

Variation in juvenile fish density along the mangrove–seagrass–coral reef continuum in SW Puerto Rico

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ABSTRACT: While the composition of the fish community of SW Puerto Rico has been studied extensively, little information is available on the importance of different shallow-water areas (i.e. back reef systems) as juvenile habitat. We investigated the extent to which 20 selected, reef-associated fish species use mangrove and seagrass as juvenile habitat in contrast to shallow-water coral reefs. A stratified sampling procedure was applied to quantify the variability of juvenile fish densities along the mangrove–seagrass–coral reef continuum of an inshore–offshore gradient. We recorded 28 758 individuals, mainly Haemulidae, Lutjanidae, Scaridae, and Acanthuridae, with juveniles accounting for 80 % of total sightings. For each fish species, juveniles were distinguished according to maturation size reported in literature. Significant variations in juvenile density were evident, and the importance of mangroves and seagrass as juvenile habitat was relative and species-specific. Frequently, shallow coral reefs showed higher densities than mangroves and seagrass. Ontogenetic migrations (i.e. progressive displacement of a given fish life stage from a given habitat to another) were inferred to occur throughout the continuum. Results highlight the importance of including this continuum within coastal management using marine reserves.

KEY WORDS: Reef fishes · Mangroves · Seagrass · Coral reefs · Puerto Rico

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INTRODUCTION

Many marine organisms display life histories involving the use by juveniles of certain habitats that differ from those used by adults (Beck et al. 2001). These habitats mostly consist of mangroves, seagrass beds, and shallow coral reefs, and appear to represent important habitats, functioning mainly as juvenile habitats (Adams et al. 2006, Dahlgren et al. 2006). According to Beck et al. (2001), a juvenile habitat or nursery results from the combination of at least 4 factors promoting certain beneficial components for the marine species: (1) density, (2) growth, (3) survival, and (4) movement to adult habitats. Adams et al. (2006) mention that the nursery function of a given habitat has been inferred by numerous studies rather than

directly demonstrated, and the inference is based on 1 or 2 of factors 1 to 3 above. Such a nursery function can be defined as the growth and survival of juvenile fishes and invertebrates followed by a successful ontogenetic habitat shift into their adult habitat (Adams et al. 2006).

In the western Atlantic, mangroves and seagrass (i.e. back reef habitats; Dahlgren & Marr 2004) are used by many reef fishes as potential nursery habitats (Parrish 1989, Roberts 1996, Dahlgren & Eggleston 2000, Faunce & Serafy 2006). From these habitats, many reef fishes perform ontogenetic migrations to deeper adult habitat areas (e.g. coral reefs) to complete their life cycle (Appeldoorn et al. 1997, Lindeman et al. 2000, Mumby et al. 2004, Dahlgren et al. 2006). In Caribbean islands, juvenile reef fishes are highly

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abundant in bays (Nagelkerken et al. 2000), and their densities are a function of the presence of nearby mangroves and seagrass habitats (Nagelkerken et al. 2001). Additionally, lagoonal patch-reef areas of back-reefs are preferred juvenile habitat for many fishes (Adams & Ebersole 2002).

In Puerto Rico, a Caribbean archipelago, the reef fish community has been extensively studied (Austin 1971, Austin & Austin 1971, Kimmel 1985, Rooker & Dennis 1991, McGehee 1994, Acosta 1997, Appeldoorn et al. 1997, Christensen et al. 2003), but relatively little information is available for analyzing the relative importance of back reef systems as important habitats for juvenile fishes. In the present study off the La Parguera shelf, SW Puerto Rico, we investigated the extent to which 20 selected, reef-associated fish species use mangroves and seagrass as juvenile habitats, and how that use, expressed as fish juvenile density variation, differs from that of shallow-water coral reefs.

MATERIALS AND METHODS

Study site. The study was conducted at the eastern part of La Parguera, SW Puerto Rico, from January 2003 to May 2004. The La Parguera shelf presents a complex physiographic relief, including submerged and emergent reefs (Morelock et al. 1977), and a variety of biotopes (e.g. mangroves, seagrass beds, algal plains, sandy-mud lagoons, and patch reefs; Kimmel 1985). Sampling sites were allocated along an inshore–offshore gradient, including a mangrove–seagrass–coral reef continuum, at 4 major locations: Montalva Bay (inshore), Romero Key and Corral Key (midshore), and Turrumote (offshore) (Fig. 1). All locations, with the exception of Turrumote, are dominated by seagrass *Thalassia testudinum* beds and fringed by mangroves *Rhizophora mangle*. Montalva Bay ($17^{\circ}57'55''$ N, $66^{\circ}59'34''$ W) is a non-estuarine, coastal system (3.7 km^2) with shallow-water areas (i.e. sand, mud). Romero Key ($17^{\circ}56'52''$ N, $66^{\circ}59'48''$ W), located 2.3 km from shore at the entrance of Montalva bay, is an emergent reef (0.7 km^2) with relatively small mangrove areas and shallow reefs. Corral Key ($17^{\circ}56'43''$ N, $67^{\circ}00'34''$ W), located 2.9 km from shore and off Montalva Bay, is an emergent reef (1.5 km^2) with shallow coral reefs and little mangrove areas. Turrumote ($17^{\circ}56'12''$ N, $67^{\circ}01'09''$ W), where there is a proposed marine reserve (7.6 km^2), is a small emergent key (0.1 km^2) located at mid-distance between the coastline and the insular shelf edge (4.6 km), comprised by emergent coral reefs and several submerged reefs with an extensive hard ground, low relief platform with shallow and deeper coral reefs and profuse soft-coral (e.g. gorgonians) areas.

