

Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds

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ABSTRACT: Mangroves and seagrass beds are considered important nursery habitats for coral reef fish species in the Caribbean, but it is not known to what degree the fish depend on these habitats. The fish fauna of 11 different inland bays of the Caribbean island of Curaçao were compared; the bays contain 4 different habitat types: seagrass beds in bays containing mangroves, seagrass beds in bays lacking mangroves, mud flats in bays containing mangroves and seagrass beds, and mud flats in bays completely lacking mangroves and seagrass beds. Principal component analysis showed a high similarity of fish fauna among bays belonging to each of the 4 habitat types, despite some differences in habitat variables and human influence between bays. Juveniles of nursery species—fish species using mangroves and seagrass beds as juvenile nurseries before taking up residence on reefs—showed highest abundance and species richness on the seagrass beds, and on the mud flats near mangroves and seagrass beds, but were almost absent from bays containing only mud flats. The high abundance and species richness on the mud flats near nursery habitats can be explained by fishes migrating from the adjacent mangroves/seagrass beds to the mud flats. Seagrass beds near mangroves showed a higher richness of nursery species than did seagrass beds alone, suggesting an interaction with the mangroves resulting in an enhancement of species richness. Comparison of fish densities from the 4 different habitat types indicates that for the nursery species the degree of dependence on a combination of mangroves and seagrass beds as nurseries for juvenile fish is high for *Ocyurus chrysurus* and *Scarus iserti*, the dependence on seagrass beds is high for *Haemulon parrai*, *H. sciurus*, *Lutjanus apodus*, *L. griseus*, *Sparisoma chrysopterum* and *Sphyrna barracuda*, and the dependence on mud flats near mangroves/seagrass beds is high for *L. analis*. The dependence on mangroves and/or seagrass beds is low for *Chaetodon capistratus*, *Gerres cinereus*, *H. flavolineatum* and *L. mahogoni*, which can also use alternative nursery habitats.

KEY WORDS: Coral reef fishes · Inland bays · Nursery · Mangroves · Seagrass beds · Mud flats

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INTRODUCTION

Many studies in several parts of the world have recognised the importance of mangroves and seagrass beds as nurseries for fishes (see reviews by Pollard 1984, Parrish 1989, Robertson & Blaber 1992), although

in some regions of the Indo-Pacific the nursery function of these habitats is doubtful (Quinn & Kojis 1985, Blaber & Milton 1990, Thollot 1992). In the Caribbean, the nursery function is especially apparent for the juvenile stages of fishes that inhabit reefs as adults (reef fishes). Several hypotheses have been proposed to explain the high abundance of (juvenile) fishes in these habitats; they are based on avoidance of preda-

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tors, abundance of food, and interception of fish larvae. They include the following: (1) the structural complexity of these habitats provides excellent shelter against predators (Parrish 1989, Robertson & Blaber 1992, Nagelkerken et al. 2000b); (2) these habitats are often located at a distance from the coral reef or from off-shore waters and are therefore less frequented by predators (Shulman 1985, Parrish 1989); (3) the relatively turbid water of the lagoons and estuaries decrease the foraging efficiency of predators (Blaber & Blaber 1980, Robertson & Blaber 1992); (4) these habitats provide a great abundance of food for fishes (Odum & Heald 1972, Carr & Adams 1973, Nagelkerken et al. 2000a); and (5) these habitats often cover extensive areas and may intercept planktonic fish larvae more effectively than the coral reef (Parrish 1989).

Many studies have been done on the fish community structure of either mangroves or seagrass beds (Pollard 1984, Birkeland 1985, Parrish 1989, Robertson & Blaber 1992). Few studies have tried to compare these 2 habitats simultaneously (e.g. Sheridan 1992, van der Velde et al. 1992, Sedberry & Carter 1993), and some studies used different methodologies to make a comparison (e.g. Thayer et al. 1987). Once juvenile fish outgrow the protection provided by these habitats, they migrate to the coral reef or other off-shore habitat, but quantitative data on this ontogenetic shift were lacking (Ogden & Ehrlich 1977, Weinstein & Heck 1979, Rooker & Dennis 1991). Hence, the linkages between mangroves, seagrass beds and the adjacent coral reef remained largely unknown for fishes (Ogden & Gladfelter 1983, Birkeland 1985).

Some qualitative descriptions of the ontogenetic shifts of fishes between mangroves, seagrass beds and the adjacent coral reef have been made by Heald & Odum (1970) and Rooker & Dennis (1991). Only recently have quantitative size-frequency data been provided on the ontogenetic shifts of Caribbean reef fish species between these 3 habitats (Nagelkerken et al. 2000c); in addition, studies have also been made to investigate the linkages of fish faunas among 6 different shallow-water bay habitats and the adjacent coral reef (Nagelkerken et al. 2000a,b). From these studies, all based on a single survey methodology, it has been established that at least 17 different fish species which inhabit coral reefs as adults utilise mangroves, seagrass beds, and other shallow-water bay habitats as nurseries during the juvenile part of their life cycle (nursery species). These studies furthermore showed that the juveniles of most of the 17 nursery species are only found in shallow-water bay habitats and do not occur on the coral reef, suggesting a high dependence on these habitats.

