p=0.001; Fig. 2). One group (A) included all reef samples and the other group (B) included all mangrove samples. Within the reef habitats, two subgroups were significantly separated (Pi=3.69, p=0.001): the A1 including patch reefs and the A2 fore-reef plus inner crest habitats. Mangrove stations showed a greater heterogeneity and split into four subgroups (B1-B2, B3, B4: Pi=2.83, p=0.03; B2-B3, B4: Pi=2.82, p=0.04 and B3-B4: Pi=3.96, p=0.024). Group B2 included mostly June, and group B4 included mostly September stations. Group B1 and

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TABLE 2

Fish species observed and their average density (D)±1 standard error (number/80m^2) in four habitat types of Northwestern Cuba in summer and fall, 2009

Species	Code	D	D%	FR	IC	PR	MA
Cephalopholis cruentatus	Cepcru	0.11±0.03	0.4	M	L	L	
Cephalopholis fulva	Cepful	0.29±0.11	1.0	H	L		
Epinephelus adscencionis	Epiads	0.01±0.01	<0.1	L			
Epinephelus guttatus	Epigut	0.16±0.04	0.6	M	M	L	
Epinephelus striatus	Epistr	0.03±0.01	<0.1	L	L		
Mycteroperca bonaci	Mycbon	0.02±0.01	<0.1	L	L	L	
Mycteroperca tigris	Myctig	0.02±0.01	<0.1	L			
Lutjanus analis	Lutana	0.01±0.00	<0.1	L		L	
Lutjanus apodus	Lutapo	1.34±0.33	4.7	M	M	H	H
Lutjanus cyanopterus	Lutcya	0.02±0.01	<0.1	L	L		
Lutjanus griseus	Lutgri	2.88±0.82	10.0			H	H
Lutjanus jocu	Lutjoc	0.01±0.01	<0.1	L			
Lutjanus synagris	Lutsyn	0.05±0.02	0.2	L	L	L	
Ocyurus chrysurus	Ocychr	2.67±0.59	9.3	H	H	H	
Haemulon aurolineatum	Haeaur	6.15±2.95	21.4		M	H	L
Haemulon carbonarium	Haecar	0.09±0.06	0.3				M
Haemulon chrysargyreum	Haechr	0.01±0.01	<0.1		L		
Haemulon flavolineatum	Haefla	0.38±0.09	1.3	M	M		
Haemulon plumieri	Haeplu	2.31±0.55	8.0	H	H	H	
Haemulon sciurus	Haesci	0.42±0.15	1.5	M	M	M	M
Chaetodon capistratus	Chacap	0.02±0.01	<0.1				L
Chaetodon ocellatus	Chaoce	0.02±0.01	<0.1				L
Chaetodon striatus	Chastr	0.01±0.00	<0.1				L
Lachnolaimus maximus	Lacmax	0.17±0.04	0.6	M	L	M	
Scarus taeniopterus/iseri	Scat-i	5.04±0.59	17.5	H	H	H	L
Sparisoma atomarium	Spaato	0.13±0.06	0.4	M	L	L	
Sparisoma aurofrenatum	Spaaur	2.49±0.28	8.6	H	H	H	L
Sparisoma chrysopterum	Spachr	0.23±0.06	0.8	M	M	L	
Sparisoma rubripinne	Sparub	0.05±0.04	0.2	L	L	M	
Sparisoma viride	Spavir	1.36±0.18	4.7	H	H	H	L
Acanthurus bahianus	Acabah	0.94±0.15	3.3	H	H	M	L
Acanthurus chirurgus	Acachi	0.05±0.02	0.2	L	L	M	L
Acanthurus coeruleus	Acacoe	1.22±0.16	4.2	H	H	H	
Sphyraena barracuda	Sphbar	0.11±0.02	0.4	M	L	M	M
Total		28.77±3.41					

