Preference of early juveniles of a coral reef fish for distinct lagoonal microhabitats is not related to common measures of structural complexity

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ABSTRACT: Coral reef populations of a variety of fish and invertebrate species are replenished by individuals that use inshore coastal habitats as temporary juvenile habitats. These habitats vary greatly in their architecture, and different characteristics of structure could play a role in their selection and utilization by resident fauna. To solely investigate the role of structural complexity in micro-habitat selection, *in situ* habitat preference of 48 individuals of the early juvenile stage of a common reef fish (*Haemulon flavolineatum*) was studied for 4 structurally very different lagoonal microhabitats (i.e. mangrove, seagrass, rubble, coral), using a multiple-choice experiment in field enclosures. This fish species was selected as it utilizes these habitats during different parts of its life cycle. The structural complexity of each microhabitat was changed in each replicate experiment and assessed on the basis of 7 commonly used measures of structure using digitized photographs. We tested the hypothesis that in isolation of other factors, fish prefer the structurally most complex microhabitat that is available, independent of habitat type. However, fish always preferred seagrass and coral micro-habitats even when offered at low complexity, and this choice was rather consistent over a 24 h time period. Structural characteristics appeared to be marginally important for the seagrass microhabitat only. Therefore, the differential preference for distinct lagoonal microhabitats does not appear to be driven by measures of structural complexity that are known to be important at the level of individual habitat types. In this light, continuing loss of coral and seagrass habitats in lagoonal environments due to anthropogenic effects is alarming as it affects preferential habitat of certain stages of the life cycle of fishes.

KEY WORDS: Habitat selection · Structure · *Haemulon flavolineatum* · Mangrove · Seagrass · Coral rubble · Choice experiment

INTRODUCTION

Ecosystems are intricately linked by the flow of organisms across their boundaries. Many coral reef-associated species have pelagic larvae which settle selectively in spatially segregated juvenile habitats, such as inshore mangroves and seagrass beds (Pollux et al. 2007, Haywood & Kenyon 2009), before replenishing adult populations on coral reefs (Verweij et al. 2008, Nagelkerken 2009). Yet, there is little information about the underlying mechanisms causing such

habitat shifts (Grol et al. 2011) and the role that various habitat attributes may play in this.

Higher food abundance and reduced predation risk are mechanisms which are thought to drive habitat shifts (Werner & Gilliam 1984, Dahlgren & Eggleston 2000, Haywood & Kenyon 2009). Habitat complexity positively affects both of these mechanisms. Therefore, structure-rich habitats (e.g. mangroves, seagrass beds, macroalgae) are preferred as settlement and juvenile habitats by many fish and invertebrate species, and are often associated with higher densities and species rich-

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ness compared to less structured or unvegetated habitats (Orth et al. 1984, Jenkins & Wheatley 1998). Vegetated habitats harbor higher abundances of certain food items which can enhance growth rates of juveniles compared to unvegetated habitats (Orth et al. 1984, Laegdsgaard & Johnson 2001, Cocheret de la Morinière et al. 2004). In addition, species may have evolved a preference for shelter-rich habitats driven by predation risk. Such habitats provide prey with more shelter holes, which reduces predation (Hixon & Beets 1993, Beukers & Jones 1997) and competition (Almany 2004, Schmitt et al. 2009) among species, both leading to enhanced survival.

Inshore coastal habitats vary greatly in their architecture, and different characteristics of structure may play a role in their selection and utilization by fish. In mangroves, for example, positive correlations have been found between fish abundance and pneumatophore and root density (Cocheret de la Morinière et al. 2004, Payne & Gillanders 2009) or epibiont complexity on mangrove roots (MacDonald et al. 2008). In seagrass beds, fish abundance is influenced by seagrass cover, height, and density (Orth et al. 1984, Bell & Westoby 1986, Gullström et al. 2008). On coral reefs, numbers of shelter holes, rugosity, and percent live coral have been identified as important aspects of complexity determining fish distribution (Luckhurst & Luckhurst 1978, Jones & Syms 1998, Gratwicke & Speight 2005a,b).

Abiotic factors may also affect habitat selection by fishes and invertebrates, e.g. shade, water clarity, depth, temperature, or salinity (Blaber & Blaber 1980, Verweij et al. 2006b, Rypel et al. 2007, Gullström et al. 2008). Mangroves, for example, may be selected by juvenile fish not only for their dense prop-root system that provides shelter and reduces predator maneuvers, but also because the shade makes prey more difficult to detect by predators and thus reduces predation risk (Helfman 1981, Cocheret de la Morinière et al. 2004).

Reef fishes that settle and temporarily reside in shallow inshore or lagoonal areas as juveniles have a choice of a suite of very dissimilar microhabitats in terms of structural architecture (e.g. shelter holes in corals, shade in mangroves, flexible structure of seagrass leaves). Despite this, many studies have focused on single habitats, taking only 1 or a few characteristics of complexity into account, and have investigated total fish abundance and species richness irrespective of species- and size-specific habitat preferences. This leaves us with little understanding of how structure contributes to selection and utilization of habitats by fish in a complex seascape, such as often found in shallow back-reef, lagoonal, or estuarine areas. In single habitat studies, Heck et al. (2003) found that the presence of structure *per se* appeared to be a more impor-

tant determinant of the nursery value of a habitat than the type of structure for a variety of fish and invertebrate species, and similarly, Nagelkerken & Faunce (2007) suggested that the use of mangrove structure is not related to a predetermined preference by certain species but more likely to the presence of structure. Additionally, Jenkins & Wheatley (1998) concluded that while the presence of structure *per se* is sufficient for the recruitment of many species, some taxa will discriminate amongst habitats based on structural characteristics.

In this study, the role of solely habitat complexity in microhabitat preference by early juvenile fish was tested experimentally in enclosures, in isolation from other abiotic and biotic variables (e.g. predation, competition, turbidity, salinity). *In situ* habitat preference was quantified in a multiple-choice experiment for 48 individual early juveniles of the common Caribbean coral reef fish species French grunt *Haemulon flavolineatum* for 4 structurally very different microhabitats (i.e. mangrove, seagrass, rubble, coral). Through ontogeny, juvenile *H. flavolineatum* are found in shallow-water coastal habitats such as lagoonal patch reefs, mangroves, seagrass beds, whereas adults mainly reside on coral reefs (Nagelkerken 2007, Grol et al. 2011). Digitized photographs of each microhabitat from each enclosure were used to measure various commonly studied structural complexity variables. Because for single habitat types it has been shown that the preference for structure is typically driven by its degree of complexity, we hypothesized that for multiple microhabitats of very different architecture fish would also prefer the structurally most complex microhabitat available rather than a specific microhabitat type *per se*.