Although more knowledge has recently been gained on the linkages of fish faunas between mangroves,

seagrass beds and the adjacent coral reef, the question remains as to how high the dependence on mangroves and seagrass beds as nurseries is for juveniles of fishes which inhabit reefs as adults. Theoretically, one method to test this would be to remove all mangroves and seagrass beds from a bay and study the effects on the existing juvenile reef fish population in the bay and the degree of new recruitment of juveniles into the bay. This is a very destructive method, however, which is unacceptable since these habitats are diminishing fast world-wide (Spalding 1998). Furthermore, such an experimental approach in 1 bay gives an insight into the utilisation of habitats by fishes in 1 bay only, and cannot be used for testing the nursery hypothesis on a wider geographical scale (e.g. different bays or different islands/countries).

An indirect method to test the dependence of juvenile reef fishes on mangroves and seagrass beds would be to compare different bays with different combinations of absence/presence of mangroves and seagrass beds, as suggested by Parrish (1989), which are located in the same geographic area and sampled with the same survey methodology. Hardly any studies exist in the Caribbean, however, that have examined the fish communities of mangroves and seagrass beds in more than 1 bay or lagoon of a single island/country. Comparison of the nursery function of bays from different studies is difficult because of the great differences in sampling techniques and observers, season of the year in which the studies were done, geographic locality, environmental variables, and geomorphology of the bays and lagoons.

The Caribbean island of Curaçao, which contains 15 different inland bays with a similar geomorphology, provides an excellent opportunity to study different combinations of bays with absence/presence of mangroves and seagrass beds, such as described above. In the present study, fish faunas of inland bays containing only seagrass beds, bays containing seagrass beds as well as mangroves, and bays completely lacking mangroves and seagrass beds were compared for 1 island, using the same survey methodology, within a time span of 3 mo. The objective of this study was to establish the degree of dependence of juvenile reef fishes on mangroves and seagrass beds as nurseries.

MATERIALS AND METHODS

Study design. The fish community of seagrass beds and mud flats of 11 inland bays was sampled during the daytime on the island of Curaçao, Netherlands Antilles (Fig. 1). Except for Spanish Water Bay, Piscadera Bay and to a lesser extent also Fuik Bay, coastal development, fishing or other human activities are lim-

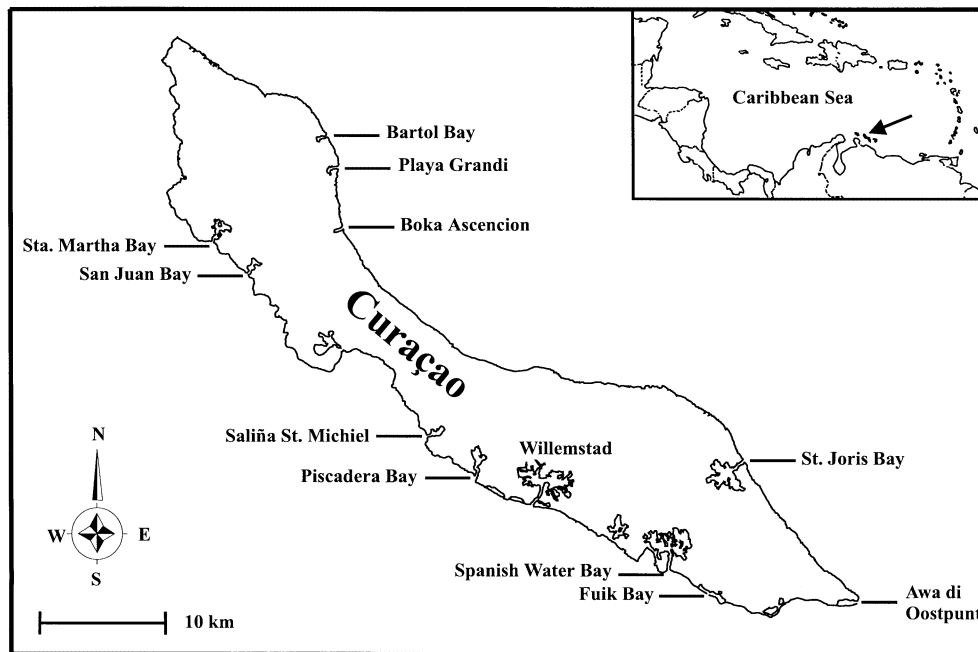


Fig. 1. Map of Curaçao, Netherlands Antilles, showing the 11 bays studied

ited to absent in all bays; these activities are more concentrated along the coastline of the island itself.

The seagrass beds and mud flats of the different bays were assigned to 4 different habitat types: (1) seagrass beds in bays containing mangroves, (2) seagrass beds in bays lacking mangroves, (3) mud flats in bays containing mangroves and seagrass beds, and (4) mud flats in bays lacking mangroves and seagrass beds (Table 1). Hereafter, habitat type 1 is referred to as seagrass beds (+m), type 2 as seagrass beds (-), type 3 as mud flats (+m+s), and type 4 as mud flats (-), respectively.

The seagrass beds studied consist of monospecific stands of turtle grass *Thalassia testudinum*, except in Piscadera Bay, where they consist of manatee grass *Syringodium filiforme*. Mean *T. testudinum* density ranged from 236 to 690 shoots m^{-2} , height from 8 to 17 cm, and cover from 55 to 89% (Table 1). Mud flats had some cover of fleshy algae ranging from 4 to 37%. The bottom of the mud flats and seagrass beds in most bays consists of fine terrestrial sand (grain size between approx. 53 and 600 μm), which washes into the bays by natural flow of rainwater. The bottom of Awa di Oostpunt and Fuik Bay consists largely of marine sediment, with a similar grain size as the other bays. The average daily tidal range in Curaçao is about 30 cm (de Haan & Zaneveld 1959).

