Deel II: Wetenschappelijk rapport

Are mangroves and seagrass beds obligate or facultative nurseries for reef fishes? 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 biotopes for coral reef fishes, but it is not known whether these biotopes are obligate or facultative nurseries. The fish fauna of 11 different inland bays of the Caribbean island of Curaçao containing four different biotope types were mutually compared: 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 lacking mangroves and seagrass beds. Fish species using mangroves and seagrass beds as nurseries (nursery species) showed highest abundance and species richness on the seagrass beds and on the mud flats surrounded by mangroves and seagrass beds, but were almost absent from the bare mud flats. The high abundance and species richness on the mud flats near to nursery biotopes is likely explained by fishes migrating from the adjacent mangroves/seagrass beds to the mud flats. Seagrass beds surrounded by mangroves showed a higher species richness of nursery species than bare seagrass beds, suggesting an interaction with the mangroves resulting in an enhancement of species richness. For the nursery species, mangroves and seagrass beds are obligate nursery biotopes for *Ocyurus chrysurus* and *Scarus iserti*, seagrass beds are obligate nurseries for *Haemulon parrai*, *H. sciurus*, *Lutjanus apodus*, *L. griseus*, *Sparisoma chrysopterum* and *Sphyraena barracuda*, mud flats near mangroves/seagrass beds are obligate biotopes for *L. analis*, and mangroves and/or seagrass beds are facultative nurseries for *Chaetodon capistratus*, *Gerres cinereus*, *H. flavolineatum*, and *L. mahogoni*.

INTRODUCTION

Many studies in various parts of the world have recognised the importance of mangroves and seagrass beds as nurseries for reef fishes (see reviews by Pollard 1984, Parrish 1989, Robertson & Blaber 1992). Several hypotheses have been proposed to explain the high abundance of (juvenile) fishes in these biotopes, and are based on avoidance of predators, the abundance of food, and interception of fish larvae. They include the following:

1) the structural complexity of these biotopes provide excellent shelter against predators (Parrish 1989, Robertson & Blaber 1992, Nagelkerken et al. 2000b).

2) these biotopes 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 biotopes provide a great abundance of food for fishes (Odum & Heald 1972, Carr & Adams 1973, Nagelkerken et al. 2000a).

5) these biotopes 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 two biotopes 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 biotopes they migrate to the coral reef or off-shore water, but quantitative data on this ontogenetic shift is lacking (Ogden & Ehrlich 1977, Weinstein & Heck 1979, Rooker & Dennis 1991). Hence, the linkages of fishes between the mangroves, seagrass beds and the adjacent coral reef remain largely unknown (Ogden & Gladfelter 1983, Birkeland 1985).

Some qualitative descriptions on 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, quantitative size-frequency data have been provided on these ontogenetic shifts for selected Caribbean reef fish species (Nagelkerken et al. 2000c), using a single methodology. Studies were also done to investigate the linkages of fish faunas among six different shallow-water bay biotopes and the adjacent coral reef (Nagelkerken et al. 2000a, b). From these studies it has been established that at least 17 different reef fishes species utilise mangroves, seagrass beds, and other shallow-water bay biotopes as nurseries during the juvenile part of their life cycle.

Although more knowledge has recently been gained on the interlinkages of fish faunas between mangroves, seagrass beds and the adjacent coral reef, the question remains whether mangroves and seagrass beds are obligate or facultative nurseries for juvenile reef fishes. Do reef fishes utilise bays or lagoons containing mangroves and seagrass beds as nurseries just because of the abundance of food and the reduced predation pressure, or do they also depend on the shelter or other advantages provided specifically by mangroves and seagrass beds? 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 biotopes are diminishing fast, world-wide (Spalding 1998).