MATERIALS AND METHODS

Study area and studied species. This study was carried out at 2 Caribbean islands: Curaçao and Aruba. Field experiments were conducted in front of Piscadera Bay on Curaçao (12° 07′ N, 68° 51′ W) and in a lagoon near Mangel Halto on Aruba (12° 27′ N, 69° 58′ W) on a sandy bottom (~2 to 4 m depth) away from other habitat types such as mangroves, seagrass beds, or coral reefs (Curaçao: >80 m, and Aruba: >300 m away).

Larvae of the model species *Haemulon flavolineatum* recruit from the plankton into shallow-water coastal habitats such as lagoonal patch reefs, mangroves, and seagrass beds (Shulman 1985, Nagelkerken et al. 2000, Pollux et al. 2007) at a size of 7.9 to 11.5 mm fork length (FL) (Gaut & Munro 1983, Lindeman & Richards 2005). At the onset of maturity, fish

migrate to coral reefs to join adult populations (Gaut & Munro 1983, Grol et al. 2011). Until approximately 4 to 5 cm FL they are diurnal planktivores and mainly feed on Copepoda (Ogden & Ehrlich 1977, Verweij et al. 2006a, Grol et al. 2008). Through ontogeny, they shift to a nocturnal zoobenthivoric feeding pattern (Randall 1967, Ogden & Ehrlich 1977, Cocheret de la Morinière et al. 2003). Fish for the experiments (mean ± SD; Curaçao: 3.7 ± 0.2 cm FL, 0.8 ± 0.3 g total weight; and Aruba: 3.9 ± 0.3 cm, 1.0 ± 0.2 g) were collected in 2 different habitat types: on seagrass beds at Barcadera (12° 28′ N, 69° 59′ W) and a sandy/rubble zone near the lagoon entrance at Mangel Halto on Aruba, and on seagrass beds and rubble located in the channel area of Spanish Water Bay on Curaçao (12° 04′ N, 68° 51′ W; see Grol et al. 2008 for details on the locations).

Experimental design. Microhabitat preference by diurnally active early juvenile *Haemulon flavolineatum* was studied *in situ* during January and February 2009 on Aruba and Curaçao using experimental cages. Experiments with an identical set-up were carried out at the 2 islands to investigate whether habitat preference of early juvenile *H. flavolineatum* was location dependent or a general pattern for at least these 2 Caribbean islands. Cages excluded predators as well as competitors, but allowed inflow of planktonic food items. Fish could therefore feed while associating with their preferred habitat, but due to the small size of the cages this did not lead to differences in water inflow among microhabitats. The cage placement on a large shallow sandy area near the coast reduced the influence of factors such as strong ocean currents, nearby presence of other complex benthic habitat or aquatic vegetation, nearby presence of schools of other fish, and strong auditory or olfactory cues created by nearby fish or habitats. As a result, fish were forced to make a choice related to microhabitat structural complexity variables, and choice was neither predator, nor food, nor environmentally induced.

The framework of the square experimental cages (1.5 × 1.5 × 0.7 m) was constructed using iron rods (∅ 8 mm) covered with galvanized wire (mesh size 6 mm), except for the bottom part which rested on the sandy bottom (Fig. 1). In total, 6 cages per island were placed at least 25 m apart from each other. Each cage was placed with 1 of its sides perpendicular to the direction of the waves and water current. In each of the 4 corners of a cage, a different microhabitat was created in an area of roughly 50 × 50 cm using pieces collected freshly in the field: pieces of live coral (predominantly *Diploria strigosa*, *Millepora complanata*, *Porites astreoides*, *P. porites*, and *Siderastrea siderea*; on Aruba a few microhabitats included branches of soft corals belonging to the family Plexauridae), coral rubble (mainly dead fragments of branching corals such as
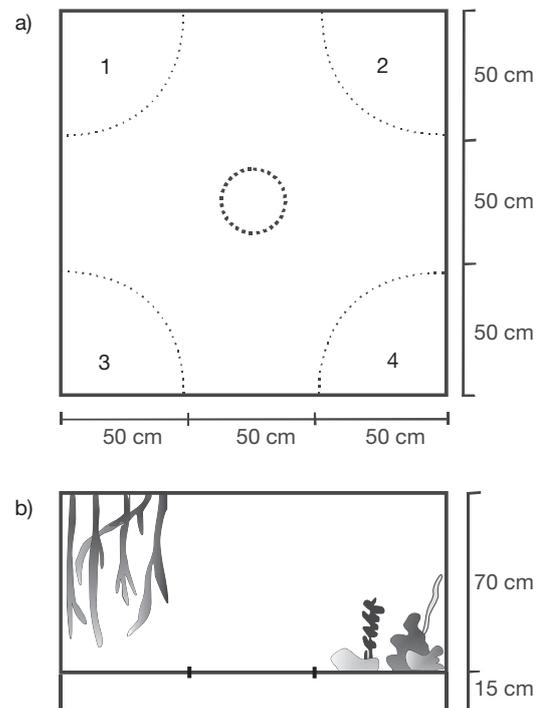

Fig. 1. Experimental cage placed on sand (an unvegetated and unstructured substratum). View from (a) the top and (b) the side. Per island, 6 cages were placed perpendicular to the current and wave direction. Different microhabitats (seagrass, coral, rubble, and mangrove) with variable numbers of structures were randomly distributed at the 4 corners (1–4) of each cage. Dashed circle: location where *Haemulon flavolineatum* were released in a transparent wire mesh cylinder on the sand before the experiment started

Acropora cervicornis and *Madracis mirabilis*), mangrove prop roots (*Rhizophora mangle*), and seagrass plants (*Thalassia testudinum*). Rubble consisted of broken pieces of dead hard coral of irregular size and shape, and was often colonized by macroalgae. In contrast, corals were erect and complex structures which had a wide variety of growth forms. All microhabitats were placed on the sandy substratum, except mangrove roots. To mimic a hanging mangrove prop-root habitat, the roots were attached to the top of the cage, and the top of this corner was covered with a cloth to create shade. All substratum that was not covered by microhabitats consisted of bare sand and is referred to as 'sandy microhabitat.' For each multiple-choice experiment, the number of structures of each of the 4 microhabitats (viz. the number of coral pieces, rubble pieces, mangrove roots, and seagrass shoots) was changed (Table 1), as was the mutual configuration of the 4 microhabitats in the corners within a cage. The latter was to reduce bias in choice behavior due to e.g. wave motion, currents, or the angle of sunlight. In addition, changing the mutual placement of the micro-