D (%) represent the proportion of each species calculated combining all the sites and sampling dates. FR: Fore reef, IC: Inner crest, PR: Patch reefs, MA: mangrove roots; Values of mean densities for each habitat are classified as L=D<0.1, M=0.1<D<1.0, H=D>1.0. Empty spaces indicate that the species was no found in those habitats.
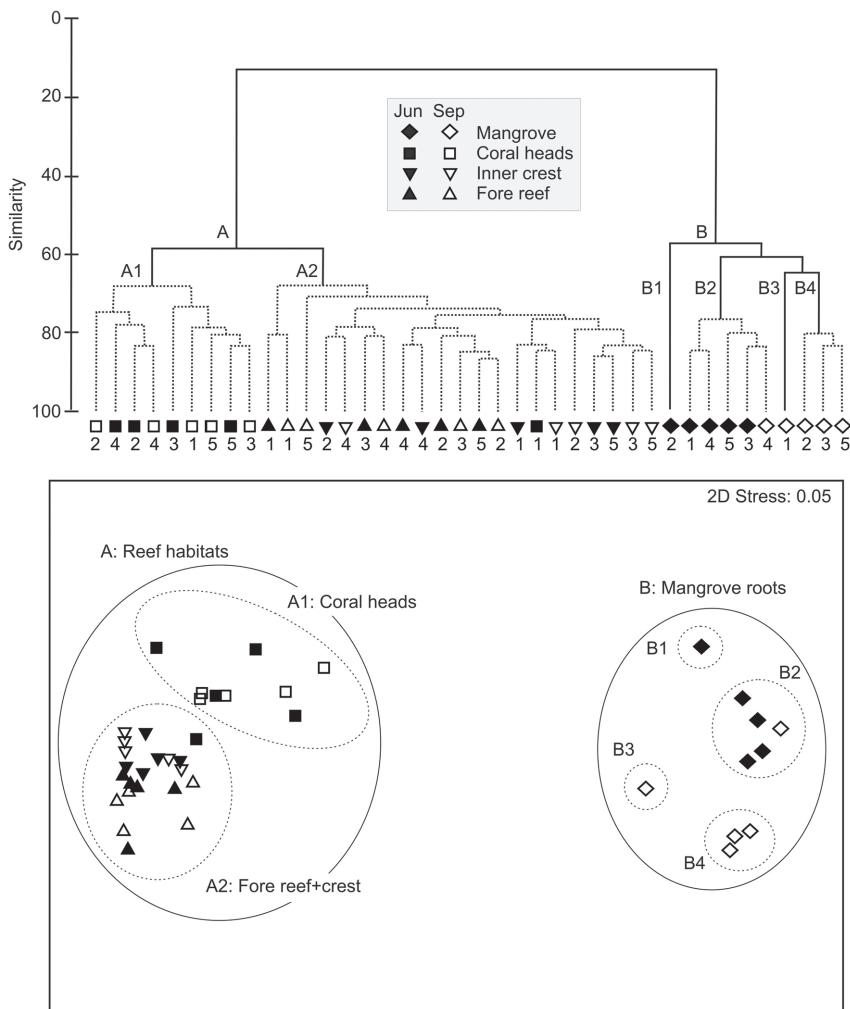
Fig. 2. Numerical classification (top panel) and MDS diagram (bottom panel) of samples. Numbers identify replicates. Envelopes indicate groups and subgroups of cluster analysis.

group B3 included only one station in June and September, respectively.

The nine species used for two factorial analyses made an important contribution to the dissimilarity among habitats (Table 3). Other species were also important because they were abundant in one habitat (*H. aurolineatum*) or were observed in just one habitat (*Cephalopholis fulva* in FR). Some rare species also made smaller contributions (>4%) to total dissimilarities (e.g., *Cephalopholis cruentata*, *Epinephelus guttatus*, *Haemulon flavolineatum*,

and *Sparisoma chrysopterum*) in reef habitats but not mangrove roots (<1/80m^2). *Haemulon sciurus* was present in all habitats with a low average density (<1/80m^2) but densities in patch reefs and mangroves were more than twice the inner crest and fore reef habitats.

