

The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries

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Abstract

Visual census surveys were used to study the distribution of coral reef fishes that are associated with seagrass beds and mangroves in their juvenile phase, on various coral reef sites along the coast of the Caribbean island of Curaçao (Netherlands Antilles). The hypothesis tested was that various reef fish species occur in higher densities on coral reefs adjacent to nursery habitats than on reefs located at some distance to these habitats. Of 17 coral reef fish species that are known to use bays with seagrass beds and mangroves as nurseries (nursery species), 15 were observed in quadrats on the reef. Four nursery species, *Haemulon sciurus*, *Lutjanus apodus*, *Ocyurus chrysurus* and *Scarus coeruleus* occurred in significantly higher densities on coral reefs adjacent to bays with seagrass beds and mangroves. *Lutjanus analis*, *Lutjanus mahogoni* and *Sphyraena barracuda* also had their highest densities on reefs adjacent to these bays, although differences between the distinguished reef categories were not always significant. It is suggested that these seven species are highly dependent on the presence of bays with seagrass beds and mangroves as nurseries on an island scale. Eight other species that are known to use seagrass beds and mangroves as nurseries did not have their highest densities on reefs adjacent to bays with seagrass beds and mangroves. For six of these species, juveniles were also observed on the reef. It is suggested that these species are able to use the reef as an alternative nursery and do not depend strictly on the presence of bays with seagrass beds and mangroves as nurseries.

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1. Introduction

In various parts of the world, shallow coastal areas containing mangroves and seagrass beds are considered important nurseries for juvenile fish (Pollard, 1984; Parrish, 1989; Baelde, 1990; Robertson and Blaber, 1992). Pelagic fish larvae settle into these habitats, and grow from juveniles to subadults or adults that leave these habitats by means of post-settlement migrations (Jones, 1991; Blaber, 2000). In the Caribbean, shallow waters with mangroves and seagrass beds are characterised by the presence of high densities of juveniles of several coral reef species that are assumed to migrate to the coral reef on reaching the (sub)adult stage (Austin, 1971; Louis and Guyard, 1982; Nagelkerken et al.,

2000a; Cocheret de la Morinière et al., 2002; Adams and Ebersole, 2002; Nagelkerken and van der Velde, 2002). On the island of Curaçao (Netherlands Antilles), Nagelkerken et al. (2000b) showed that an inland marine bay with seagrass beds and mangroves served as a nursery habitat for at least 17 coral reef species (indicated below as nursery species). It has been shown on various islands that a reduced density of several of these nursery species on the coral reef is related to the absence of seagrass beds and mangroves (Nagelkerken et al., 2002). This suggests that these nursery species depend on the presence of seagrass beds and mangroves as a nursery habitat. If this is the case, coral reefs adjacent to mangrove and seagrass nursery areas might be expected to harbour higher densities of adults of these nursery species than reefs located at greater distance to these nursery areas, assuming that adult migration along the coast between reefs is limited.

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The island of Curaçao provides an opportunity to test this hypothesis along the coast of a single island. The occurrence of both seagrass beds and mangroves is restricted to several shallow inland marine bays situated at the southwestern part of the island, allowing a clear distinction to be made between reefs adjacent to bays with seagrass beds and mangroves, reefs adjacent to bays without seagrass beds and mangroves, and reefs located at some distance from bays. In a pilot study, Nagelkerken et al. (2000b) already observed reduced densities of six nursery species on the reef at an increasing distance from a single bay with nursery habitats. However, their study focused on only a few species and a small part of the reef, and did not consider the possible relation with fish size.

While subadult or adult bay-to-reef migrations are likely to supply coral reefs adjacent to bays with nursery species, reefs at some distance from these habitats can be colonised either by fish dispersal on reefs along the coast or by small populations of juvenile fish larvae that settle and survive on these reefs. Several studies (Tulevech and Recksiek, 1994; Macpherson, 1998; Zeller, 1998) suggest that it is predominantly the larger individuals that undertake migrations along the reef over larger distances. Whereas the population of nursery species on coral reefs adjacent to bays with seagrass beds and mangroves is represented by older juveniles, subadults and adults (Nagelkerken et al., 2000b; Cocheret de la Morinière et al., 2002; Nagelkerken and van der Velde, 2002), it might be expected that the population of nursery species on coral reefs at great distances to bays with seagrass beds and mangroves would consist predominantly of adults.