Study design. A stratified sampling was applied to investigate the variability of juvenile fish densities along the inshore–offshore gradient and between mangroves, seagrass and coral reefs (Fig. 2). At each of the 4 locations, strata selection was according to a combination of biotope (mangrove, seagrass, coral reef), depth (shallow: 0 to 3 m; deep: 3 to 10 m), position from shore (inside or outside the bay), and wave exposure (fore reef, back reef). In each stratum, 3 randomly

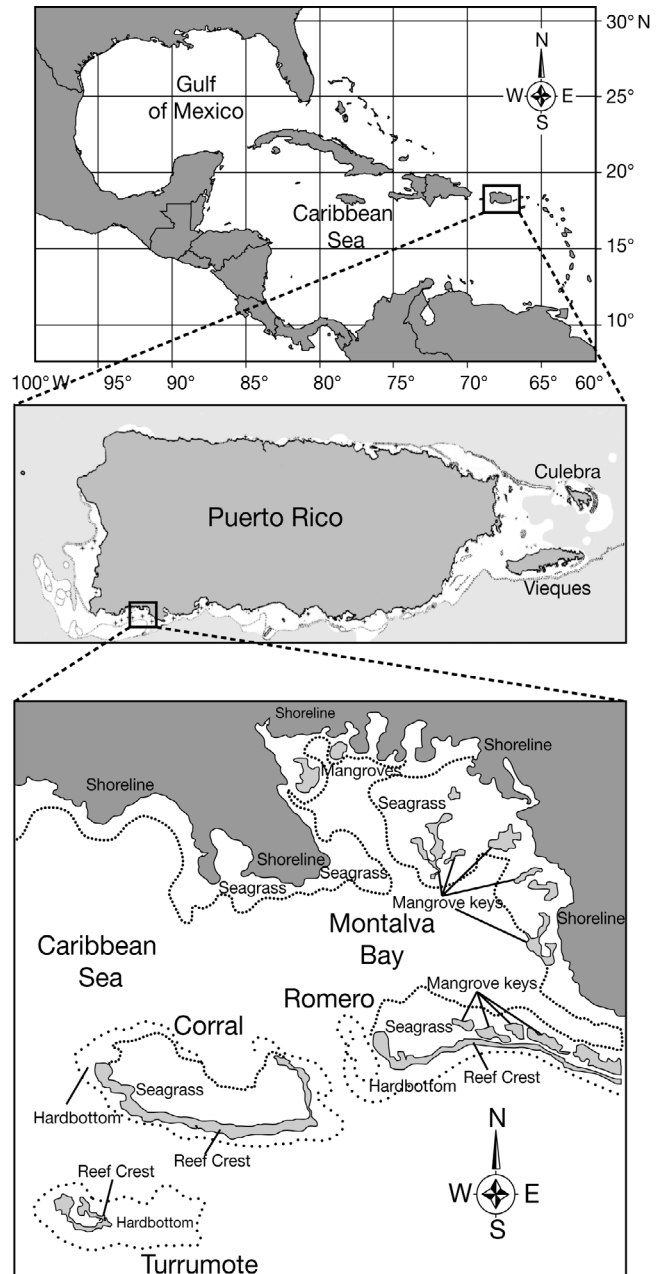


Fig. 1. Geographic location of Puerto Rico and major habitat components (e.g. biotopes) and locations (Montalva Bay, Romero Key, Corral Key, Turrumote Key) in the study area

selected sites were allocated. At each site, 10 transects (each 100 m²) were sampled totaling 1000 m² per site (3000 m² per stratum, Fig. 2). For Montalva Bay, the strata selection based on biotope and orientation from shore resulted in 2 strata for mangroves (Mang-In and Mang-Out) and 2 for seagrass beds (Seag-In and Seag-Out). For Romero Key, the selection was based on biotope, wave exposure and depth, resulting in 1 stratum for seagrass beds, 2 strata for shallow coral reefs (back reef: SBR; and fore reef: SFR) and 1 stratum for deep coral reefs (fore reef: DFR). For Corral Key, strata selection was similar to that of Romero Key. For Turrumote, the same criteria applied; however, there were 2 strata for shallow reefs (SBR and SFR) and 2 for deep reefs (DBR and DFR).

Fish censuses. We considered 20 fish species in the study based on (1) high relative abundance, (2) commercial (i.e. fisheries, aquarium trade; e.g. Haemulidae, Lutjanidae) and ecological (i.e. coral feeders, herbivores; e.g. Acanthuridae, Scaridae) importance, and (3) nursery habits. Nagelkerken et al. (2000) coined the terms 'nursery species' and 'reef species' for categorizing fishes showing differential use of habitat according to life stage. Such a distinction was used in this study of Puerto Rico to discern reef fishes that as juveniles

use habitats other than coral reefs (e.g. mangroves, seagrass). However, we used the term 'reef resident species' instead of 'reef species'. The species in this study from Puerto Rico comprised 4 grunts (Haemulidae), 3 surgeonfishes (Acanthuridae), 5 parrotfishes (Scaridae), 4 snappers (Lutjanidae), 1 butterflyfish (Chaetodontidae), 1 barracuda (Sphyraenidae), 1 mojarra (Gerreidae), and 1 damselfish (Pomacentridae) (see Table 1). Distinction of juveniles was based on information of maturation sizes available in literature (García-Cagide et al. 2001) and FishBase (Froese & Pauly 2003).