No significant differences in relative abundance were found between sampling periods for any species. Significant differences in fish densities were found between habitats in all cases (Table 4; Fig. 3). *L. apodus* showed significantly higher density at mangrove and

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TABLE 3

The overall average dissimilarity (AD) and single species contributions (%) to total dissimilarity between habitat pairs in four habitat types of Northwestern Cuba in summer and fall, 2009

	AD	FR-IC	FR-PR	IC-PR	FR-MA	IC-MA	PR-MA
		28.1	43.2	37.9	91.1	90.6	77.9
Acabah		4.4	5.7	5.9	6.0	5.8	3.6
Acachi		—[1]	—	1.9	—	—	—
Acacoe		2.6	2.9	2.7	6.5	7.2	6.8
Cepcru		5.3	3.5	2.9	2.8	—	—
Cepful		10.8	7.9	—	5.3	—	—
Epigut		6.1	4.7	2.7	3.7	1.7	—
Epistr		2.5	—	—	—	—	—
Haecar		—	—	—	1.9	2.1	2.2
Haeaur		2.5	15.5	16.8	—	—	12.7
Haefla		7.4	4.1	9.5	2.8	5.6	—
Haeplu		4.7	3.5	3.9	7.5	7.4	8.3
Haesci		5.1	4.3	4.7	2.2	2.6	3.7
Lacmax		3.6	4.7	4.8	—	—	4.7
Lutapo		5.5	6.2	6.8	6.2	6.4	3.9
Lutgri		—	5.8	6.8	10.5	11.6	7.5
Myctig		1.9	—	—	—	—	—
Ocychr		6.7	5.2	3.9	5.6	8.1	10.9
Scat-i		2.3	2.3	2.8	9.6	10.1	9.5
Spaato		4.7	2.7		1.8	—	—
Spaaur		1.9	2.9	2.9	8.1	8.6	8.5
Spachr		5.1	3.7	4.9	2.8	3.6	—
Sparub		1.6	—	—	—	—	—
Spavir		2.4	2.8	3.3	6.4	7.7	7.8
Sphbar		3.5	2.5	2.9	1.4	1.6	—
Total		90.6	90.9	90.1	91.1	90.1	90.1

FR: fore reef, IC: inner crest, PR: patch reefs, MA: mangrove roots. The cut off for low contributions was 90%. Species codes are presented in table 2.

[1] Species was not found or density was below the cutoff %.

patch reefs. Density of *L. griseus* in mangrove roots was the highest, followed by a lower value in patch reefs, but this species was not recorded in other habitats. *O. chrysurus* was not recorded in mangrove habitats and had higher densities in patch reefs with a progressive decrease towards the fore reef. *H. plumieri, S. taeniopterus/iseri, S. aurofrenatum, S. viride* and *A. coeruleus* showed no significant differences in density among reef habitats, and were mostly absent in mangrove roots. Density of *A. bahianus* was higher in fore reef and inner crest habitats, lower in patch reefs, and observed the lowest values in mangrove roots.

Juvenile proportions changed among habitats and species, but showed less variability between sampling dates (Table 5). Based in our results, we grouped juvenile species in three categories: a) species that were not present in mangrove roots; b) species present in all sampled habitats; and c) species that were more abundant in mangrove roots. For the three species that were not present in mangrove roots habitats, no clear trend in size composition was found. For *A. coeruleus,* the percentage of juvenile individuals was high (45-71%) in fore reef and inner crest habitats; while *O. chrysurus* was found in most habitats