An indirect method to test the dependence of juvenile reef fishes on mangroves and seagrass beds would be to compare different types of bays located in the same geographic area using a single survey methodology. Such a comparison should be focussed on different combinations of bays with absence/presence of mangroves and seagrass beds (Parrish 1989). Hardly any studies exist in the Caribbean, however, which have studied the fish community of mangroves and seagrass beds in more than one bay or lagoon of a single island/country. Comparison between different studies is difficult as a result of differences in fishing technique, 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 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 lacking mangroves and seagrass beds were compared for one island, with the same survey methodology, and carried out within a time span of three months. The objective of this study was to establish the degree of dependence of fishes on mangroves and seagrass beds.

MATERIALS AND METHODS

Sampling design. The fish community of seagrass beds and mud flats of 11 inland bays was sampled during daytime on the island of Curaçao, Netherlands Antilles (Fig. 1). The seagrass beds and mud flats of the different bays were assigned to one of four different biotope 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, biotope 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 consist of monospecific stands of turtle grass *Thalassia testudinum*, except in Piscadera Bay where they consist of manatee grass *Syringodium filiforme*. Mean

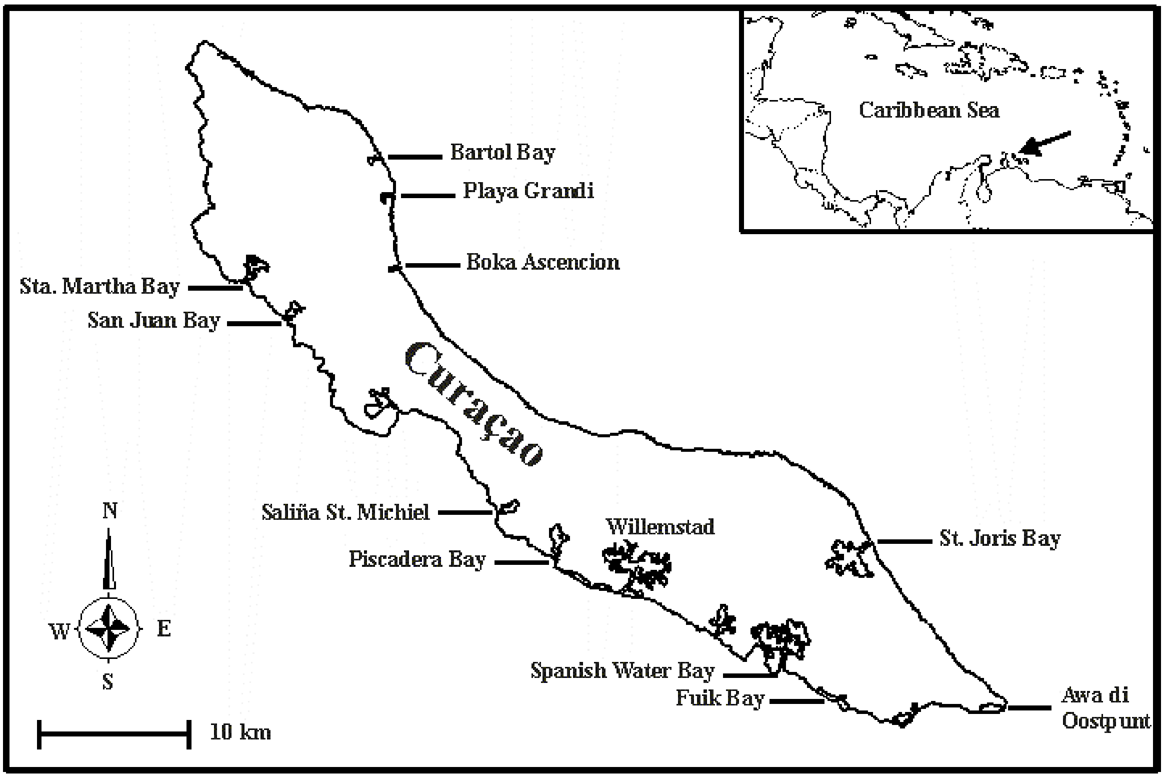

Fig. 1. Map of Curaçao showing the different bays

seagrass (*Thalassia*) density ranged from 236 to 690 seagrasses per m^2, seagrass height from 8 to 17 cm, and seagrass cover from 55 to 89% (Table 1). Mud flats had some cover of fleshy algae ranging from 4 to 37%, but showed no presence of seagrass.