The fish communities of the different seagrass beds and mud flats were sampled with a beach seine, since most bays were too turbid for the use of visual census.

The beach seine is less selective for fish species than a variety of other collecting gear, but a disadvantage of the beach seine is that it may ride up over dense seagrass beds (English et al. 1994). The latter problem was observed during the present study, and resulted in an underestimation of abundance for some fish species. These species dove between the seagrass shoots when the net approached, and sheltered there until the net had passed over. On the mud flats this problem did not occur, since a chain along the bottom of the net for its full length ploughed through the mud, making it difficult for fishes to escape the net. To quantify the degree of selection of the beach seine in the seagrass beds, a total of 9 visual censuses were done at 3 seagrass sites in the Spanish Water Bay and compared with 9 beach seine hauls at the same sites. Spanish Water Bay was selected because it is one of the few bays with sufficient visibility for visual censuses. Another problem of the beach seine is that very small fishes are not caught because they can pass through the meshes of the net.

The beach seine measured 30 m in length and 1.8 m in height, and had a mesh size of 1 cm (stretched). During each haul, the beach seine was laid out from the shore into the water in the form of a semi-circle, and pulled ashore. The mean maximum water depth of the seine samples varied between 0.5 and 2.0 m (Table 1), and the sampled surface area measured approximately 150 m^2 haul $^{-1}$. All fishes caught were identified and counted in a bin filled with seawater, and released afterwards. For each seagrass bed and mud flat of each

Table 1. Sampling regime, environmental variables and habitat characteristics of the seagrass beds and mud flats of the 4 habitat types. At the mud flats (+m+s), mangroves and seagrass beds are present in the vicinity of the mud flats and not on the mud flats themselves

	No. of sites sampled	Mangroves present in bay	Seagrass present in bay	Maximum sampling depth (m)	Salinity (‰)	Temp. (°C)	Water clarity (m)	Seagrass shoot density (m ⁻²)	Seagrass height (cm)	Seagrass cover (%)	Algal cover (%)	Mud cover (%)
Seagrass beds (+m)												
(1) Spanish Water Bay	6	+	+	2.0	35.7	30.3	3.6	279	17.2	67.1	10.8	22.1
(2) St. Joris Bay	5	+	+	1.2	33.8	30.5	1.7	276	12.0	66.9	10.2	22.9
(3) Fuik Bay	3	+	+	1.7	33.9	30.8	3.7	246	7.7	62.9	12.8	24.3
(4) Piscadera Bay	3	+	+	1.5	33.1	29.6	0.9	–	39.1	100.0	0.0	0.0
Seagrass beds (-)												
(5) Awa di Oostpunt	3	–	+	1.0	33.3	31.9	5.5	690	11.4	89.0	0.0	11.0
(6) Boka Ascension	2	–	+	0.6	34.7	29.9	2.1	473	9.6	75.5	0.0	24.5
(7) Bartol Bay	1	–	+	0.5	35.5	29.9	0.4	236	9.8	55.0	7.0	38.0
Mud flats (+m+s)												
(8) St. Joris Bay	5	+	+	1.8	33.8	30.4	1.3	0	0.0	0.0	11.8	88.2
(9) Piscadera Bay	3	+	+	1.8	32.9	29.7	1.0	0	0.0	0.0	15.6	84.4
(10) Playa Grandi	2	+	+	1.5	34.9	30.1	1.1	0	0.0	0.0	36.5	63.5
Mud flats (-)												
(11) San Juan Bay	4	–	–	1.3	34.1	29.7	0.6	0	0.0	0.0	0.0	100.0
(12) Salina St. Michiel	4	–	–	0.9	47.8	31.2	0.7	0	0.0	0.0	0.0	100.0
(13) Sta. Martha Bay	4	–	–	2.0	34.7	30.0	0.7	0	0.0	0.0	3.5	96.5

bay, 1 to 6 sites were sampled at each occasion (Table 1), depending on the size of the bay (see Fig. 1). Each site in each bay was sampled on 3 different occasions (3 replicates) between September and November 1999; all sampling was done during daytime.

Fish species were divided into 3 groups with respect to their use of coral reefs and bays, which was largely based on studies of (ontogenetic shifts in) habitat utilisation by fishes in Spanish Water Bay and the adjacent reef (see Nagelkerken et al. 2000b): (1) nursery species: fishes which inhabit coral reefs as adults and of which the juveniles use mangroves and seagrass beds in bays as nurseries; (2) bay species: fish species which are relatively abundant in bays and not present or found in lower abundance on the reef; and (3) reef species: the remaining reef fishes of which all life stages are normally found on the reef.

During each survey, water temperature, salinity, and transparency were measured at 1 m depth. Temperature and salinity were measured using a YSI 30 salinity, conductivity, temperature meter, and water transparency was measured as horizontal Secchi disk visibility. Cover of *Thalassia testudinum*, *Syringodium filiforme* (Piscadera Bay), macro-algae and mud, and density and height of *T. testudinum* were measured once at each site, in 6 randomly selected quadrats of 50 × 50 cm. Seagrass density is expressed as the number of seagrass shoots m⁻². Density of *S. filiforme* in Piscadera Bay was not measured because this was difficult due to the high density and great length of the narrow leaves.