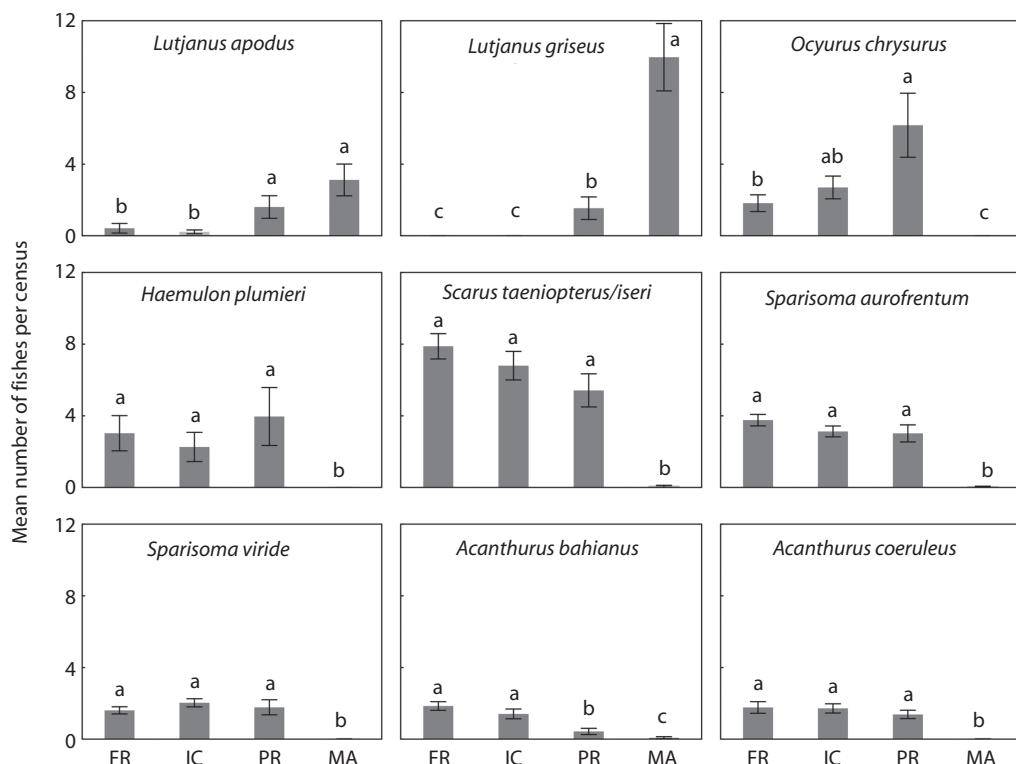| Species	Habitats		Dates		Habitat x date	
	F(3.32)	p	F(1.32)	p	F(3.32)	p
Lutapo	10.6	<0.001	3.3	0.080	0.3	0.815
Lutgri	58.1	<0.001	0.8	0.392	0.4	0.754
Ocychr	39.9	<0.001	0.2	0.686	1.0	0.385
Haeplu	51.3	<0.001	1.0	0.315	0.6	0.646
Scat-i	86.1	<0.001	0.1	0.805	0.3	0.829
Spaaur	126.7	<0.001	3.1	0.089	0.8	0.487
Spavir	79.0	<0.001	0.7	0.400	0.2	0.921
Acabah	18.9	<0.001	0.2	0.623	0.3	0.792
Acacoe	101.1	<0.001	1.4	0.241	0.1	0.951

Fig. 3. Average number of individuals/80m^2 (±1 standard error) for selected species. Similar letters are not significantly different (SNK test).

(62-94%). *H. plumieri* were mostly adults (68-88%) in all habitats.