An adaptation of the belt-transect (Brock 1954), an underwater visual census (UVC), was used for the survey. In general, UVCs are non-destructive techniques used to estimate reef fish populations that enable the selection of specific species, require only one worker and relatively little time, and are inexpensive (Fowler 1987). Among the disadvantages of UVCs are the potential variations in observer swimming speed (Lincoln Smith 1988), transect width (Cheal & Thompson 1997), fish length estimation variations (Bellwood & Alcalá 1988), accuracy of species identification (Brock 1982), and optimal number of transect replication (Samoilys & Carlos 2000). Despite such disadvantages,

UVCs allow rapid estimates of relative abundance, biomass, and length frequency distributions of fishes. This technique is practical and extensively used to study a wide range of demersal species taken by shallow-water fisheries on coral reefs (Nagelkerken et al. 2000, Appeldoorn et al. 2003, Christensen et al. 2003).

When an individual of the selected fish species was encountered within a given belt-transect, the body length (i.e. fork length, FL, in cm) was visually estimated and recorded. Each transect was 25 m in length by 2 m to each side of the line transect (25 × 4 m). Such dimensions were chosen (1) to render an area of 100 m² per replicate (i.e. transect), (2) to allow easy comparisons with previous studies, and (3) because they were amenable for use in the biotopes selected. For reducing potential census bias and improving accuracy in fish length estimation, wooden fish models of several lengths (5 to 40 cm), tied to the reef bottom (Rooper & Recksiek 1992), were used as calibration objects before the study. Transect survey duration (i.e. fish counting)

	Location	Biotope	Position	Depth	Wave exposure	Stratum	No. of Sites	No. of Transects	
Inshore	Montalva Bay	Mangroves	In	Shallow	NA	Mang-In	3	3 × 10	
			Out	Shallow	NA	Mang-Out	3	3 × 10	
		Seagrass	In	Shallow	NA	Seag-In	3	3 × 10	
			Out	Shallow	NA	Seag-Out	3	3 × 10	
	Romero	Seagrass	NA	Shallow	NA	Seag-Rom	3	3 × 10	
		Coral reefs	NA	Shallow	Back-Reef	SBR-Rom	3	3 × 10	
NA	Shallow		Fore-Reef	SFR-Rom	3	3 × 10			
NA	Deep		Fore-Reef	DFR-Rom	3	3 × 10			
GRADIENT	Corral	Seagrass	NA	Shallow	NA	Seag-Corr	3	3 × 10	
		Coral reefs	NA	Shallow	Back-Reef	SBR-Corr	3	3 × 10	
			NA	Shallow	Fore-Reef	SFR-Corr	3	3 × 10	
	NA		Deep	Fore-Reef	DFR-Corr	3	3 × 10		
	Offshore	Turrumote	Coral reefs	NA	Deep	Back-Reef	DBR-Turr	3	3 × 10
				NA	Shallow	Back-Reef	SBR-Turr	3	3 × 10
NA				Shallow	Fore-Reef	SFR-Turr	3	3 × 10	
NA				Deep	Fore-Reef	DFR-Turr	3	3 × 10	
Totals	4	3		2	2	16	48	480	

Fig. 2. Sampling intensity and sampling design along the inshore-offshore gradient in SW Puerto Rico. The stratification is based on location, biotope (in: inside the bay; out: outside), depth (shallow: 0–3 m; deep: 3–10 m), exposure, and stratum. We selected 3 sites per stratum, totalling 48 sites along the gradient, and 10 transects per site, totalling 480 transects in all. SBR: shallow back reef; SFR: shallow fore reef; DFR: deep fore reef; DBR: deep back reef. NA: not applicable; Mang: Mangrove; Seag: Seagrass

was standardized to 20 min per transect and censuses were conducted 15 min after lying the transect line down on the bottom, this latter to allow the fish to resume normal behavior after setting the line. SCUBA was used in deeper locations (>5 m), whereas snorkeling was used during shallow surveys (<5 m), mainly in the mangrove prop-roots and seagrass beds. Transect width in the mangrove prop-roots was adapted, as much as possible, to the selected transect dimension. For schooling fishes (e.g. *Haemulon flavolineatum*) comprising more than 50 individuals, previous trials were performed to calibrate number estimation using counting techniques for shorebirds (Haig 2004). Range of visibility in all locations investigated was relatively homogeneous; therefore, it did not represent a factor interfering with visual recordings of fish density.