Statistical analysis. The fish data from the various study sites and bays were used to calculate the average values for each habitat type. Fish data for the 4 different habitat types were compared using a nested ANOVA on log- or square-root-transformed data, followed by a Tukey HSD multiple comparison test (Sokal & Rohlf 1995), with the 3 temporal census replicates (sites pooled per bay) nested under the bays of each habitat type. The same procedure was followed for comparison of the environmental variables. Fish data were statistically compared among the 4 habitat types for total fish abundance and species richness, total abundance and species richness of nursery species, bay species and reef species, abundance of each of the 28 most common fish species, and difference in fish density estimates by visual censuses and beach seine hauls. Small pelagic species of the water column forming large schools (Atherinidae, Clupeidae, Engraulidae) were excluded from all analyses.

Principal component analysis (PCA) was carried out on the log-transformed abundance (averaged for the different sites) of each fish species on the seagrass beds and mud flats of the different habitat types, using the ordination programme Canoco 4.0 (ter Braak &

Smilauer 1998). Scaling was focussed on inter-sample distances (similarity in fish abundance among the seagrass beds and mud flats of the different habitat types, Fig. 2a), and on inter-species correlations (correlations between species on the basis of their abundance in the seagrass beds and mud flats of the different habitat types, Fig. 2b). Species scores were divided by the standard deviation, and the data were centred by species.

RESULTS

The 4 habitat types did not differ significantly in salinity and water temperature ($p > 0.05$, nested ANOVA, Table 1). Water clarity was higher on the seagrass beds than on the mud flats ($p < 0.001$), and higher on the mud flats (+m+s) than on the mud flats (-) ($p < 0.005$, Tukey HSD test).

Almost all individuals of the nursery species caught were juvenile fishes (see mean sizes in Table 2). The adults of these species are normally not found in bays and live on the coral reef (see Nagelkerken et al. 2000b,c).

For 4 out of 14 fish species, catches with the beach seine net showed significantly lower densities than estimations with the visual census technique (Table 2). The difference between the 2 methods was largest for *Haemulon flavolineatum* and *Archosargus rhomboidalis*.

PCA showed a clear dissimilarity between the 4 distinguished habitat types, based on abundance of the different fish species (Fig. 2a). Despite differences between bays due to, for example, water clarity, habitat characteristics, human influences, etc., bays clustered within one habitat type showed a high similarity. Only the mud flats (+m+s) of Playa Grandi showed some similarity to the seagrass beds (+m). The *Syringodium filiforme* beds in Piscadera Bay (with mangrove present) showed a high similarity to the *Thalassia testudinum* beds (+m) in other bays, despite the difference in seagrass species.

The 4 habitat types displayed differences in fish abundance and species richness (Fig. 3). Total fish abundance was lower on seagrass beds than on mud flats, but the difference was only significant ($p = 0.034$, nested ANOVA) between the seagrass beds (-) and the mud flats (+m+s). Total species richness, on the other hand, was highest in habitats with presence of mangroves ($p < 0.035$, nested ANOVA), i.e., on seagrass beds (+m) and mud flats (+m+s), although the difference was not significant between seagrass beds (+m) and seagrass beds (-). Nursery species showed a significantly lower abundance ($p < 0.001$) on mud flats (-) than in the 3 other habitats with presence of either sea-

grass beds or mangroves. Species richness of nursery species was highest in the 2 habitats with presence of mangroves ($p < 0.008$), and as was the case with abundance, it was lowest on the mud flats (-). Bay species were more abundant on the mud flats than on the seagrass beds ($p < 0.003$). Species richness of the bay species was highest on the mud flats (-) ($p < 0.022$) and lowest in the seagrass beds (-) ($p < 0.001$). Reef species contributed little to the total fish fauna, and their abundance and species richness were greatest on the seagrass beds (-) ($p < 0.045$).

PCA of the fish species showed 3 different species clusters (Fig. 2b). These clusters partly correspond to the 4 distinguished habitat types: fishes of the seagrass beds (-) and mud flats (-) formed separate clusters, but seagrass beds (+m) and mud flats (+m+s) were clustered together. Three fish species had a wide habitat utilisation and did therefore not form part of the three clusters (Fig. 2b).

With the exception of 1 species (*Lutjanus analis*), all fish species found in the 4 habitat types can be divided into 2 groups: (1) species associated with mangroves and/or seagrass beds, and (2) species associated with mud flats. These 2 groups comprise 5 different categories (Table 2). The first category is characterised by fish species which are most abundant on the seagrass beds (+m), and show a significantly lower abundance or complete absence in the seagrass beds (-) and on the mud flats (-). The lack of a significant difference between the seagrass beds (+m) and the mud flats (-) for *Archosargus rhomboidalis* and *Scarus iserti* may be explained by the underestimation of their abundance in the beach seine catches in the seagrass beds (Table 2). Three nursery species furthermore showed a significantly higher abundance on the mud flats (+m+s) than on the mud flats (-).

The second category is characterised by fish species that are significantly more abundant in any of the 3 habitats with presence of mangroves or seagrass beds, but show a much lower abundance or complete absence on the mud flats (-), which lack these nursery habitats. In contrast to the first category, the nursery species in this category show no significantly higher abundance on the seagrass beds (+m) than on the seagrass beds (-). The abundance of *Lutjanus griseus* was underestimated on the seagrass beds in the beach seine catches, which may explain the lack of a significant difference with the mud flats (-). The second category consists mainly of nursery species.

The third category is characterised by mainly reef species that are only found on the seagrass beds (-). However, they were present in only 1 bay (Boka Ascencion), and only at 1 site or during 1 sampling date. Hence, this species category does not represent a species group which depends on seagrass beds.