Additionally, four species (*S. taeniopterus/iseri*, *S. viride*, *S. aurofrenatum* and *Acanthurus bahianus*) were present in all habitats but were scarce in mangrove roots. No clear trend was evident in three species of parrotfishes (*S. taeniopterus/iseri*, *S. viride* and *S. aurofrenatum*) and most of these species were juveniles (40-82%). *A. bahianus* individuals were larger in patch reefs with a low representation of juvenile fish (10-25%). In the rest of the habitats,

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Species	Date	Percentage below ML			
		FR	IC	PR	MA
Acabah	Jun	57	61	10	100
	Sep	56	53	25	75
Acacoe	Jun	49	45	19	—[1]
	Sep	61	71	40	—
Haeplu	Jun	16	32	23	—
	Sep	14	12	17	—
Lutapo	Jun	0	57	40	100
	Sep	31	13	48	100
Lutgri	Jun	—	—	53	100
	Sep	—	—	57	97
Ocychry	Jun	62	94	87	—
	Sep	46	82	87	—
Spauro	Jun	40	42	39	—
	Sep	51	43	40	63
Spavir	Jun	44	47	49	50
	Sep	31	57	52	—
Scatae	Jun	50	80	61	75
	Sep	69	81	72	82
Median		48	55	44	90
		a	a	a	b

FR=Fore reef; IC=Inner crest; PR=Patch reef; MA=Mangrove roots. Similar letters are not significantly different (post-hoc pairwise test).

[1] Species not present.

however, the percentages of juveniles for this species were greater (53-100%).

L. apodus and *L. griseus* were the only species that were abundant in mangrove root habitats as juveniles, yet they were larger in body size at reef habitats. For this reason, we presented a detailed analysis of size distributions by habitat for these two species (Fig. 4). Juveniles of *L. apodus* were present in all habitats and their proportion decreased from mangrove to fore reef habitats (mangrove, 100%; patch, 40-48%; inner crest, 13-57%; fore reef, 0-31%). Individuals of *L. griseus* were almost only juveniles in mangrove root habitats (97-100%), while juvenile fish decreased notably

in patch reefs (53-57%). This species was not observed in inner crest and fore reef stations.

The estimated percentage of juvenile fish per species per habitat showed a significant correlation between sampling dates (r_s=0.787, p<0.001, n=30). Kruskal-Wallis test pooling all nine species data yielded a significant value indicating differences among habitats (H=18.04, p=0004, n=60). After a post-hoc pairwise comparison of the medians, mangrove habitat values were significantly higher compared to other habitats (not significantly different, Table 5).

DISCUSSION

The presence of adult fish in all sampled habitats was consistent with Sheaves (2005) and Chittaro et al. (2005) conclusions that the term 'nursery area' applied for mangroves and seagrass habitats should be used with discretion. Based in our results, we consider the term 'adult habitat' applied for coral reefs should be used also with discretion. As Gillanders, Able, Brown, Eggleston & Sheridan (2003) discuss, it is important to measure the life history and specific movements of individuals, if we were to better understand the location and function of nursery habitats for marine organisms. Supporting former ideas, we found adults of scarid species in mangrove roots, and juvenile of all most abundant fish species in reef habitats.

Our data did not allow a quantitative approach to define nursery areas (sensu Beck et al., 2001) or essential juvenile habitats (Dahlgren et al., 2006; Layman et al, 2006). Instead, we discuss juvenile habitats as a qualitative labeling for those places where a relative high percent (>40%) of individuals were classified as juveniles. Generally, juveniles were relatively abundant in reef habitats and most abundant in mangrove roots. Nagelkerken et al. (2000) showed that fish had a preference for specific nursery habitats, but that most species used multiple nursery habitats simultaneously. The value of nursery habitats is species specific and a combination of habitats is used by high densities of juveniles (Aguilar-Perera, 2004).