The fish community of the different seagrass beds and mud flats was 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 the disadvantage of the beach seine is that it may ride up over dense seagrass beds (English et al. 1994). The latter was also observed during the present study, and resulted in an underestimation in abundance of some fish species. These species dive in-between the seagrasses when the net approaches and shelter there until the net passes over. On the mud flats this problem does not occur, since the iron chain at the underside of the net ploughs trough the mud, making it difficult for fishes to escape at the underside of the net. To quantify the degree of selection of the beach seine in the seagrass beds, a total of nine visual censuses were done at three seagrass sites in the Spanish Water Bay and compared with nine beach seine hauls at the same sites. Spanish Water Bay was selected as this was 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 mazes 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). An iron chain and lead weights were attached to the underside of the net to keep the net on the bottom along its entire length. 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 depth at which the biotopes were sampled varied between 0.5 and 2.0 m (Table 1), and the sampled surface area measured approximately 150 m^2 per haul. All fishes caught were identified and counted in a bin filled with seawater, and released afterwards. For each seagrass bed and mud flat one to six sites were sampled (Table 1), depending on the size of the bay (see Fig. 1). Each site in each bay was sampled three different times during September to November 1999, and all sampling was done during daytime

Fish species were divided into three groups (Nagelkerken et al. 2000b): 1) nursery species (= reef fishes 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 occurring in low abundances on the coral reef), and 3) reef species (= the remaining reef fishes of which all life stages are normally found on the coral 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*, macro-algae, and mud, and density and height of seagrass were measured once at each site, in six randomly selected quadrats of 50 x 50 cm. Seagrass density is expressed as the number of seagrasses per m^2. Density of *Syringodium* 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 of the different study sites were averaged per bay for the different seagrass beds and mud flats. Fish data of the four different biotope types were then compared with a nested Anova on log or square root transformed data (Sokal & Rohlf 1995), with the three temporal census replicates nested under the different seagrass beds and mud flats. The same procedure was followed for comparison of the environmental variables. Fish data were compared among the four biotope 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 for difference in fish density between visuals censuses and beach seine hauls. Small species of the pelagic water column forming large schools (Atherinidae, Clupeidae, Engraulidae) were excluded from all analyses.

Principal Component Analysis (PCA) was carried out on log-transformed fish abundances of the different seagrass beds and mud flats, using the ordination programme Canoco 4.0 (ter Braak & Smilauer 1998). Scaling was focussed on inter-sample distances (similarity in fish community structure among the different seagrass beds and mud flats) and on inter-species correlations (correlations between species on basis of their abundance in the different seagrass beds and mud flats), species scores were divided by the standard deviation, and the data were centred by species.

RESULTS

The four biotope types did not differ significantly in salinity and water temperature (Table 1). Only Saliña St. Michiel had a significantly higher salinity than the other seagrass beds and mud flats ($p < 0.001$, 1-way Anova). Water clarity was higher on the seagrass beds than on the mud flats ($p < 0.001$, nested Anova), and higher on the mud flats (+m+s) than on the mud flats (-) ($p < 0.005$).

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

Table 1. Sampling regime, environmental variables and biotope characteristics of the seagrass beds and mud flats of the four biotope types

	No. of sites sampled	Mangroves present	Seagrass present	Maximum sampling depth (m)	Salinity (‰)	Temperature (^{0}C)	Water clarity (m)	Seagrass 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 Ascencion	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. Saliña 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

The four biotope types showed a clear difference in fish community structure as revealed by PCA (Fig. 2a). The mud flats (+m+s) of Playa Grandi, however, showed some similarity to the seagrass beds (+m). The fish community structure of the *Syringodium filiforme* beds in