Table 2. Mean abundances of the 28 most common (abundance > 0.26 haul⁻¹) fish species in the 4 habitat types. First 3 columns with p-values: values refer to statistical comparison (nested ANOVA) between the respective habitat type and the mud flats (-) (beach seine catches). *Significantly higher (p < 0.005) than catches on the seagrass beds (-), **Significantly higher than catches on the seagrass beds (+m) and seagrass beds (-). In addition, densities ± SE (individuals per 100 m²) are shown for the visual census versus the beach seine method on the seagrass beds of Spanish Water Bay, together with the p-value (last column) of their statistical comparison (nested ANOVA). Mean size refers to the mean fish size of the 13 different seagrass beds and mud flats. b: bay species, n: nursery species, r: reef species (see text for definitions)

Species group	Mean size ± SD (cm)	Seagrass beds (+m)	p	Mud flats (+m+s)	p	Seagrass beds (-)	p	Mud flats (-)	Visual census	Beach seine	p
Category 1: Associated with mangroves and seagrass beds											
(1) <i>Archosargus rhomboidalis</i> sea bream	b 12.6 ± 4.0	0.6*	0.2	0.2	0.0	0.0	0.1	0.1	3.0 ± 0.7	0.2 ± 0.1	0.000
(2) <i>Chaetodon capistratus</i> four-eye butterflyfish	n 5.1 ± 0.7	0.9*	0.4	0.035	0.1	0.0	0.0	0.0	0.1 ± 0.1	0.3 ± 0.2	
(3) <i>Haemulon flavolineatum</i> french grunt	n 7.9 ± 1.8	2.4*	0.8	0.022	0.0	0.0	0.0	0.0	7.2 ± 1.0	2.8 ± 1.5	0.010
(4) <i>Hyporhamphus unifasciatus</i> silverstripe halfbeak	b 19.9 ± 0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	-	-	
(5) <i>Ocyurus chrysurus</i> , yellowtail snapper	n 8.8 ± 1.9	2.7*	1.0	0.003	0.3	0.0	0.0	0.0	2.4 ± 0.8	4.0 ± 1.6	
(6) <i>Scarus iserti</i> , striped parrotfish	n 3.8 ± 1.1	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.8 ± 0.3	0.0 ± 0.0	0.029
Category 2: Associated with seagrass beds											
(7) <i>Diodon holocanthus</i> balloonfish	b 13.6 ± 2.2	0.4	0.012	0.2	0.3	0.0	0.0	0.0	0.1 ± 0.1	0.4 ± 0.1	
(8) <i>Haemulon parrai</i> sailors choice	n 12.5 ± 4.9	0.1	0.0	0.0	0.9	0.026	0.0	0.0	-	-	
(9) <i>Haemulon sciurus</i> bluestriped grunt	n 11.8 ± 3.2	1.2	0.004	0.3	0.3	0.0	0.0	0.0	1.6 ± 0.5	1.2 ± 0.6	
(10) <i>Lutjanus apodus</i> schoolmaster	n 10.0 ± 1.7	1.6	1.6	0.000	5.1	0.000	0.4	0.4	0.2 ± 0.2	0.0 ± 0.0	
(11) <i>Lutjanus griseus</i> gray snapper	n 13.4 ± 3.5	0.3	0.3	0.000	0.4	0.0	0.1	0.1	0.4 ± 0.2	0.0 ± 0.0	0.021
(12) <i>Lutjanus mahogoni</i> mahogany snapper	n 9.3 ± 0.2	0.1	1.3	0.000	0.3	0.0	0.0	0.0	-	-	
(13) <i>Mulloidichthys martinicus</i> yellow goatfish	r 11.8 ± 0.4	0.3	0.0	1.1	0.9	0.045	0.0	0.0	0.2 ± 0.1	0.6 ± 0.4	
(14) <i>Spanisoma chrysopterum</i> redtail parrotfish	n 9.1 ± 1.1	0.3	0.4	0.0	0.9	0.045	0.0	0.0	-	-	
(15) <i>Sphyaena barracuda</i> great barracuda	n 25.2 ± 4.0	0.7	0.005	0.5	0.4	0.0	0.1	0.1	0.0 ± 0.0	0.4 ± 0.3	

Table 2 (continued)

Species group	Mean size ± SD (cm)	Seagrass beds (+m)	p	Mud flats (+m+s)	p	Seagrass beds (-)	p	Mud flats (-)	Visual census	Beach seine	p
Category 3: Association with seagrass beds uncertain											
(16) <i>Abudefduf saxatilis</i> sergeant major	4.6 ± 2.2	0.0		0.0		0.4		0.0	-	-	
(17) <i>Acanthurus bahianus</i> ocean surgeon	7.3 ± 1.1	0.0		0.0		0.5		0.0	-	-	
(18) <i>Haemulon carbonarium</i> caesar grunt	8.3 ± 0.0	0.0		0.0		0.7	0.000	0.0	-	-	
(19) <i>Lactophrys trigonus</i> trunkfish	25.2 ± 23.8	0.0		0.0		0.4	0.000	0.0	-	-	
Category 4: Associated with mud flats—not found on seagrass beds											
(20) <i>Achirus lineatus</i> lined sole	7.1 ± 2.3	0.0	0.000	0.3	0.000	0.0	0.000	2.0	-	-	
(21) <i>Albula vulpes</i> bonefish	16.0 ± 4.9	0.0	0.007	0.0	0.046	0.0	0.011	0.3	-	-	
(22) <i>Cyprinodon variegatus</i> sheepshead minnow	2.0 ± 0.0	0.0		0.0		0.0		3.3	-	-	
(23) <i>Elops saurus</i> ladyfish	19.8 ± 2.1	0.0	0.000	0.0	0.000	0.0	0.000	0.3	-	-	
Category 5: Associated with mud flats—also found on seagrass beds											
(24) <i>Eucinostomus gula</i> silver jenny	6.9 ± 0.9	1.8		2.7		0.2	0.004	2.2	1.3 ± 0.5	0.5 ± 0.2	
(25) <i>Eucinostomus jonesi</i> slender mojarra	6.5 ± 1.7	2.8	0.043	11.2**		1.3	0.001	6.0**	1.8 ± 1.1	2.2 ± 1.1	
(26) <i>Gerres cinereus</i> yellowfin mojarra	10.7 ± 5.7	1.0	0.000	1.1	0.000	0.6	0.000	7.5	0.8 ± 0.5	0.3 ± 0.2	
(27) <i>Mugil curema</i> white mullet	14.0 ± 5.9	0.0	0.004	3.5**		0.1	0.016	1.8**	-	-	
Category 6: Associated with mud flats near mangroves/seagrass beds											
(28) <i>Lutjanus analis</i> mutton snapper	10.6 ± 1.3	0.5		1.5**	0.027	0.4		0.3	-	-	