Table 1. *Haemulon flavolineatum.* Experimental design used to investigate microhabitat preference of early juveniles on Aruba and Curaçao. In total, 24 fish were tested on each island in 4 series of 6 cages each. The number of structures per microhabitat (SG: no. of seagrass shoots, CR: no. of coral pieces, RB: no. of rubble pieces, and MG: no. of mangrove roots) varied per cage and between series 1–2 and 3–4. Catch location (SG: seagrass, RB: rubble), fork length (FL), and wet weight (WW) are provided for each fish

Series	Cage	Number of structures				Catch location	FL (cm)	WW (g)
		SG	CR	RB	MG			
Aruba								
1	1	47	12	47	10	RB	4.0	1.1
	2	16	13	43	5	SG	3.4	0.7
	3	41	5	25	2	RB	3.7	0.9
	4	37	11	37	11	SG	3.8	1.1
	5	53	14	41	3	RB	3.8	0.7
	6	47	7	23	13	SG	3.9	1.0
2	1	47	12	47	10	SG	3.8	0.9
	2	16	13	43	5	RB	4.2	1.1
	3	41	5	25	2	SG	3.8	0.9
	4	37	11	37	11	RB	4.0	1.2
	5	53	14	41	3	SG	4.0	1.1
	6	47	7	23	13	RB	4.0	1.1
3	1	29	15	27	7	RB	4.0	1.0
	2	42	6	31	12	SG	3.2	0.5
	3	59	9	45	8	RB	4.3	1.3
	4	20	10	35	6	SG	3.7	0.9
	5	11	16	21	4	SG	3.3	0.5
	6	31	8	33	9	RB	4.1	1.2
4	1	29	15	27	7	SG	3.7	0.9
	2	42	6	31	12	RB	3.9	0.8
	3	59	9	45	8	SG	3.8	0.8
	4	20	10	35	6	RB	4.1	1.3
	5	11	16	21	4	RB	4.0	1.0
	6	31	8	33	9	SG	3.9	1.0
Curaçao								
1	1	31	10	47	10	SG	3.6	0.4
	2	51	5	33	12	RB	3.2	0.3
	3	12	15	23	5	RB	3.6	0.5
	4	41	9	25	9	SG	3.9	1.1
	5	25	6	37	3	RB	3.6	0.6
	6	20	12	31	2	SG	3.5	0.5
2	1	31	10	47	10	RB	3.8	1.2
	2	51	5	33	12	SG	3.6	0.7
	3	12	15	23	5	SG	3.7	0.7
	4	41	9	25	9	RB	3.7	0.6
	5	25	6	37	3	SG	3.6	0.8
	6	20	12	31	2	RB	3.8	1.0
3	1	41	14	23	7	SG	3.7	0.8
	2	39	16	43	11	RB	3.9	1.0
	3	48	7	27	8	SG	3.6	0.7
	4	51	8	35	13	RB	3.6	0.9
	5	25	11	21	4	RB	3.9	1.2
	6	31	9	41	6	SG	3.6	0.8
4	1	41	14	23	7	RB	3.9	1.3
	2	39	16	43	11	SG	3.6	0.8
	3	48	7	27	8	RB	3.8	1.2
	4	51	8	35	13	SG	3.7	0.9
	5	25	11	21	4	SG	4.0	1.2
	6	31	9	41	6	RB	3.8	1.1

habitats avoided habitat choice being influenced by non-random search behavior of the fish in a cage, i.e. fish are more likely to move to another microhabitat along the edges of a cage than to swim across the sand to the opposite microhabitat. The iron gauze of the cages was scrubbed on the outside after each experiment to remove algal growth and to preserve a good flow of water through the cages.

Early juvenile *Haemulon flavolineatum* were caught using nets and fish traps in seagrass and rubble habitats. On Curaçao, the collected fish were directly transported over land from Spanish Water Bay to the laboratory and were housed in 2 separate aquaria with flowing seawater. On Aruba, collected fish were directly transported to the experimental site near Mangel Halto and temporarily held in 2 small cages (40 × 40 × 50 cm) made of wire (mesh size 6 mm) and placed on the sand bottom, as no aquaria with flowing seawater were available. Fish collected from seagrass and rubble habitats were kept separately and acclimatized for at least 24 h in the holding tanks before experiments started. Every other day, new fish were collected from the field. Per island, 6 cages were used simultaneously. A replicate experiment consisted of a single fish that was tested during 4 time periods over 2 d within the same cage and released afterwards. Microhabitat preference was tested for a total of 24 fish on Curaçao and 24 on Aruba (i.e. 4 series of 6 replicates each; Table 1). We specifically tested single individuals of this generally gregarious fish species (Verweij et al. 2006a), as decision-making in fish schools is significantly affected by the behavior of bolder individuals (Magnhagen & Bunnefeld 2009). If preference for a specific microhabitat is a species-specific trait, then we would expect the majority or all of the individuals, bold as well as timid, to make similar choices.

Fish were transported from the holding tanks to the experimental cages within 5 min in a semi-closed dark box through which fresh seawater could

flow. Fish caught from seagrass or rubble habitats were selected randomly for each experiment (see catch location in Table 1). One fish was introduced into each cage using a wire mesh cylinder (∅ 25 cm, 1.2 m in length) that was stuck through a closable window (25 × 25 cm) in the center on top of the cage (Fig. 1a). To acclimatize to the environment in the cage and to provide the fish with the opportunity to see all 4 microhabitats before making a choice, fish were kept in the cylinder on the sandy substratum for 3 min. Thereafter, the cylinder was slowly removed and the experiment started. Each fish was observed for 15 consecutive minutes at a distance of at least 5 m using SCUBA on Curaçao and snorkeling equipment on Aruba. Every between-microhabitat movement within these 15 min was recorded by an observer, resulting in a time budget spent in each microhabitat.

Each experiment with the same fish lasted for almost 24 h. Repetitive observations were done from 14:30 to 15:30 h (t_1) and 17:00 to 18:00 h (t_2, just before sunset) on Day 1, and from 07:00 to 08:00 h (t_3, just after sunrise) and 09:30 to 10:30 h (t_4) on Day 2. Different time periods were chosen because this could affect microhabitat preference; small fish feed continuously on zooplankton during daytime and do not shift habitats to feed (Verweij et al. 2006a, Grol et al. 2008), while larger individuals (approximately >5 cm FL) feed on zoobenthos and migrate in shoals at dusk and dawn to and from their benthic feeding areas (Ogden & Ehrlich 1977, Helfman et al. 1982). After the fourth and last observation, fish were released from the cages, cages were scrubbed, rearranged, and the experiments were repeated with newly-caught fish.