Lutjanus apodus

Lm=25cm
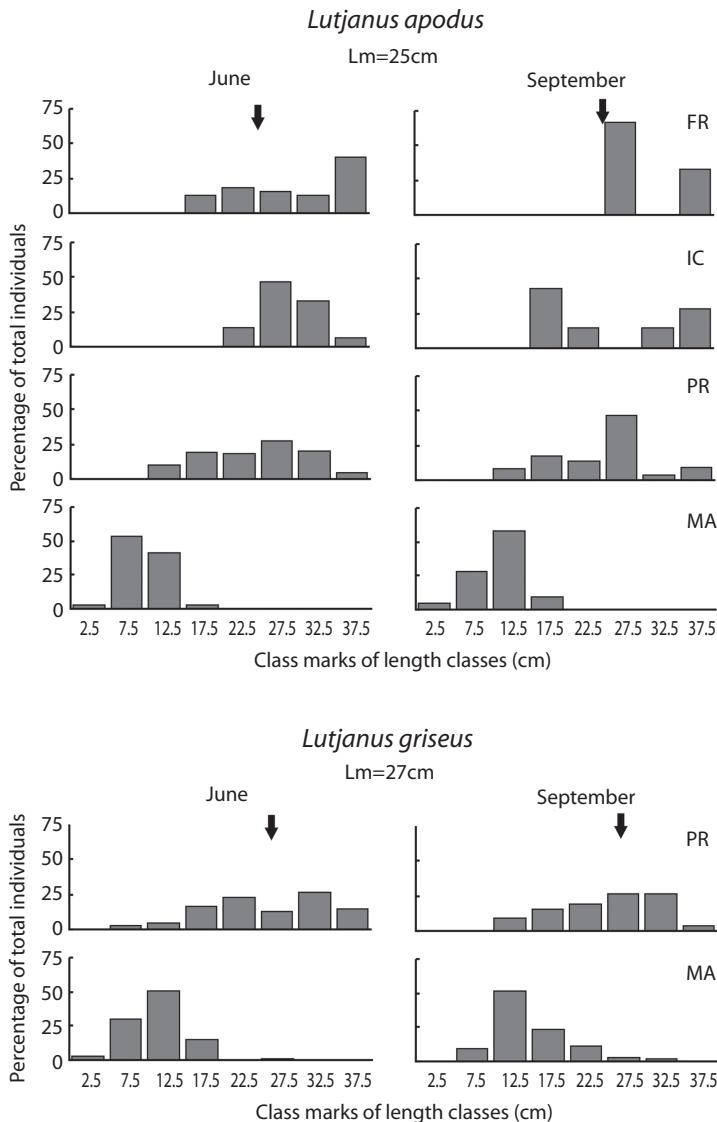
Fig. 4. Length composition of fish from the mangrove habitat for two species of Lutjanids. ML=Length at maturation. MA: mangrove, PR: patch reefs, IC: inner crest, FR: Fore reef.

Our results for *A. bahianus* and *A. coeruleus* corroborate earlier findings. Nagelkerken et al. (2000) found that juveniles of Acanthuridae were restricted to the shallow water biotopes (mangrove, notches in fossil reef rock, seagrass bed and fossil reef boulders), whereas adults were found on the reef. In contrast, Cocheret de la Moriniere et al. (2002) reported

that *A. bahianus* was not observed in mangroves. Aguilar-Perera & Appeldorn (2007) found a similar trend for *A. coeruleus* and *A. bahianus* which were almost absent from mangroves in their study.

Habitat and size distribution patterns of Lutjanidae in our study agree with those reported by other authors. Nagelkerken et al. (2000)

found that *L. apodus* and *L. griseus* were more abundant in mangrove habitats and that *L. apodus* showed an ontogenetic shift to deeper coral reefs. Cocheret de la Moriniere et al. (2002), Chittaro et al. (2005), and Aguilar-Perera & Appeldoorn (2007) found that *L. apodus* and *L. griseus* showed strong preferences for mangroves over seagrass beds at all size-classes.

Juvenile yellowtail snapper (*O. chrysurus*) prefer seagrass over mangrove roots and other habitats (Nagelkerken et al., 2000; Aguilar-Perera & Appeldoorn, 2007), but they have been recorded in both habitats (Cocheret de la Moriniere et al., 2002). Huijbers, Nagelkerken, Debrot & Jongejans (2013) found that the contribution of the coral reef as a nursery habitat for *O. chrysurus* was minimal. We found relatively high abundances of juveniles of this species in all reef habitats except mangrove roots.