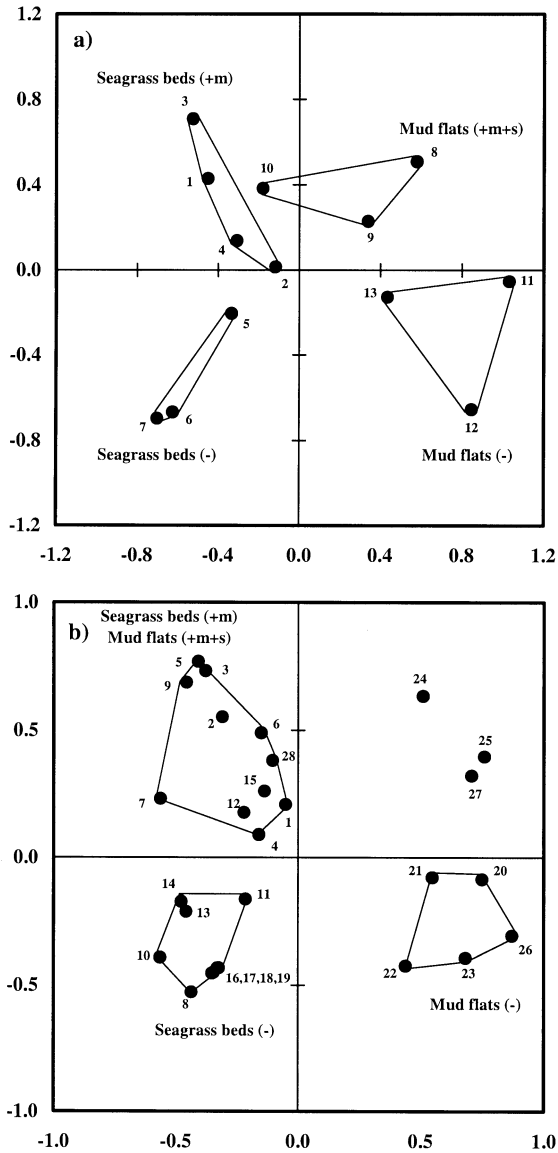


Fig. 2. Principal component analysis (PCA) of fish abundance (a) for the different seagrass bed and mud flat sites of the 4 habitat types and (b) for the different fish species. The horizontal axes represent the first PCA axis, the vertical axes represent the second PCA axis. The first 2 axes account for 50.9% of the total variance. Site and species clusters are encircled by solid lines and are based on the similarity in fish abundances among sites, and on sites in which a particular species is most abundant, respectively. Only the 28 most abundant fish species are shown (abundance > 0.26 haul⁻¹). Numbers refer to the different seagrass bed and mud flat sites in Table 1 and to the fish species in Table 2

The fourth category is characterised by bay species that occur only on mud flats, showing the highest abundance on the mud flats (-).

The fifth category consists of bay species that occur on mud flats as well as seagrass beds, but show the highest abundance on 1 or both types of mud flats.

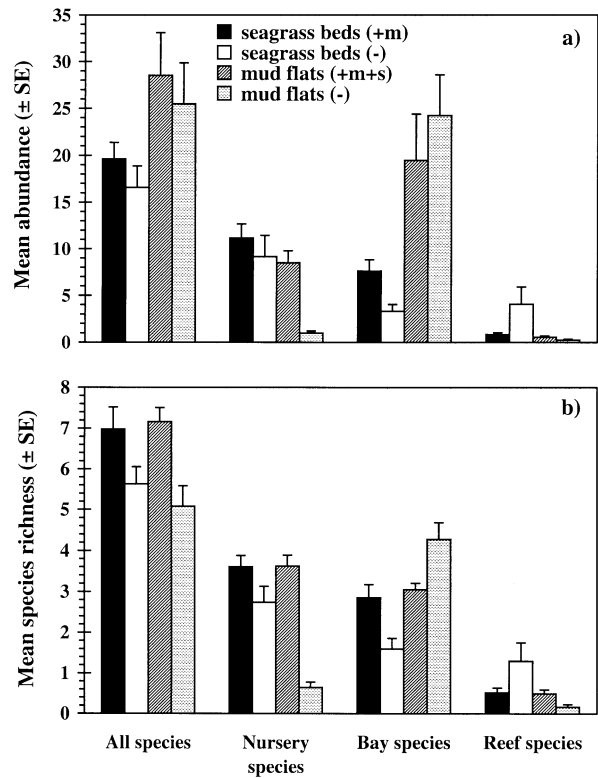


Fig. 3. (a) Mean abundance (per haul) and (b) mean species richness (per haul) for all, nursery, bay, and reef species (see text for definition) in the 4 different habitat types

The exception to the 2 groups was *Lutjanus analis* (Category 6, Table 2). This species showed highest densities on mud flats (+m+s), but low densities on mud flats (-) and seagrass beds. This category is thus characterised by fish associated with mud flats located near mangroves/seagrass beds.