Photo analyses. Each microhabitat in each cage for all replicate experiments was photographed at a distance of about 1.5 to 2.0 m to determine the degree of habitat complexity. Photos were taken in the horizontal (from above) and vertical (from the side) plane of each microhabitat, and reflected the approximate positions from which a fish could see the microhabitat. A measuring rod was placed in each microhabitat to scale the images. Photographs were printed and digitized, and using the measuring rod's scale, pixels in each photo were converted to dimensions (cm) of the structural complexity variables using the program Coral Point Count with Excel extensions (CPCe; Kohler & Gill 2006). Automatic processing of the photographs was not possible due to low contrast. Therefore, the outlines of each microhabitat in every photo from above and from the side were drawn manually using the image analysis software GIMP version 2.6 (GNU Image Manipulation Program), an open source image editing software package (www.gimp.org).

Per photo, 6 different structural complexity variables that are often used in structure-related studies were measured within the manually-drawn habitat outlines: (1) top and (2) side percent cover of the microhabitat, (3) microhabitat rugosity, (4) maximum and (5) mean height of the microhabitat above the substratum, and (6) number of shelter holes. Total number of structures (7) was not determined from the photos as these were pre-selected for the experiments (Table 1). For microhabitat cover, a self-written script using PHP (PHP hypertext pre-processor; www.php.net) was used to count the total number of pixels of covered versus uncovered microhabitat per photo, and the percent area covered was calculated for photos taken from above (top cover, where uncovered substratum consisted of sand) and from the side (side cover, where uncovered substratum consisted of the open water layer). For rugosity, the contour of the microhabitat was measured from photos taken from the side, and was calculated as the ratio of contour-following versus straight distance between 2 end points of the microhabitat in the photo (Risk 1972). Maximum and mean heights of the microhabitats were also calculated from the photos taken from the side: per 'pixel column' the difference between the highest and lowest elevation of the microhabitat was determined to calculate the maximum microhabitat height per column in pixels. Mean microhabitat height was calculated by averaging the heights of all pixel columns. Maximum and mean heights were converted from pixels to length in cm using CPCe. For number of shelter holes, the number of holes was counted from the photos that were taken from above the microhabitat.

Microhabitats differed greatly in complexity variables (Table 2). Seagrass was characterized by a high number of shelter holes and structures, coral by a high top and side cover, rubble by a high top and side cover and number of structures, and mangroves by a high rugosity and mean and maximum height.

Data and statistical analyses. For each fish, total time spent in each microhabitat was expressed as a percentage of each 15 min test period. First, temporal variation in microhabitat preference within cages was tested over the four 15 min observations per microhabitat per island using repeated-measures analysis of variance (ANOVA; GLM), followed by Bonferroni multiple comparisons using SPSS (version 16.0, Field 2005). A Mauchly's test was used to test for sphericity. When the assumption of sphericity was violated, the Greenhouse-Geisser correction was used. Since fish were very consistent in their choice and no significant differences in habitat choice were found over time, the four 15 min observations for each fish were averaged per microhabitat for further data analysis. Differences in mean microhabitat preference were then tested per island using repeated-measures ANOVA (GLM) for all fish pooled as well as for fish caught on seagrass beds

Table 2. Mean and range values (in parentheses) of the 7 complexity variables for each microhabitat, pooled for Aruba and Curaçao. P-values show results of Kruskal-Wallis tests, while different superscripts (a–d) within the same row indicate significant differences (p ≤ 0.050) in means among microhabitats (Games-Howell post hoc test)

Complexity variables	Seagrass		Coral		Rubble		Mangrove		p
Top cover (%)	51.6[a]	(27–71)	69.5[b]	(49–87)	66.8[b]	(56–81)	36.0[c]	(22–48)	<0.001
Side cover (%)	42.3[a]	(24–59)	58.8[b]	(47–72)	52.3[c]	(36–64)	33.1[d]	(16–54)	<0.001
Rugosity	6.6[a]	(3–15)	2.6[b]	(2–6)	2.1[c]	(2–3)	24.6[d]	(7–60)	<0.001
Mean height (cm)	18.4[a]	(10–27)	13.9[b]	(9–22)	12.1[c]	(8–17)	42.2[d]	(27–59)	<0.001
Maximum height (cm)	26.5[a]	(16–37)	19.6[b]	(13–38)	17.4[b]	(12–25)	57.2[c]	(37–70)	<0.001
Number of shelter holes	40.9[a]	(11–121)	8.5[b]	(4–17)	19.0[c]	(12–31)	11.0[b]	(1–28)	<0.001
Number of structures	35.3[a]	(11–59)	10.3[b]	(5–16)	33.1[a]	(21–47)	7.5[c]	(2–13)	<0.001

or rubble habitats, followed by Bonferroni multiple comparisons.

The 7 complexity variables of each microhabitat type were analyzed by multivariate principal component analysis (PCA) to reduce the number of variables per habitat type. Data were scaled before PCA analysis. For further analysis, the first 2 PCA axes were used for each microhabitat. These explained 66 to 74% of the total variation in habitat complexity as measured by all 7 variables. Next, the matrix (48 fish × 4 microhabitats) of average percent time spent by each fish in each habitat was transformed to a distance matrix comparing all the time budgets using Euclidean distance and analyzed by non-metric multi-dimensional scaling (nMDS). Per individual, the microhabitat in which most time (i.e. >50%) was spent was set as the ultimate habitat (only applicable to the multivariate ANOVA test), to test whether there was a significant difference among microhabitats and a significant effect of the factors catch location and island, using permutational MANOVA (Anderson 2001, McArdle & Anderson 2001). To test which aggregated complexity variables had an effect on the choice of the fish, a procedure was used that determines the projection of nMDS points on vectors that have a maximum correlation with corresponding values of the PCA axes, or in case of factors (island and fish catch location) the correlation with the average at each factor level (Legendre & Legendre 1998). The vectors point to the direction of most rapid change in the environmental variable. The length of the vector is proportional to the correlation between the ordination and environmental variable. The resulting correlations were tested using 9999 permutations. Fitted vectors are commonly used in displaying environmental variables in ordination such as, for example, constrained correspondence analysis. In unconstrained ordination like nMDS, the relation between external variables and ordination configuration may be less linear and methods other than fitting arrows may be more useful. We tried non-linear fitting (i.e. a surface using splines) as well, but results indicated that linear fitting

was sufficient. The method used here effectively uses the locations of the points from the 2-dimensional nMDS space to predict the PCA axis values. It is a least squares fit of the form PCA-axis ~ nMDS1 + nMDS2. The arrow heads are the normalized coefficients for nMDS axes, and hence represent the normalized change in response for a unit change in the nMDS axes. As these are normalized, the larger the coefficient is (change in response for unit change in the site scores) the stronger the relationship between the nMDS scores and the vector is. The multivariate analyses were done using R (version 2.10.1, R Development Core Team 2009) and the packages 'vegan' (Oksanen et al. 2010) and 'mgcv' (Wood 2006).