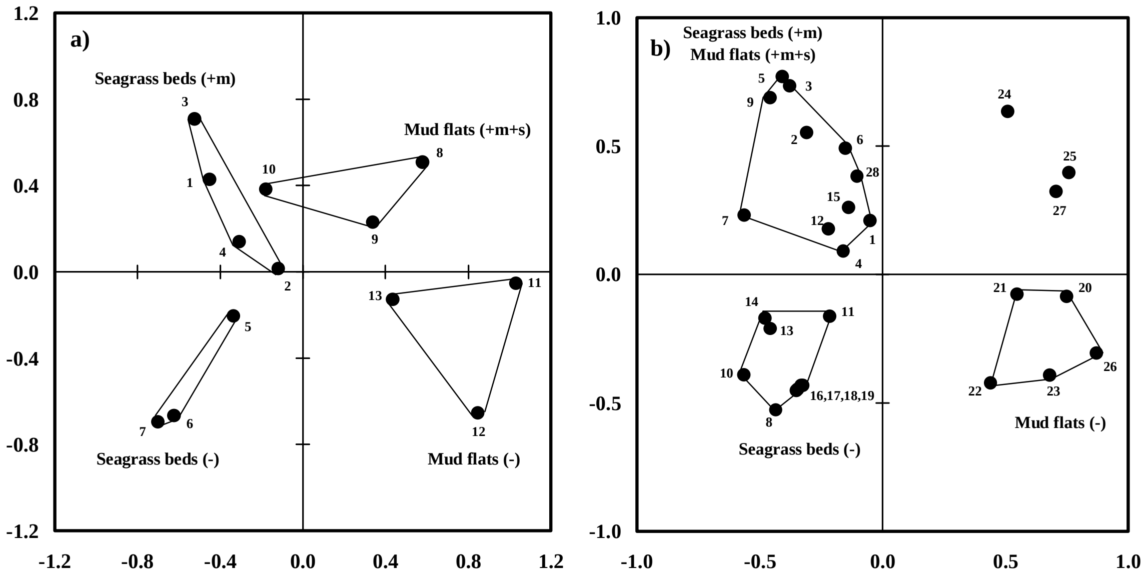

Fig. 2. Principal Component Analysis (PCA) of fish abundance for (a) the different seagrass bed and mud flat sites of the four biotope types, and for (b) the different fish species. The horizontal axes represent the first PCA axis, the vertical axes represent the second PCA axis. The first two axes accounted for 50.9% of the total variance. Site and species clusters are encircled by solid lines and are based on the similarity in fish community structure 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 per haul). Numbers refer to the different seagrass bed and mud flat sites in Table 1 and to the fish species in Table 2

Piscadera Bay showed a high similarity with that of the *Thalassia testudinum* beds (+m).

The four biotope types also differed 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 biotopes with presence of mangroves ($p < 0.035$, nested Anova), viz. on seagrass beds (+m) and mud flats (+m+s), although the difference was not significant between seagrass beds (+m) and seagrass bed (-). Nursery species showed a significantly lower abundance ($p < 0.001$) on mud flats (-) than in the three other biotopes with presence of either seagrass beds or mangroves. Species richness of nursery species was highest in the two biotopes 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 most abundant on the seagrass beds (-) ($p < 0.045$).

PCA of the different fish species showed three different species clusters (Fig. 2b). These clusters partly corresponded to the four distinguished biotope 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 showed a wide biotope utilisation and were therefore separated from the clusters.

With the exception of one species (*Lutjanus analis*), all fish species found in the four biotope types can be divided into two groups: (1) species associated with mangroves and/or seagrass beds, and (2) species associated with mud flats. These two groups can be divided into