DISCUSSION

This study shows that the presence of mangroves and/or seagrass beds in bays has a significant effect on the fish communities of the bays, despite some habitat and environmental differences between bays. Several other comparative studies have shown that seagrass beds harbour higher fish densities than adjacent bare sand flats (see review by Orth et al. 1984). In the present study, total fish abundance was higher on the mud (sand) flats than on the seagrass beds. However, this is caused by a high abundance of bay species (especially mojarras) that are associated with mud flats and are independent of mangroves and seagrass beds as nurseries. For the nursery species, on the other hand, total fish abundance and species richness were much

higher on both types of seagrass beds than on the mud flats (-), suggesting a dependence on these nursery habitats for at least some of the nursery species.

Fish abundance and species richness of nursery species were also high on mud flats (+m+s) which were located near seagrass beds and mangroves. The most likely explanation for this pattern is that these fish do not remain on the seagrass beds or in the mangroves, but roam around in the bay and also enter the adjacent mud flats. This idea is supported by the single PCA cluster for (mainly nursery) species utilising seagrass beds (+m) and those utilising mud flats (+m+s). The data thus indicate that adjacent mangroves and seagrass beds enhance densities and species richness of nursery species on mud flats.

A similar pattern was observed for the seagrass beds (-). Species richness of nursery species was significantly higher on the seagrass beds (+m) than on the seagrass beds (-), suggesting that presence of adjacent mangroves enhances the species richness on seagrass beds. This may be related to the fact that most nursery species utilise seagrass beds as well as mangroves as nursery habitats (Nagelkerken et al. 2000b,c). Presence of both types of vegetation diversifies the available habitat in bays, making them suitable for a wider range of species. The interaction between mangroves and seagrass beds is probably mutual, with seagrass beds also enhancing species diversity in the mangroves, although this has yet to be tested.

The present study shows a variable dependence of fishes on mangroves and seagrass beds. Six different categories of habitat utilisation could be distinguished, of which 1 was uncertain, 2 were associated with mangroves/seagrass beds, 2 associated with mud flats, and 1 associated with mud flats located near mangroves and seagrass beds. The first category represents species that are associated with mangroves and seagrass beds. In this category, all 4 nursery species, *Chaetodon capistratus*, *Haemulon flavolineatum*, *Ocyurus chrysurus* and *Scarus iserti*, showed a significantly lower abundance to complete absence on seagrass beds (-) and on mud flats (-) compared to the abundance on seagrass beds (+m), suggesting a high dependence on a combination of mangroves and seagrass beds as nursery habitats. Two bay species also fell into this category. The bay species *Hyporhamphus unifasciatus* probably does not belong to this category, since it is not a nursery species and its high abundance was caused by a high number of fishes caught in just 1 bay at just 1 site.

In the second category, the nursery species *Haemulon parrai*, *H. sciurus*, *Lutjanus apodus*, *L. griseus*, *L. mahogoni*, *Sparisoma chrysopterum* and *Sphyræna barracuda* did not show a significantly higher abundance on seagrass beds (+m) than on seagrass beds (-), but did show a strong reduction in abundance or com-

plete absence on mud flats (-). This indicates a high dependence of juveniles of these species on seagrass beds, but not on mangroves. Nagelkerken et al. (2000b) showed that all of these species are much more abundant in the mangroves than in the seagrass beds, but apparently these species do not strictly depend on the presence of mangroves. The association of the non-nursery species *Diodon holocanthus* (bay species) and *Mulloidichthys martinicus* (reef species) with the seagrass beds is probably related to a high abundance of food in the seagrass beds (Nagelkerken et al. 2000a). The association of *D. holocanthus* with the seagrass beds is not related to a nursery function, since this species shows rare mass recruitment not only into bays, as is the case with nursery species (Nagelkerken et al. 2000b), but also onto the coral reef (Debrot & Nagelkerken 1997).

Fish species associated with mud flats (categories 4 and 5) all belonged to the bay species. *Gerres cinereus* is partly also a nursery species since some of its juveniles use mangroves as a nursery habitat, and since a part of the adult population is found on the coral reef (Nagelkerken et al. 2000b). Their densities were highest on the mud flats (-), where juveniles were also common, indicating that the dependence of *G. cinereus* on mangroves is low.

Lutjanus analis (category six) showed a high abundance on mud flats (+m+s), but a low abundance on both types of seagrass beds and on the mud flats (-). This suggests that *L. analis* favours mud flats, but still depends on mangroves and seagrass beds. Nagelkerken et al. (2000b) showed that this species utilises both mangroves and seagrass beds as nursery habitats.