RESULTS

Microhabitat preference

Microhabitat preference of *Haemulon flavolineatum* was highly consistent over time (Fig. 2) and showed no significant differences among the 4 time periods (separate repeated-measures ANOVA per microhabitat: Aruba, p ≥ 0.290; Curaçao, p ≥ 0.218).

Averaged across the 4 time periods (Fig. 3), significant differences were only found for all fish pooled (GLM: Aruba, $F_{1.7, 38.4}$ = 6.8, p = 0.005; Curaçao, $F_{3, 69}$ = 3.9, p = 0.013) and for seagrass fish on Aruba (GLM: $F_{1.7, 18.6}$ = 3.2, p = 0.050). In general, fish showed the highest mean preference for seagrass, although significant differences in preference were only observed between seagrass and mangrove for all fish pooled (Bonferroni: Aruba, p = 0.002; Curaçao, p = 0.016), between seagrass and rubble for all fish on Aruba (Bonferroni: p = 0.034), and between seagrass and mangrove for seagrass fish on Aruba (Bonferroni: p = 0.024). Coral was the next most preferred microhabitat, especially on Aruba. Significant differences between coral and other microhabitats were only found between coral and mangrove on Aruba for all

fish pooled (Bonferroni: p = 0.004). Lack of other significant differences among microhabitats resulted from the relatively large variability within habitats. This was caused by individual fish choosing predominantly either seagrass or coral microhabitats instead of both seagrass and coral microhabitats; both scenarios would lead to a similar average preference for these 2 habitats. In such a case, averages give a false representation of individual choice. Therefore, microhabitat preference was further investigated on an individual level using nMDS.

The nMDS plot showed a clear grouping for the predominant preference of each of the tested individuals (Fig. 4). The ordination into the 4 microhabitat groups was highly significant (permutational MANOVA: $F_{3,43}$ = 58.9, p < 0.001). No significant correlation was found between the ordination and the island or habitat where fish were caught (r^2 = 0.024, p = 0.326, and r^2 = 0.004, p = 0.834, respectively). The preference for seagrass and coral is clear since most of the nMDS points are either in the top right or top left part of the plot. The farther the points are towards the left or right sides of the plot, the more the time spent in the preferred habitat approached 100%. Clearly, there were very few individuals that chose mangrove and rubble (only 2 and 5, respectively). Furthermore, individual preference for seagrass and coral microhabitat was rather persistent over time. Out of 48 fish, 27 (56%) were still found in their initial microhabitat
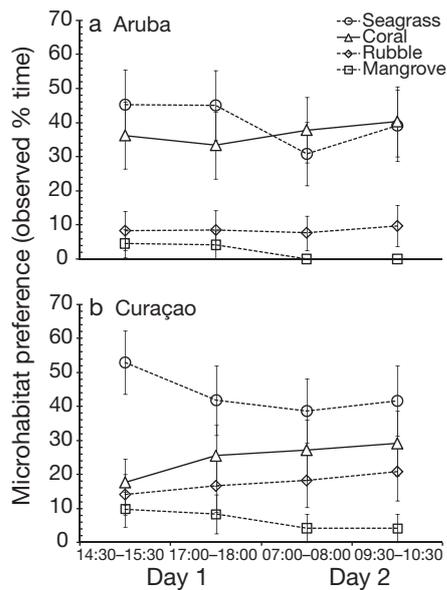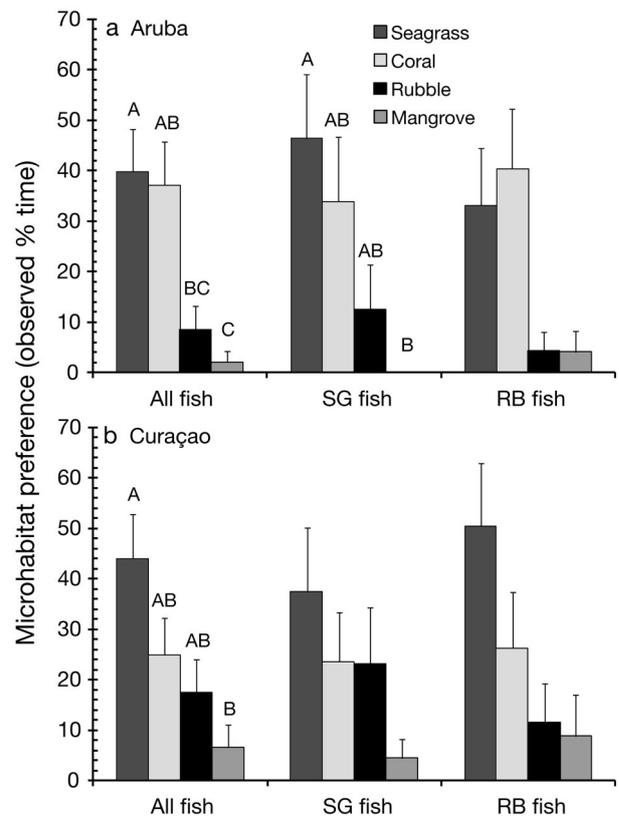
Fig. 3. *Haemulon flavolineatum.* Preference of early juveniles for 4 different microhabitats (seagrass, coral, rubble, and mangrove) on (a) Aruba and (b) Curaçao, for all fish pooled (all fish), fish collected in seagrass beds (SG fish), and fish collected on rubble (RB fish). Mean + SE; letters above bars indicate significant differences among microhabitats (Bonferroni multiple comparisons, p ≤ 0.050) when bars do not share a same letter (A, B, or C); tests were done separately per island and for all, SG, and RB fish

Fig. 2. *Haemulon flavolineatum.* Preference of early juveniles for 4 different microhabitats (seagrass, coral, rubble, and mangrove) as a function of time of day on (a) Aruba and (b) Curaçao during the 2 observation days (mean ± SE; all fish pooled per time period)

of choice on the second day of the experiment; for seagrass and coral microhabitats separately, this was 48 and 69% (Fig. 5). However, of the fish that switched habitat during the course of the experiment, the majority moved to either seagrass or coral microhabitat, resulting in 63% of all fish persisting in these 2 microhabitats on Day 2 of the experiment for 94 to 100% of their time, or 77% of all fish for >50% of their time.