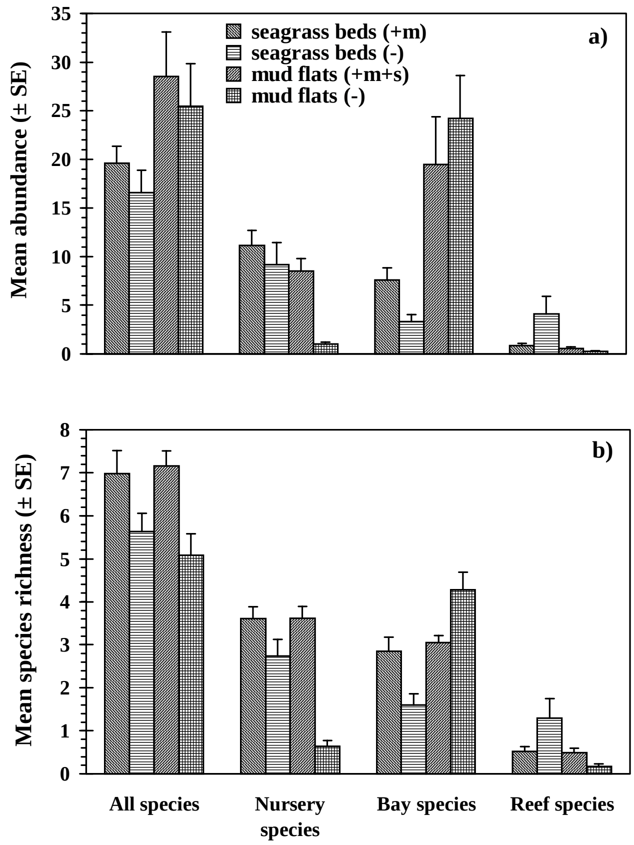

Fig. 3. (a) Mean abundance and (b) mean species richness for all, nursery, bay, and reef species in the four different biotope types

five different categories (Table 2). The first category is characterised by fish species which are most abundant on the seagrass beds (+m), and show significantly lowered abundances or complete absence at the seagrass beds (-) and 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 abundances in the beach seine catches (Table 2). Three nursery species show significantly higher abundances on the mud flats (+m+s) than on the mud flats (-).

The second category is characterised by fish species which are significantly more abundant in any of the three biotopes with presence of mangroves or seagrass beds, but show highly lowered abundances or complete absence on the mud flats (-), which lack these nursery biotopes. 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 abundances of *Lutjanus griseus* were 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 which are only found on the seagrass beds (-). However, they were present in only one bay (Boka Ascencion), and only at one site or during one sampling date. Hence, this species category does not represent a species group which depends on seagrass beds.

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

The fifth category consists of bay species which occur on mud flats as well as seagrass beds, but which show highest abundances on one or both types of mud flats.

The exception to the two groups was formed by *Lutjanus analis* (category six). This species showed high densities on mud flats in the vicinity of mangroves and seagrass beds, but low densities on mud flats (-). This category is thus characterised by fishes associated with mud flats located near mangroves/seagrass beds.

DISCUSSION

The present study shows that the presence of mangroves and/or seagrass beds in bays has a significant effect on the fish community. Several 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 flats than on the seagrass beds. However, this is caused by high abundances of only bay species (especially mojarras) associated with mud flats, which are independent of mangroves and seagrass beds as nurseries. For the nursery species, comparable to other studies, fish abundance and species richness were much higher on both types of seagrass beds than on the mud flats (-), suggesting an obligate dependence on these nursery biotopes 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 just stay on the seagrass beds or in the mangroves, but roam around in the bay and also enter the adjacent mud flats. This is supported by the single PCA species cluster for (mainly nursery) species utilising seagrass beds (+m) as well as mud flats (+m+s). The data thus suggest that adjacent mangroves and seagrass beds enhance densities and species richness of nursery species on bare mud flats.