The present study tested the hypothesis that juveniles and adults of nursery species occur in higher densities on coral reefs adjacent to nursery habitats than on reefs located at some distance to these habitats. In accordance with this, reduced densities of adults and the absence of juveniles on coral reefs away from these bays, are expected. The degree to which nursery species might utilise the coral reef as an alternative juvenile habitat instead of seagrass and mangrove habitats was also investigated.

2. Materials and methods

2.1. Study area

The present study was carried out on the coral reef at the leeward southwestern coast of the Caribbean island of Curaçao, Netherlands Antilles (Fig. 1). The coast on this side of the island is characterised by the presence of a continuous fringing coral reef that consists of a small surf zone and a reef flat that gradually slopes down to a 'drop-off' at 7–12 m (Bak, 1975). At the drop-off, the reef slopes off steeply and ends in a sandy plain at depths

of 80–90 m. The southwestern coast features eight large inland bays (Fig. 1), which are dominated by mangroves, seagrass beds and a muddy/sandy seabed (Table 1). Rocky substratum, in the form of boulders and erosional notches, is present to some degree only in Spanish Water Bay. Notches are formed at and under the water line through biochemical solution of the fossil reef terrace along the shoreline (de Buissonjé and Zonneveld, 1960). Fringing mangroves grow in stands along the sandy shoreline of the bays and consist of *Rhizophora mangle* (see Nagelkerken et al., 2000b and Nagelkerken et al., 2001 for a detailed description of these habitats). Seagrass beds in Spanish Water Bay and Fuik Bay consist of *Thalassia testudinum* whereas those in Piscadera Bay consist of *Syringodium filiforme*. All bays have a narrow entrance from the open sea. The water of Zakito Bay is polluted with heavy metals from a desalination plant and has an elevated temperature and salinity (Nagelkerken, unpubl. data). The average daily tidal range in Curaçao is about 30 cm (de Haan and Zaneveld, 1959), and the bays are not subject to strong tidal currents.

2.2. Study design

The distribution of the 17 nursery species (listed in Table 2) was studied at 11 coral reef sites in a gradient along the southwestern coast at varying distances from two types of bays. The 11 reef sites were subdivided into four 'reef categories' (Fig. 1): (1) three coral reef sites adjacent to bays featuring major seagrass beds and mangrove habitats, indicated below as sg–mg bays (distance to the bay <1 km); (2) three coral reef sites adjacent to bays dominated by bare sediment without marine vegetation (distance to the bay <1 km), but situated at some distance to sg–mg bays, indicated below as mud/sand bays (distance to nearest sg–mg bay between 3.2 and 25.6 km); (3) two coral reef sites situated between sg–mg bays (distance to nearest sg–mg bay between 3.1 and 3.5 km, and to nearest mud/sand bay between 8.0 and 15.5 km); and (4) three coral reef sites located at greater distance to sg–mg bays (distance to nearest sg–mg bay between 11.6 and 38.5 km, and to nearest mud/sand bay between 4.7 and 13.4 km). The reef at Holiday Beach was located close to a bay (St. Anna Bay), but was nevertheless defined as a reef situated between sg–mg bays (Fig. 1). Due to industrial activities in St. Anna Bay (involving the presence of a large harbour, oil refinery and shipyards), all natural marine vegetation and muddy/sandy habitats have been destroyed, and the water is highly polluted (van den Hoek et al., 1972). Therefore, the ecological function of this bay cannot be considered typical for a mud/sand bay, and the reef close to this bay cannot be considered typical for a reef adjacent to an unpolluted mud/sand bay.