Relationship with habitat complexity

Mean microhabitat preference (see Fig. 3) was not reflective of the mean value of any structural characteristic of the microhabitats. Although values of each of the 7 structural variables overlapped among microhabitats, their means differed significantly (Table 2).
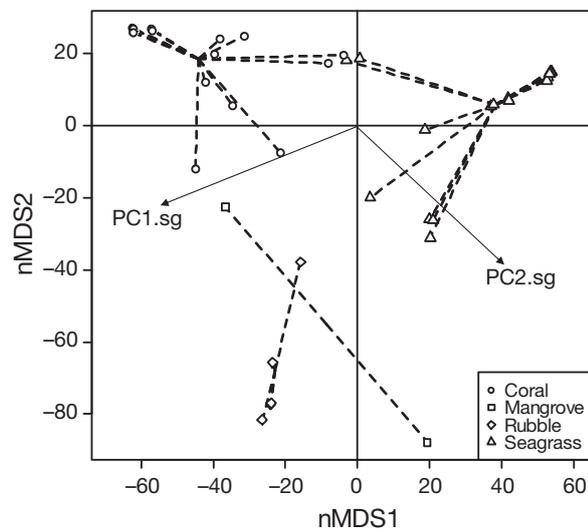
Fig. 4. *Haemulon flavolineatum.* Non-metric multi-dimensional scaling (nMDS) plot indicating the choices made by each fish (N = 47; 1 fish did not spend time in any of the 4 microhabitats and was removed from this analysis). Each point denotes a distribution of the true time spent by a single fish in the 4 microhabitats (i.e. seagrass, coral, rubble, and mangrove). The closer points are to one another, the more similar the preference of the fish is. For illustrative reasons, each individual was given a symbol to indicate the habitat in which it spent most of its time (>50%). Individuals in the far top-left area spent almost all of their time in the coral microhabitat, whereas individuals in the far top-right corner spent all their time in the seagrass microhabitat. The 2 principal component analysis (PCA) axes for the seagrass microhabitats (PC1.sg and PC2.sg), which represent an aggregated structural complexity variable, were the only ones that showed a marginally significant correlation; their direction of highest correlation is shown in the graph. The dashed lines connect the individual points to the centroids of the 4 groups

Fig. 5. *Haemulon flavolineatum.* Habitat persistence in microhabitats that were favored at the start of the experiment shown seperately (in columns with different symbols) for different initially preferred microhabitats. Depicted is the percent time spent during t_3 and t_4 (total duration: 30 min) in the microhabitat that was favored at t_1 for each of the 48 test fish. Grey symbols indicate fish that had switched from coral or rubble to seagrass (◉) or from seagrass or mangrove to coral (▲) microhabitats on Day 2 at t_3 and t_4; these fish spent on average 95% of their time (range: 60–100%) in the new habitat. SG = seagrass, CR = coral, RB = rubble, MG = mangrove, SD = sandy microhabitat

Top cover was significantly highest in coral and rubble microhabitats, but much lower for the preferred seagrass microhabitat. Side cover increased significantly from mangrove to seagrass to rubble to coral, while average microhabitat preference increased from mangrove to rubble to coral to seagrass. Mean values for rugosity, mean height, and maximum height were all much higher for mangrove than for the other microhabitats, yet this microhabitat was seldom selected. The number of shelter holes was highest for seagrass, but lowest for coral, which was the second most-preferred microhabitat. Finally, the number of structures was highest for seagrass and rubble, but the latter habitat was much less preferred than the former.

With respect to individual preference, the only 2 aggregated habitat complexity variables that appeared to have some effect on the choice of the fish were the first and second axes of the seagrass PCA
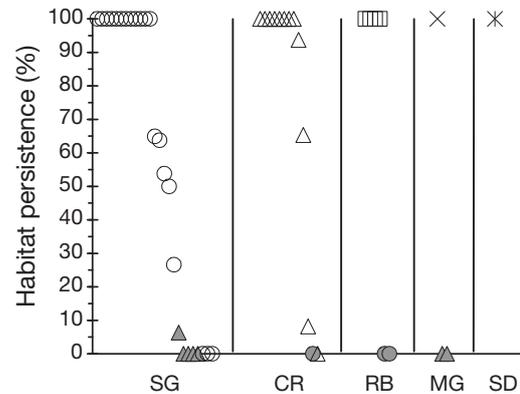
(Fig. 4; Pearson correlation: first axis r = 0.135 and p = 0.040; second axis r = 0.121 and p = 0.057). The first seagrass PCA axis is mainly related negatively to side and top cover of seagrass and number of seagrass structures and shelter holes, while the second axis is related negatively to seagrass rugosity. The vectors show that when seagrass cover or number of seagrass shoots or shelter holes decreased (i.e. increase of PC1.sg vector that has large negative coefficients for these variables) or when seagrass rugosity increased (i.e. decrease of PC2.sg vector that has a large negative coefficient for this factor), the fish tended to move towards the coral microhabitat. Note, however, that the correlations explained only a very small part of the variability (r < 0.14) and were only marginally significant. Correlations between the nMDS points and the PCA variables of the other microhabitats were much lower and far from significant. We also investigated whether the ordination could be explained by a nonlinear relationship using the PCA variables as the dependent variable and the nMDS axes as a flexible surface, but the results were similar, i.e. no correlations between individual microhabitat preference and the complexity variables, and indicated again that the relationship with the seagrass PCA axes was the only significant relationship and that these were linear. Also a 1-dimensional representation of habitat choice, in which the percent time spent in just 1 microhabitat was considered while disregarding that in the other microhabitats, showed no relationship with the 2 PCA axes (Fig. 6).
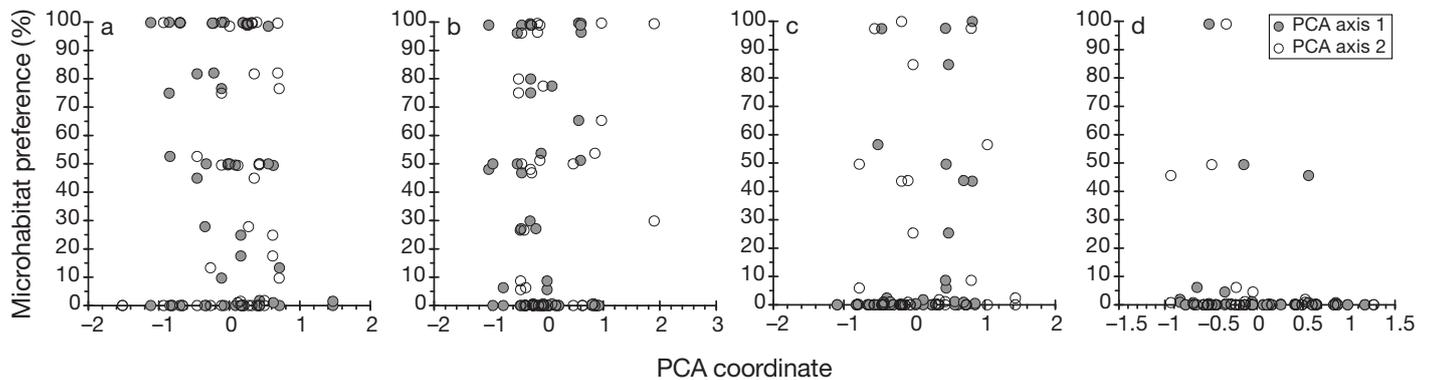
Fig. 6. *Haemulon flavolineatum.* Mean percent time spent in a microhabitat by each fish as a function of structural complexity of that habitat for (a) seagrass, (b) coral, (c) rubble, and (d) mangrove separately. Complexity is represented by an aggregated complexity value (coordinates of first and second axis, respectively), as calculated by principal component analysis (PCA) of 7 different structural complexity variables per microhabitat. The difference with Fig. 4 is that percent time spent in the other microhabitats by individual fish is not considered here