Statistical analysis. For testing the null hypothesis that there are no differences in fish juvenile densities between mangroves, seagrass beds and shallow-water coral reefs of lagoon areas, the proportional abundances of juveniles of selected fish species were calculated and compared using a 1-way ANOVA among (1) strata (Mang-In, Seag-Out, SBR-Rom, see Fig. 2) and biotope (Mangrove, Seagrass) and (2) species among strata and biotope along the gradient using the multiple comparison Tukey HSD test ($\alpha = 0.05$) (Sokal & Rohlf 1995). Homogeneity of variances was tested with a Bartlett's test, and normality was tested using the Kolmogorov-Smirnov 1-sample test after a square root data transformation, while homogeneity of variances was determined by Gabriel's post hoc test. For each fish species, evidence of ontogenetic migration/habitat shifts was considered as changes in the length composition recorded across the inshore–offshore shelf gradient. To compare the spatial distribution of fishes between strata, and infer ontogenetic migrations along an inshore–offshore gradient, a cluster analysis was used. Densities per species and size class per each stratum were transformed to percentages of total composition of a given species and were square root-transformed for cluster analyses using the program MultiVariate Statistical Package 3.1 (Kovach Computing Services). The average-linkage method (with weighted pair group average) was used in combination with the Bray-Curtis coefficient.

RESULTS

A total of 28 758 individuals of 20 species in 8 families were recorded from mangroves, seagrass beds, and coral reefs (Table 1). Juveniles accounted for 80 % of this total, reaching amounts greater than 60 % per stratum. The proportional abundance of juveniles was higher in mangroves, seagrass beds, and shallow reefs of Montalva Bay and Romero (inshore) compared to that in shallow and deep coral reefs of Corral and Turrumote (offshore) (Table 2, Fig. 3). There was a significantly higher proportional abundance of juveniles in the shallow back reef (SBR) of Romero and the mangroves and seagrass of Montalva Bay relative to the shallow and deep fore reefs (SFR and DFR) of Romero ($F = 7.64$, $p < 0.0005$; Fig. 4). However, regarding the proportional abundance of juveniles, the Seag-Corr stratum was significantly different ($p < 0.05$) from the other strata (50 %) in Corral and from those of Turrumote ($p < 0.05$).

In terms of mean density (N per 100 m²) of juveniles, there were significant differences among strata ($F = 13.15$, $p < 0.0005$; Fig. 5) and biotope ($F = 14.42$, $p < 0.0005$; Fig. 6). At the level of strata, densities in SBRs, SFRs, and DFRs of Romero and Corral, and Mang-Out and Seag-In of Montalva Bay were higher than those in the remaining strata. The lowest density was found in DFR of Turrumote. However, at the level of biotope,

Table 1. Maturation sizes, percentage of juveniles (% juv.), total density (per 100 m²), and relative species abundance (%) of the 20 selected fish species. Maturation data taken from Nagelkerken et al. (2000), García-Cagide et al. (2001), and FishBase (Froese & Pauly 2003). N: nursery species; R: reef species (after Nagelkerken et al. 2000; see text for definition); FL: fork length

Species	Code	Group	Maturation size (FL, cm)	% juv.	Density	%
<i>Haemulon flavolineatum</i>	Hfla	N	10	86	138.4	14.4
<i>Haemulon plumieri</i>	Hplu	N	10	82	87.1	9.1
<i>Haemulon parrai</i>	Hpar	N	10	18	7.1	0.7
<i>Haemulon sciurus</i>	Hsci	N	15	78	43.4	4.5
<i>Gerres cinereus</i>	Gcin	N	15	80	7.1	0.7
<i>Ocyurus chrysurus</i>	Ochr	N	15	91	14.0	1.5
<i>Lutjanus apodus</i>	Lapo	N	20	96	49.4	5.2
<i>Lutjanus griseus</i>	Lgri	N	15	95	9.2	1.0
<i>Lutjanus mahogoni</i>	Lmah	N	10	30	2.8	0.3
<i>Acanthurus bahianus</i>	Abah	R	10	46	46.4	4.8
<i>Acanthurus coeruleus</i>	Acoe	R	10	57	93.9	9.8
<i>Acanthurus chirurgus</i>	Achi	N	15	94	76.7	8.0
<i>Sphyaena barracuda</i>	Sbar	N	40	96	9.3	1.0
<i>Sparisoma aurofrenatum</i>	Saur	R	15	90	63.8	6.7
<i>Sparisoma chrysopterum</i>	Schry	N	15	91	21.1	2.2
<i>Sparisoma rubripinne</i>	Srub	R	15	79	5.5	0.6
<i>Sparisoma viride</i>	Svir	R	15	87	98.5	10.3
<i>Scarus taeniopterus</i>	Stae	R	15	95	96.3	10.0
<i>Chaetodon capistratus</i>	Chcap	N	5	27	49.0	5.1
<i>Abudefduf saxatilis</i>	Asax	R	10	98	39.8	4.1
Total				80	59.9	

Table 2. Total density (per 100 m²), percent of juveniles, species richness (S), and relative fish abundance (%) for the 16 strata along the inshore–offshore gradient. Mang: Mangrove; Seag: Seagrass; SBR: Shallow back reef; SFR: Shallow fore reef; DFR: Deep fore reef; MB: Montalva Bay; Rom: Romero Key; Corr: Corral Key; Turr: Turrumote Key