Mumby et al. (2004) reported that juveniles of the white grunt, *H. plumieri,* were common in mangrove habitats. Appeldoorn, Recksiek, Hill, Pagan & Dennis (1997) presented length-frequency distributions that indicated an offshore ontogenetic migration. Along the Northwest coast of Cuba, we observed no white grunt in mangrove roots, and the length composition in reef habitats did not suggest an ontogenetic migration, because proportions of juveniles were similar in all reef habitats. Aguilar-Perera & Appeldoorn (2007) reported that mean densities of juveniles were significantly higher in seagrass relative to mangroves and coral reefs.

Our results for species in the family Scaridae indicated that these species were found at all stages in all reef habitats. Aguilar-Perera & Appeldoorn (2007) found significant differences among habitats for *S. aurofrenatum* and *S. viride* juveniles*,* but not for *S. iseri* juveniles. The preference of *S. aurofrenatum* and *S. iseri* for reef habitats has also been reported by others (Adams & Ebersole, 2002; Chittaro et al., 2005).

In summary, we found significant differences in densities and size compositions of fishes among reef and mangrove habitats of Northwestern Cuba. These suggest a species-specific, differential use of coastal habitats during ontogeny. Adults were found in all habitats. Reef habitats, mainly patch reefs, seem to be very important for juvenile fish of most species in our study area. These results differ notably from the main trend found in the Caribbean, where studies report that most or all nursery fish species studied herein had the highest juvenile densities in mangrove areas only (Nagelkerken, 2009). In our study area, mangroves were especially important for the two snapper species (*L. apodus* and *L. griseus*) which were also the only species that showed well defined gradients in length composition from mangrove to the fore reef.

RESUMEN

Variación entre hábitats de la densidad y composición por tallas en peces de arrecife de la región noroccidental de Cuba. El movimiento e intercambio de individuos entre hábitats son aspectos críticos para la dinámica y el éxito de las poblaciones de peces arrecifales. La segregación de tallas entre hábitats puede ser considerada como evidencia para la conectividad de hábitats y esta podría ser el primer paso para la formulación de hipótesis sobre migraciones ontogenéticas entre hábitats. El objetivo principal de nuestra investigación fue encontrar evidencia de diferencias entre hábitats en la distribución de tallas y densidad de especies de peces de arrecifes, las cuales pueden ser clasificadas, *a priori*, como especies con cambios ontogénicos en el hábitat, en una área extensa (~600 km^2) de plataforma en el Caribe. Se realizaron censos visuales (métodos estacionario y de recorrido) de especies de peces seleccionadas en 20 sitios localizados en raíces de mangle,

arrecifes de parche, la zona interna de la cresta arrecifal y el arrecife frontal (12-16m de profundidad). Se hicieron diez censos en cada sitio de los cuatro tipos de hábitat y se repitió este esquema en junio y septiembre 2009. Fueron contados un total de 11 507 individuos de 34 especies en un total de 400 censos. Se encontraron diferencias significativas en la densidad y composición por tallas entre los hábitats de arrecife y manglar. Estas diferencias, indicaron un uso variable de los hábitats costeros dependiendo de la especie. Los adultos fueron encontrados en todos los hábitats. Los hábitats de arrecifes, principalmente los arrecifes de parche, parecen ser muy importantes para los juveniles de peces de la mayoría de las especies en nuestra área de estudio. Los manglares fueron especialmente importantes para dos especies (*L. apodus* y *L. griseus*), que a lo largo de la plataforma fueron las únicas que mostraron gradientes bien definidos en las tallas.

Palabras clave: peces de arrecife, Caribe, hábitat, composición por tallas, Cuba, cambios ontogenéticos.

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