Although the present study shows a close association of nursery species with mangroves and/or seagrass beds in bays, it cannot be ruled out that other types of shallow-water habitats inside or outside bays can be used as alternative nurseries by these species. The shallow coral reef is used to some degree by a few species as a nursery habitat (Nagelkerken et al. 2000c), which implies that the dependence of some nursery species on mangroves and seagrass beds may not be completely obligate (i.e. unable to use other habitats as nurseries). This is the case for 3 nursery species: *Chaetodon capistratus*, *Haemulon flavolineatum* and *Lutjanus mahogoni*. On Caribbean islands completely lacking bays with mangroves/seagrass beds, these 3 species use alternative nursery habitats (Nagelkerken et al. unpubl.). For all other nursery species of the present study, however, the densities on reefs of islands completely lacking mangroves/seagrass beds are very low or close to zero, supporting the idea of a high dependence of these fishes on mangroves and/or seagrass beds as nurseries. An exception is *Gerres cinereus*, which did not show a high dependence on

mangroves/seagrass beds (this study), but was nevertheless absent from islands lacking bays with mangroves and seagrass beds (Nagelkerken et al. unpubl.). This suggests that *G. cinereus* simply depends on the presence of shallow coastal areas as nurseries, such as inland bays.

With all of the above comparisons of abundance of juvenile nursery species between the different habitat types it should be kept in mind that the juveniles of these species are highly associated with shallow-water bay habitats, in particular mangroves and seagrass beds, and are normally not found on the coral reef (Nagelkerken et al. 2000a,b,c). The data thus imply that the observed differences in abundance of nursery species between the 4 habitat types are highly related to the absence/presence of mangroves/seagrass beds and perhaps only to a lesser extent to environmental or habitat factors in the bays studied. This is further supported by the similarity of fish faunas of different bays belonging to the same habitat type (i.e. Fig. 2a).

It remains to be established if other types of bay habitats which provide sufficient shelter (e.g. patch reefs) can take over the nursery function of mangroves/seagrass beds. Since the majority of inland bays of Curaçao do not contain large surface areas of bay habitats other than mangroves, seagrass beds or mud flats, it appears that for at least the island of Curaçao mangroves and seagrass beds are very important nursery areas for several reef fish species.

The use of the beach seine net for the fish surveys in the seagrass beds resulted in an underestimation of abundance for some fish species when compared to visual censuses. Nevertheless, the abundance in the seagrass beds was high enough that statistical differences from the mud flats (-) could be shown, where the catch rate of fishes was higher. The higher abundance on the seagrass beds was statistically insignificant only for the nursery species *Scarus iserti* and *Lutjanus griseus*, which were 2 of the 4 species that were underestimated on the seagrass beds. Visual observations during seining revealed that catch rates of fish species which swim some distance above the seagrass beds (e.g. *Ocyurus chrysurus*, *Sphyraena barracuda*, mojaras) and of slow-swimming species (e.g. *Chaetodon capistratus*, *Diodon holocanthus*) were better than those of species swimming between or just above the seagrass blades (e.g. *Lutjanus* spp., *Haemulon* spp.). For the latter group, escape from the net was easier in dense seagrass beds where the beach seine sometimes rode over the seagrass shoots. Other species such as *Archosargus rhomboidalis* and *Scarus iserti* were particularly alert and immediately dove into the sediment to escape from the net. The results are probably not greatly influenced by the significant underestimation of 4 species with the beach seine in the seagrass beds

(in the mud flats this problem did not exist). Most comparisons were made between seagrass beds and mud flats and between seagrass beds (+m) and seagrass beds (-). Higher catch rates in the seagrass beds would only have increased the difference in fish abundance with the mud flats, whereas for the 2 types of seagrass beds the catch ratio should have remained the same since both experienced identical problems with the beach seine.

Small juveniles were not caught because of the mesh size used (1 cm), and hence the results with respect to the dependence of nursery species on mangroves and seagrass beds are based on medium-size and large juveniles. However, since mortality of small juveniles can be very high in the first few weeks after settlement (Shulman & Ogden 1987), results based on the standing crop of medium-size and large juveniles (i.e. those actually using the nursery habitats for a longer period of time) are probably more reliable. Hence, we assume that the absence of the very small juveniles of nursery species from the beach seine catches does not affect the general conclusions on the dependence of these fishes on mangroves and seagrass beds.

The mangrove and seagrass habitats of Curaçao are not comparable to many other mangrove and seagrass habitats (often in estuaries), particularly in the Indo-Pacific. These habitats are often very turbid and show fluctuating salinities and a larger tidal range. These features influence the nursery function and species composition of mangroves and seagrass beds (Blaber 1997). As the characteristics which are usually associated with these habitats are not present on Curaçao, the mechanisms responsible for the nursery function of the bays of Curaçao may differ from those in bays, lagoons and estuaries which have been studied in other regions. One important difference with lagoons and estuaries which have a large tidal range is, for example, that in Curaçao (tidal range 30 cm) the mangrove and seagrass habitats are continuously available to the fish, and do not fall dry as a result of the tides. The results of the present study are of importance, however, for other Caribbean islands which have comparable mangrove and seagrass systems.

In conclusion, for species designated as nursery species (Table 2), the degree of dependence on a combination of mangroves and seagrass beds as nurseries for juvenile fish is high for *Ocyurus chrysurus* and *Scarus iserti*, the dependence on seagrass beds is high for *Haemulon parrai*, *H. sciurus*, *Lutjanus apodus*, *L. griseus*, *Sparisoma chrysopterum* and *Sphyraena barracuda*, the dependence on mud flats near mangroves/seagrass beds is high for *L. analis*, whereas the dependence on mangroves and/or seagrass beds is low for *Chaetodon capistratus*, *Gerres cinereus*, *H. flavolineatum* and *L. mahogoni*.

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