Stratum	Density	% juv.	S	%
Mang-In-MB	47.6	94	17	4.97
Mang-Out-MB	78.9	87	19	8.23
Seag-In-MB	60.4	97	11	6.30
Seag-Out-MB	31.4	98	15	3.28
Seag-Rom	28.5	96	13	2.97
SBR-Rom	77.2	86	19	8.05
SFR-Rom	109.5	77	15	11.43
DFR-Rom	86.1	60	19	8.98
Seag-Corr	28.7	100	10	2.99
SBR-Corr	86.9	89	18	9.06
SFR-Corr	82.3	78	15	8.59
DFR-Corr	55.4	67	16	5.78
DBR-Turr	68.4	59	16	7.13
SBR-Turr	34.4	75	16	3.59
SFR-Turr	54.5	78	13	5.68
DFR-Turr	28.5	66	14	2.98
Total	59.9	80	20	

densities in SFRs and SBRs from all locations were higher than those in mangroves, seagrass beds, and DFRs, while mangroves had higher densities compared with those in seagrass beds and DFRs.

Haemulon flavolineatum (14.4%) showed the greatest relative abundance (for both juveniles and adults), followed by *Sparisoma viride* (10.2%), *Scarus taeniopterus* (10%), *Acanthurus coeruleus* (9.7%), and *H. plumieri* (9%; Table 1). Since the proportional abundance of juveniles per species was greater than 70% in the majority of strata, with the exception of *H. parrai* (18%), *Lutjanus mahogoni* (30%), *A. bahianus* (46%), *A. coeruleus* (57%), and *Chaetodon capistratus* (27%; Fig. 3), the mean density of juveniles per stratum was compared to determine variations among strata rather than comparing the proportional abundance of juveniles for each species per stratum along the inshore–offshore gradient.

Among Haemulidae, the mean density of *Haemulon flavolineatum* juveniles was significantly higher in mangroves and seagrass relative to coral reefs ($F = 7.83$, $p < 0.0005$) while at the level of stratum, the density was significantly higher in Mang-Out and Seag-In of Montalva Bay and SBR-Rom compared to SBR-Corr and DFR-Turr ($F = 3.26$, $p < 0.001$). The mean densities

of juveniles of *H. plumieri* ($F = 9.32$, $p < 0.0005$) and *H. sciurus* ($F = 11.43$, $p < 0.0005$) were significantly higher in seagrass relative to mangroves and coral reefs. Seagrass and mangroves were the most important biotopes for *H. plumieri* and *H. sciurus*, respectively (Table 3).

Among Lutjanidae, the mean density of *Lutjanus apodus* juveniles was significantly higher in mangroves relative to seagrass and coral reefs ($F = 6.17$, $p < 0.001$). Density in Mang-Out in Montalva Bay was significantly higher than that in the remaining strata ($F = 6.79$, $p < 0.0005$). Mangroves represented the most important biotope (see Table 3) for *L. apodus*. However, the mean density of juveniles of *Ocyurus chrysurus* was significantly higher in Turrumote (seagrass and DBR) relative to that in other coral reef strata ($F = 8.25$, $p < 0.0005$; Table 3). *Lutjanus griseus* was found almost exclusively in mangroves and seagrass but its density was very low and not significantly different (Table 3).

Among Acanthuridae, the mean density of *Acanthurus chirurgus* juveniles was significantly higher in all SBR strata relative to SFRs and DFRs ($F = 31.48$, $p < 0.0005$), being significantly

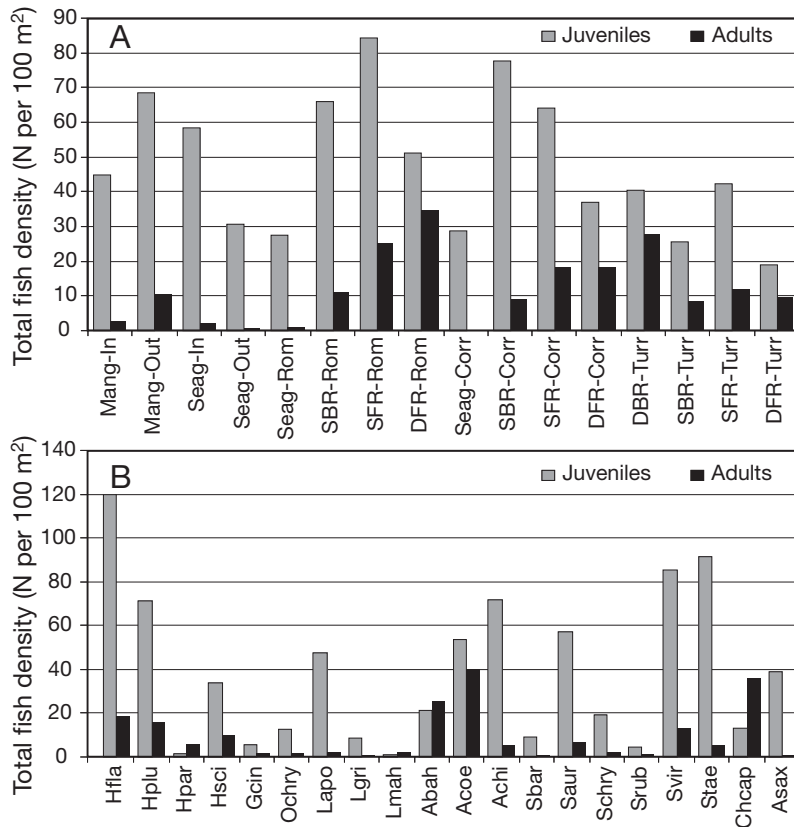


Fig. 3. Total density (N per 100 m²) of juveniles and adults per stratum (A) along the inshore–offshore gradient, and (B) for juveniles and adults of the 20 selected species. N: number of individuals. See Table 1 for species codes, and Table 2 for stratum abbreviations