DISCUSSION

In the present study, an *in situ* multiple-choice experiment was used to test the hypothesis that in isolation of other factors (e.g. predation or competition), fish prefer the structurally most complex microhabitat that is available, independent of habitat type. However, our experiment showed the opposite: fish preferred seagrass or coral habitats, independent of common measures of structural complexity. There was quite a wide range in values for complexity variables of microhabitats within and among replicate experiments, so it is unlikely that these differences were too small to induce a response of fish to the highest structure. Therefore, the hypothesis of a preference for the most 'structure-rich' habitat can be rejected for the microhabitats and structure variables compared, and other habitat selection criteria seem to play a role in the present experiment. It is likely that due to the very contrasting architectures of the microhabitats (e.g. flexible versus rigid, hanging versus standing, living versus dead), fish showed lack of the typically observed correlations between habitat preference and structural complexity that many studies have found for single habitats (Luckhurst & Luckhurst 1978, Orth et al. 1984, Cocheret de la Morinière et al. 2004). Based on our study, it is not possible to completely rule out that preference for coral and seagrass habitats is not related in any way to their structure. However, this would then be related to aspects of complexity other than those that have typically been shown to be important for fish. For example, Nakamura et al. (2007) showed that choice for distinct habitat types (coral versus seagrass) by settling fish was driven to a larger extent by the rigidity than the complexity of the microhabitats offered. Other explanations include differences in olfactory cues (attracting or deterring fish; Arvedlund & Takemura 2006), color (relevant for camouflage; Marshall & Vorobyev 2003), shape (branching, massive, crust-like; Nakamura et al. 2007), vertical orientation (standing versus hanging structure; Nagelkerken et al. 2010), and living versus dead substratum (see below).

Haemulon flavolineatum showed a lack of preference for unstructured sandy microhabitat, which is in accordance with other studies. After release of the test fish on the unvegetated sandy bottom in the experimental cages, 88% of the fish on Aruba and 79% on Curaçao moved within 30 s towards 1 of the 4 microhabitats. With a few exceptions, fish did not return to the sandy bottom after they had selected a microhabitat. The importance of the presence of structured habitat is further supported by the fact that the sandy bottom had a surface area that was more than 5 times larger than that of each of the microhabitats, but was hardly selected even though the cages excluded nearby presence of predators. Numerous studies have demonstrated higher preference for vegetated than for unvegetated habitats, irrespective of the type of bottom structure (Luckhurst & Luckhurst 1978, Orth et al. 1984). Preference for structured habitats can be driven by higher food abundance and predator avoidance, as structure has a positive effect on both factors (Beukers & Jones 1997, Cocheret de la Morinière et al. 2004, Schmitt et al. 2009).

Haemulon flavolineatum unexpectedly showed a lack of preference for the complex and shaded mangrove roots, which contrasts the results of experimental studies with other species (Verweij et al. 2006b). Although the hanging mangrove roots had the highest rugosity and maximum and mean height of structure and could potentially be more attractive because they

were shaded in addition (Cocheret de la Morinière et al. 2004), they were hardly ever selected by the test fish. This lack of mangrove preference can be explained by a recent field experiment in Spanish Water Bay, Curaçao, using 7 open artificial mangrove units (AMUs) with different combinations of root lengths in a hanging and/or standing orientation (Nagelkerken et al. 2010). The results show that all demersal species (including *H. flavolineatum*) were equally attracted to any AMU with standing roots even though they had a different architecture (i.e. different root length or 3-dimensional root structure); however, they were not attracted at all to AMUs with hanging roots. The study by Nagelkerken et al. (2010) showed that the vertical orientation (hanging versus standing) of mangrove roots was the primary explanatory factor for their observed differences in fish microhabitat selection. Likewise, Verweij et al. (2006b) found a higher density of juvenile *H. flavolineatum* in AMUs with only artificial seagrass than in those with only artificial hanging mangrove roots. Although in our experiment the factors microhabitat type and vertical orientation of the structure were confounded, it is likely that fish did not select the darker structure-rich mangrove microhabitat because hanging structure is not preferred by demersal species such as *H. flavolineatum* (Nagelkerken et al. 2010).

Live coral and dead coral rubble showed a high degree of similarity in top and side cover, rugosity, and mean and maximum height, but fish nevertheless preferred coral over rubble even though coral provided a lower number of shelter holes. Recent studies have shown that fishes prefer live over dead coral (Graham et al. 2006, Feary et al. 2007), and live coral enhances fish abundance and diversity of species that are dependent on live coral as settlement sites (Jones et al. 2004). The fact that fish showed a similarly high preference for coral and seagrass microhabitats despite their large differences in architecture, stiffness, and color, and the fact that individual fish preferentially chose either seagrass or coral independent of common elements of structural complexity (e.g. also preferred at low cover, rugosity, density, and height), supports the notion of other studies that habitat preference can also be driven by living versus dead structure; however, this remains speculative on the basis of the current study set-up. Alternatively, the availability of appropriate shelter holes in the rubble microhabitat could have played a role, as fishes prefer hole sizes near their body size (Randall 1963, Shulman 1984, Almany 2004). The rubble microhabitat provided many but small holes, and this may have been a limiting factor for *Haemulon flavolineatum*. In contrast, the coral microhabitat provided the fish with less but larger shelter holes.