A similar pattern was observed for bare seagrass beds. Species richness of nursery species was significantly higher on the seagrass beds (+m) than on the bare 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 biotopes (Nagelkerken et al. 2000b, c). Presence of both of these biotopes diversifies the available habitat in bays, making them suitable for a wider range of species. It should be noted that the interaction between mangroves and seagrass beds is probably mutual, also with seagrass beds 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 biotope utilisation could be distinguished, of which one was uncertain, two were associated with mangroves/seagrass beds, two associated with mud flats, and one associated only with mud flats located near mangroves and seagrass beds. The first category represents species which are associated with mangroves and seagrass beds. In this category, all four nursery species, *Chaetodon capistratus*, *Haemulon flavolineatum*, *Ocyurus chrysurus*, and *Scarus iserti*, showed significantly lower abundances to complete absence on seagrass beds (-) and on mud flats (-) than on seagrass beds (+m), suggesting an obligate dependence on mangroves and seagrass beds as nursery biotopes. Two bay species also belong to this category. The bay species *Hyporhamphus unifasciatus* was doubtfully categorised in this category, since this is not a nursery species. Its high abundance is caused by a high number of fishes caught in just one bay at just one site.

In the second category, the nursery species *Haemulon parrai*, *H. sciurus*, *Lutjanus apodus*, *L. griseus*, *L. mahogoni*, *Sparisoma chrysopterum*, and *Sphyraena barracuda* did not show significantly higher abundances on seagrass beds (+m) than on seagrass beds (-), but did show a strong reduction in abundance or complete absence on mud flats (-). This suggests an obligate 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 utilisation of the mangroves by these species is facultative. The association of *Diodon holocanthus* (bay species) and *Mulloidichthys martinicus* (reef species) with the seagrass beds is likely 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. The bay species *Gerres cinereus* is partly a nursery species since some of its juveniles use mangroves as a nursery biotope, 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, which suggest that *G. cinereus* uses the mangroves as a facultative nursery habitat.

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

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 biotopes inside or outside of the bays can be used as alternative nurseries by these species. The shallow coral reef is used by some species as a nursery biotope (Nagelkerken et al. 2000c), which implicates that the dependence of these species on mangroves and seagrass beds may not be as obligate as suggested in the present study. This is the case for the nursery species *Chaetodon capistratus*, *Haemulon flavolineatum* and *Lutjanus mahogoni*. On Caribbean islands lacking bays with mangroves/seagrass beds, these species use alternative nursery biotopes (Nagelkerken et al. submitted). For all other nursery species of the present study, however, the densities on these islands are highly lowered or close to zero, supporting the obligate dependence of these fishes on mangroves and/or seagrass beds. An exception is *Gerres cinereus* which did not show an obligate dependence on mangroves/seagrass beds (this study), but was absent from islands lacking bays with mangroves and seagrass beds (Nagelkerken et al. submitted). This suggests that *G. cinereus* just depends on the presence of shallow coastal areas as nurseries, such as inland bays, and only make facultative use of mangroves and/or seagrass beds. It yet remains to be established, however, if other types of bay biotopes which provide sufficient shelter (e.g. patch reefs) can take over the nursery function of mangroves/seagrass beds. Since most inland bays of Curaçao do not contain large areas of other types of bay biotopes, it appears that for at least this island mangroves and seagrass beds are obligate 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 the visual censuses. Nevertheless, abundances in the seagrass beds were sufficiently high for a statistical difference with the mud flats (-). Only for *Scarus iserti* and *Lutjanus griseus* the higher abundance on the seagrass beds was insignificant, most likely as a result of the underestimation of their abundance with the beach seine. Further, small juveniles were not caught as a result of the mesh size of 1 cm, and the results with respect to the dependence of nursery species on mangroves and seagrass beds are based on medium-sized 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 larger juveniles (i.e. those actually using the nursery biotopes 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.

In conclusion, for species designated as nursery species, mangroves and seagrass beds are obligate nursery biotopes for *Ocyurus chrysurus* and *Scarus iserti*, seagrass beds are obligate nurseries for *Haemulon parrai*, *H. sciurus*, *Lutjanus apodus*, *L. griseus*, *Sparisoma chrysopterum* and *Sphyraena barracuda*, mud flats near mangroves/seagrass beds are obligate biotopes for *L. analis*, and mangroves/seagrass beds are facultative nurseries for *Chaetodon capistratus*, *Gerres cinereus*, *H. flavolineatum*, and *L. mahogoni*.

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