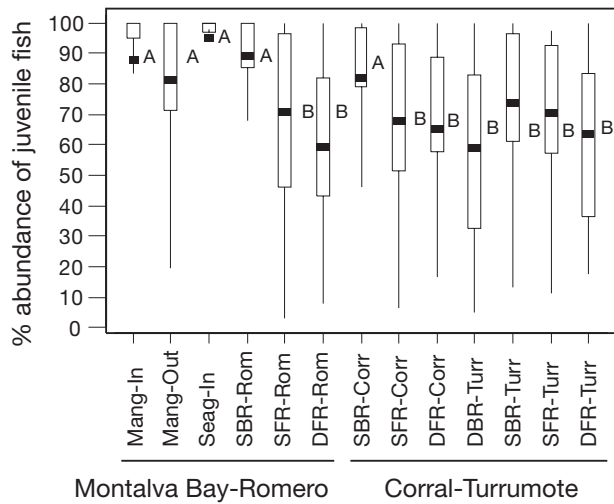


Fig. 4. Percent abundance of juveniles among strata along the inshore–offshore gradient. Groups with the same letter are not significantly different from each other as determined by Tukey-Kramer HSD tests ($p > 0.05$). Data were arcsine-transformed for analysis; however, proportionality is shown in the graph. Data from Seag-Out-MB, Seag-Rom, and Seag-Corr were not included because proportional abundance of juveniles = 100% for these strata. See Table 2 for stratum abbreviations. Whiskers: upper and lower limits; box: 95% CI; ■: mean

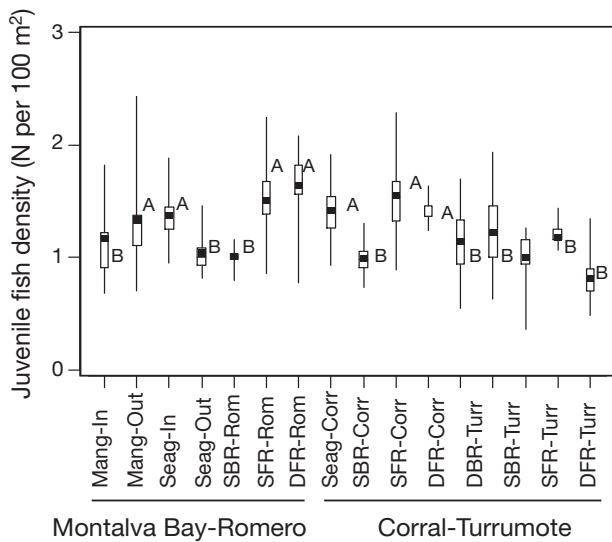


Fig. 5. Mean fish density of juveniles per stratum in the inshore–offshore gradient. Groups with the same letter are not significantly different from each other as determined by Tukey-Kramer HSD tests ($p > 0.05$). Data were square root-transformed for analysis. See Table 2 for stratum abbreviations. Whiskers: upper and lower limits; box: 95% CI; ■: mean

higher in the SFR of Romero and DFR of Corral relative to mangroves and seagrass, and coral reefs of Turumote ($F = 12.76$, $p < 0.0005$; Table 3). *A. coeruleus* showed a higher density in all SFRs relative to SBRs and DFRs ($F = 11.82$, $p < 0.0005$), while showing a

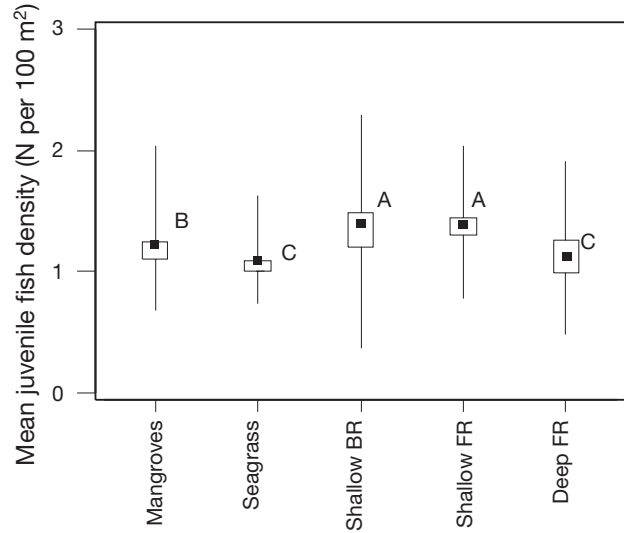


Fig. 6. Mean density of juveniles per biotope along the inshore–offshore gradient. Groups with the same letter are not significantly different from each other as determined by Tukey-Kramer HSD test ($p > 0.05$). Data were square root-transformed for analysis. BR: back reef; FR: fore reef. Whiskers: upper and lower limits; box: 95% CI; ■: mean

higher density in the SFR of Turumote relative to the other coral reefs of Corral and Romero ($F = 5.24$, $p < 0.0005$; Table 3). *A. coeruleus* and *A. bahianus* were almost absent from mangroves and seagrass; however, the latter species showed no significant differences in mean density among strata and biotopes ($F = 1.3$, $p < 0.0005$).