It is intriguing to observe that fish consistently selected either seagrass or coral microhabitats. There was not a single structure variable measured that was higher in seagrass and coral microhabitats compared to rubble and mangrove microhabitats. Lack of a clear correlation between fish preference and these structure variables may be explained by the fact that fish were offered microhabitats that had habitat characteristics that possibly operated at a higher hierarchical level than the degree of complexity in terms of habitat selection. Also, Igulu et al. (2011) found the highest preference of early juveniles of the reef fish *Lutjanus fulviflamma* for coral and seagrass microhabitats (as opposed to mangrove roots). Many studies have manipulated structural complexity for single habitat types and have confirmed a relationship with complexity (e.g. reviews by Orth et al. 1984, Horinouchi 2007, Mellin et al. 2009). Had we offered the same microhabitat but of different structural complexities within the cages, we likely would have found similar results as the above studies. Our results indeed show that fish tended to move away from seagrass to coral microhabitats when seagrass cover or number of structures or seagrass shoots decreased, although these correlations explained only a very small part of the variability and only in seagrass.

The results of our study translate well to the natural situation, even though we investigated habitat preference in isolation of other ecological factors. For the life stage studied here (i.e. diurnal zooplanktivores), early juveniles on Curaçao and Aruba are predominantly found on seagrass beds in terms of total lagoonal population size (Grol 2010), and prefer to school around coral heads in seagrass beds (I. Nagelkerken & M. Grol pers. obs. for multiple lagoons on Aruba, Curaçao, and other Caribbean islands). These fish utilize the extensive open plains of seagrass beds for daytime feeding on copepods in the water column (Cocheret de la Morinière et al. 2003, Grol et al. 2008), which is less effective in enclosed mangrove roots (Verweij et al. 2006a). As the test fish were able to feed on zooplankton within the cages while associating with their microhabitat of choice, it would indeed not be expected that they would choose the confined mangrove microhabitat. Rubble zones and mangroves are primarily used during different life stages and for different purposes: as settlement habitat and as daytime shelter habitat by larger juveniles, respectively (Nagelkerken et al. 2000, Grol 2010, Huijbers et al. in press). The fact that fish caught from rubble also showed a predominant preference for seagrass and coral microhabitats underlines that some specific element(s) of these 2 habitats are perceived to be attractive. The observation that under natural conditions fishes of the life stage studied here are to some degree

also found in alternative habitats suggests that in such cases other environmental or biotic factors may play a role, e.g. competition or predation risk. The latter probably explains the lack of high densities of early juvenile grunts on fringing coral reefs even though they show high preference for coral microhabitats: predation pressure is extremely high on reefs, leading to little or no survival (Grol et al. 2011).

Coral reefs, mangrove forests, and seagrass beds are extensively degraded worldwide as a result of continued human impacts to marine ecosystems (Valiela et al. 2001, Duarte 2002, Hughes et al. 2003). Loss of live benthic habitat is of great concern as *Haemulon flavolineatum* seem to prefer live seagrass and coral structure over dead coral structure and are not attracted to hanging mangroves and unvegetated habitats. Lagoons and estuaries harboring aquatic vegetation are often catchment areas that experience nutrient influxes from terrestrial sources (natural or anthropogenic). Corals and seagrasses are habitats that are especially susceptible to nutrient enrichment (Tomasko et al. 1996, Szmant 2002). Debrot et al. (1998), for example, showed significant loss of coral heads in Spanish Water Bay over a 30 yr period, likely due to eutrophication originating from shoreline development. Furthermore, habitat heterogeneity (e.g. configuration, accessibility) and the co-occurrence of different structured habitats in the seascape play important roles in habitat selection and fish distribution patterns (Dorenbosch et al. 2005, Nakamura et al. 2007, Nagelkerken 2009). Nakamura et al. (2007) showed that pelagic larvae preferred heterogeneous seagrass beds and settled on patch reefs within seagrass beds, rather than on monotonous seagrass fields or on sand patches. In this light, preservation of multiple preferred habitat types should be considered through, for example, establishment of marine protected areas and coastal zone management that help to protect against habitat destruction and eutrophication of inshore coastal areas. Likewise, habitat restoration of nursery habitats should focus on habitats that are preferred or essential during different life stages of fish. In our specific case, restoration of depauperate lagoonal coral populations and seagrass beds may prove beneficial for the productivity of inshore fish populations.

Limitations of habitat choice experiments are diverse, and include presence of predators, differences in food abundance, environmental effects, time of the day, and duration of the experiment. These factors did not affect our experiment as the cages excluded predators, allowed similar water flow with planktonic food items through the microhabitats, were located at a distance from other habitat structures, and were continuously rotated while also changing the mutual positioning of the microhabitats to rule out environmental and cage effects. Although microhabitats in the present study mimicked the field situation and were created of natural materials collected in the field instead of using artificial materials (e.g. PVC pipes to mimic mangroves), the experimental microhabitats were relatively small compared to naturally occurring habitats. Because microhabitats were small and very close to each other (≥50 cm) it could be expected that fish would easily shift from one habitat to another over time. Nevertheless, fish were rather consistent in their habitat choice and showed little temporal change in preference; once fish selected a specific microhabitat they mostly did not change their original preference, and if they did, it was largely towards seagrass or coral microhabitats. This indicates that their preference for these 2 microhabitats was fixed within their behavior and that true habitat selection was occurring, and that this was not a result of the experimental set-up. Finally, because the microhabitats were very different in architecture, the measured complexity variables might not have been perceived the same by fish among the different microhabitats. We cannot discard this possibility, but other studies have shown that even when using highly dissimilar artificial structures, general patterns emerge for specific structural characteristics that are most attractive to fishes, e.g. number of shelter holes or height of structure (Gratwicke & Speight 2005a,b).

In conclusion, although it has previously been shown for single habitat types that fish prefer complex structure, we have shown that at the scale of multiple habitat types of different architecture, these typical measures of habitat complexity are not an important determinant of habitat choice by our study fish. Fish consistently preferred coral and seagrass microhabitats—even when offered at low cover, rugosity, height, or number of shelter holes—over dead coral rubble and mangrove microhabitats, which could possibly be driven by preference for living benthic structure. The results of the present study contribute to an understanding of the processes that determine visual habitat selection by early juvenile fish in lagoonal environments, which still remains rudimentary. More emphasis needs to be placed on the criteria involved in habitat selection by fishes to strengthen predictions about the causes of spatial and temporal variation in the abundance and diversity of coral reef fishes.

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