Among Scaridae, the mean density of *Sparisoma aurofrenatum* juveniles was significantly higher in all SFRs relative to the remaining strata ($F = 12.96$, $p < 0.0005$), showing a significantly higher density in SBR and SFR of Romero and DBR of Turumote relative to the strata of Corral and Turumote ($F = 12.37$, $p < 0.0005$; Table 3), but being completely absent from mangroves and seagrass. Densities of *Scarus taeniopterus* were not significantly different at the level of biotopes but were higher at Romero (SBR, SFR and DFR) relative to other strata ($F = 6.36$, $p < 0.0005$; Table 3). *Sparisoma viride* showed a significantly higher density in SBRs ($F = 2.60$, $p < 0.053$; Table 3) compared to the other coral reef strata, but was absent from mangroves and seagrass, and exhibited a significantly higher density in all strata of Romero and in SBR-Corr relative to the other coral reef strata ($F = 9.02$, $p < 0.0005$; Table 3). The mean density of *Sparisoma chrysopterus* was significantly higher at all SFRs relative to SBRs ($F = 18.34$, $p < 0.0005$), and significantly higher in SBR-Rom relative to other strata ($F = 10.45$, $p < 0.0005$; Table 3). It was absent from mangroves and seagrass.

Table 3. Frequency of juvenile and adult fishes found on different strata along the inshore–offshore gradient in SW Puerto Rico. Shaded areas: relative abundance > 20%; +: relative abundance = 10–20%. FL: fork length; stratum abbreviations as in Table 2

Species	Maturation size (FL, cm)	Mang-In-MB	Mang-Out-MB	Seag-In-MB	Seag-Out-MB	Seag-Rom	SBR-Rom	SFR-Rom	DFR-Rom	Seag-Corr	SBR-Corr	SFR-Corr	DFR-Corr	DBR-Turr	SBR-Turr	SFR-Turr	DFR-Turr
<i>Haemulon flavolineatum</i>	10																
Juvenile		+	+														
Adult			+			+		+			+		+				
<i>Haemulon plumieri</i>	10																
Juvenile				+	+					+	+						
Adult								+				+	+				
<i>Haemulon parrai</i>	10																
Juvenile		+	+					+	+								
Adult		+						+	+		+						
<i>Haemulon sciurus</i>	15																
Juvenile		+	+	+													
Adult		+										+					
<i>Gerres cinereus</i>	15																
Juvenile		+	+	+		+		+				+					
Adult							+	+				+	+				
<i>Ocyurus chrysurus</i>	15																
Juvenile				+					+								
Adult								+					+				
<i>Lutjanus apodus</i>	20																
Juvenile		+	+														
Adult		+							+								
<i>Lutjanus griseus</i>	15																
Juvenile		+	+	+													
Adult		+	+														
<i>Lutjanus mahogoni</i>	10																
Juvenile			+														
Adult			+					+									
<i>Acanthurus bahianus</i>	10																
Juvenile							+	+				+			+	+	
Adult								+	+			+		+		+	+
<i>Acanthurus coeruleus</i>	10																
Juvenile								+	+	+	+	+					+
Adult								+	+			+		+			+
<i>Acanthurus chirurgus</i>	15																
Juvenile								+			+	+					+
Adult							+						+				
<i>Sphyaena barracuda</i>	40																
Juvenile		+	+														
Adult			+														
<i>Sparisoma aurofrenatum</i>	15																
Juvenile								+	+			+					
Adult									+					+	+	+	+
<i>Sparisoma chrysopterus</i>	15																
Juvenile								+				+				+	+
Adult								+				+			+	+	+
<i>Sparisoma rubripinne</i>	15																
Juvenile							+		+			+			+		
Adult									+			+					
<i>Sparisoma viride</i>	15																
Juvenile						+	+	+		+	+						
Adult								+	+			+	+				
<i>Scarus taeniopterus</i>	15																
Juvenile			+					+				+		+			
Adult								+	+			+		+			
<i>Chaetodon capistratus</i>	5																
Juvenile				+							+						
Adult								+			+	+		+			
<i>Abudefduf saxatilis</i>	10																
Juvenile								+	+			+					
Adult											+						

Among the remaining families (Chaetodontidae, Pomacentridae and Sphyraenidae), the mean density of *Chaetodon capistratus* juveniles showed a significantly higher density in coral reefs relative to seagrass and mangroves ($F = 15.23$, $p < 0.0005$), and showed a significantly higher density in SBR-Corr and Seag-Out of Montalva Bay relative to the remaining strata ($F = 8.40$, $p < 0.0005$; Table 3). *Abudefduf saxatilis* showed a high density in coral reefs relative to mangroves ($F = 31.47$, $p < 0.0005$; Table 3), and was significantly higher at Romero (SFR and DFR) and SFR-Corr relative to the remaining strata ($F = 27.03$, $p < 0.0005$), but it was absent from seagrass. *Sphyraena barracuda* and *Lutjanus griseus* exhibited a restricted distribution to mangroves and seagrass only, but their juvenile mean densities were not significantly different either among strata or biotope. The remaining fish species, *Lutjanus mahogoni* (Lutjanidae), *Gerres cinereus* (Gerreidae), *Haemulon parrai* (Haemulidae), and *Sparisoma rubripinne* (Scaridae) were not statistically compared because of their low density per stratum.

DISCUSSION

Juvenile reef fish densities along the mangrove–seagrass–coral reef continuum in SW Puerto Rico showed differences depending on habitat and fish species. Of the 20 species selected, at least 13 corresponded to ‘nursery species’ recognized by Nagelkerken et al. (2000), whereas 7 were ‘reef residents.’ In Curaçao, Nagelkerken et al. (2000) determined that seagrass was the most important nursery for *Haemulon flavolineatum*, *H. sciurus*, *Ocyurus chrysurus*, *Acanthus chirurgus*, and *Sparisoma viridae*; mangroves for *Lutjanus apodus*, *L. griseus*, *Sphyraena barracuda*, and *Chaetodon capistratus*; and shallow-water coral reefs for *H. chrysargyreum*, *L. mahogoni*, *A. bahianus*, and *Abudefduf saxatilis*. However, in SW Puerto Rico, while relatively abundant in mangroves and seagrass, *H. flavolineatum*, *L. apodus*, *O. chrysurus*, *H. sciurus*, and *H. plumieri* occurred mainly in shallow coral reefs.

The importance of mangroves and seagrass as nursery habitats is known (Parrish 1989, Beck et al. 2001, Adams et al. 2006, Dahlgren et al. 2006, Faunce & Serafy 2006). Higher densities of juveniles in mangroves and seagrass are attributed to food availability, structural complexity, shade, and reduced predation (Beck et al. 2001, Adams et al. 2006, Dahlgren et al. 2006). Chittaro et al. (2005) argued that based on density, assemblage composition and relative rates of predation, not all mangrove and seagrass beds appear to function as nurseries. Dorenbosch et al. (2004) found that some fish species use the shallow coral reefs as an

alternative nursery and do not depend strictly on the presence of bays with seagrass beds and mangroves as nurseries. In contrast, Mumby et al. (2004) showed that mangroves are indeed important, serving as intermediate nursery habitat that may increase the survivorship of juvenile fishes (e.g. *Scarus guacamaia*), strongly influencing the community structure of fishes in adjacent coral reefs of the Caribbean.

In SW Puerto Rico, we found that reef fishes within the inshore–offshore gradient along a mangrove–seagrass–coral reef continuum showed a species-specific preference for given habitats, and that the importance of mangroves and seagrass in terms of harboring high densities of juveniles of the selected 20 species was relative; for the majority of cases, shallow coral reefs (i.e. SBRs and SFRs, 0 to 3 m depth) were even more important than mangroves and seagrass. While juvenile fish showed preferences for certain habitats, the function of nursery for the habitats investigated was not evaluated. We only assume that such habitats may have a nursery function because of the high densities in juveniles, but we did not compare the relative importance to other habitats outside the inshore–offshore gradient investigated. The term ‘nursery area’ as a surrogate for mangroves or seagrass habitats should be used with discretion, since these biotopes also harbor an adult community (Sheaves 2001, 2005).

Many studies have shown that fishes accomplish ontogenetic migrations (Appeldoorn et al. 1997, Dahlgren & Eggleston 2000, Lindeman et al. 2000, Nagelkerken et al. 2000). The extent that this occurs in SW Puerto Rico, and the impact it may have on understanding the complexities of habitat use, has not been fully investigated. In this study, we inferred that juvenile densities along the continuum showed a progressive displacement from mangroves to shallow coral reefs. Inferences of fish ontogenetic migrations were not only evident from mangroves to coral reefs, using seagrass as intermediate habitat, but also from shallow-water coral reefs (i.e. SBRs and SFRs, 0 to 3 m depth) to deeper reefs (3 to 10 m depth).

In terms of management and conservation, recognizing the mosaic of structural habitat heterogeneity, represented by the mangrove–seagrass–coral reef continuum, is a fundamental aspect for promoting potential inter-linkage of reef fishes. While it is difficult to demonstrate direct evidence of inter-linkage through a life-cycle of fish migration between habitats, studies using either otolith microchemistry or tagging confirm such migrations in temperate areas (Gillanders 2002). In Puerto Rico, such an approach is still needed; however, for now it could be sufficient to include within the proposed marine protected area the mosaic of habitats along the continuum Montalva Bay–Turrumote to pro-

tect not only the adult and juvenile habitats but also the whole 'corridor' of potential post-settlement fishes.

Nowadays, there is a trend to incorporate an ecosystem-based approach into traditional fisheries management for a sustainable use of the marine environment (Browman et al. 2004). Such innovation stems from recognizing the ecological components for better management. Any conservation or management action taken to protect fish assemblages must include not only certain coral reef areas, but also their associated inshore habitats, such as mangroves and seagrass (Adams et al. 2006, Dahlgren et al. 2006).

In conclusion, the present study showed the relative importance of mangroves, seagrass, and shallow coral reef as juvenile fish habitats based on densities, and their associated contribution as ontogenetic platforms for displacement of fishes, and also showed that the apparent preference of fishes for given habitats is species-specific.

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