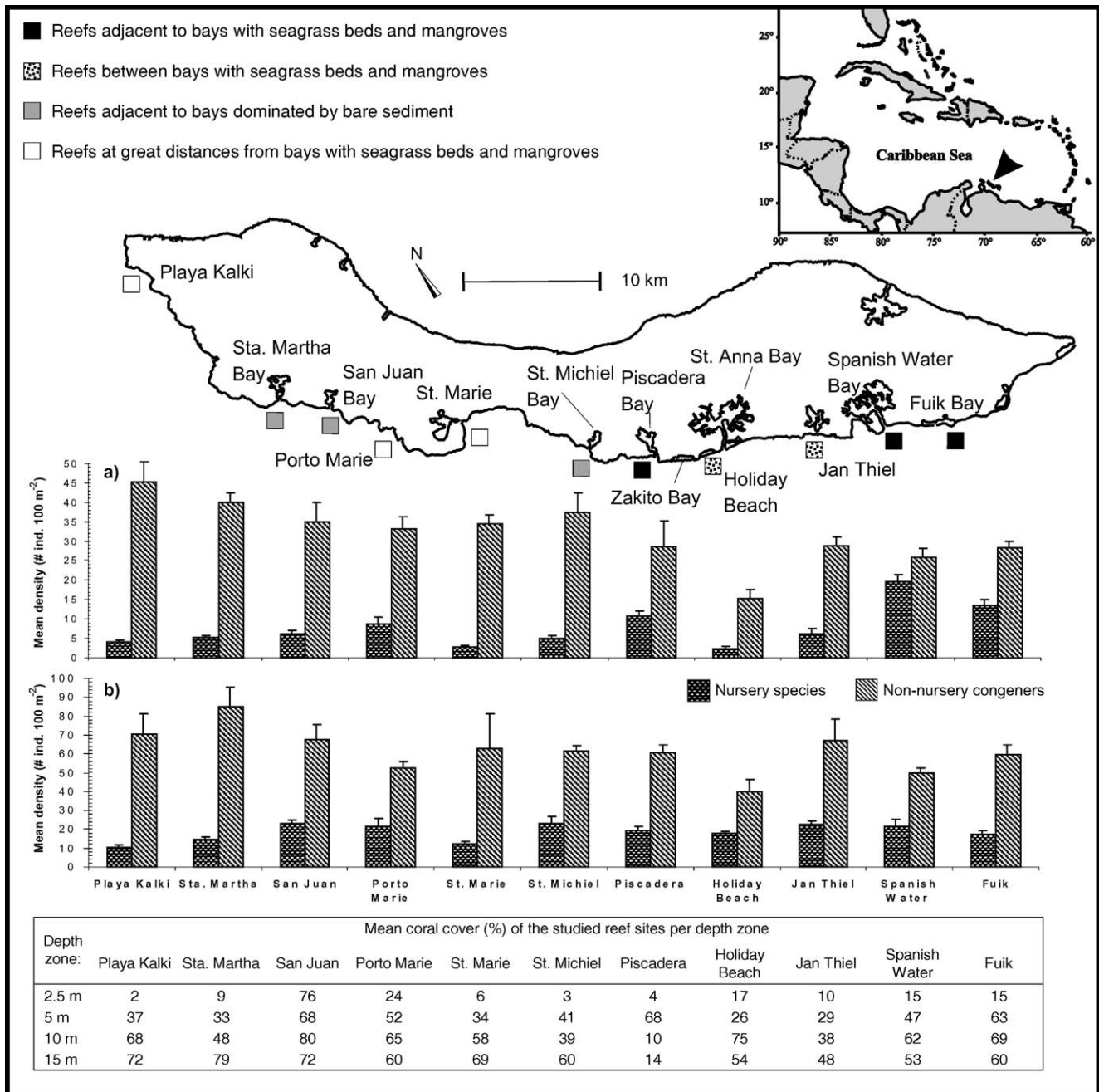


Fig. 1. Locations of the eight largest bays and 11 reef sites sampled on the island of Curaçao (latitude 12° N, longitude 68° W). The density pattern of nursery species and their non-nursery congeners along the gradient of reef sites is shown below the map of Curaçao. Separate patterns are shown (a) for pooled densities of the seven nursery species that had their highest densities at reef sites adjacent to bays with seagrass beds and mangroves (see Table 1) and their congeners, and (b) for pooled densities of the eight nursery species that did not have higher densities at reef sites adjacent to bays with seagrass beds and mangroves (see Table 1) and their congeners. Error bars indicate SEM. The table shows the mean coral cover (%) of each depth zone.

Besides the 17 nursery species, the densities of nine common non-nursery congeners of the nursery species were also determined on the reef sites: *Acanthurus bahianus*, *Acanthurus coeruleus*, *Chaetodon striatus*, *Haemulon carbonarium*, *Haemulon chrysargyreum*, *Scarus taeniopterus*, *Scarus vetula*, *Sparisoma aurofrenatum* and *Sparisoma viride*. Based on Nagelkerken et al.

(2000b) it is assumed that juveniles of these congeners do not use seagrass and mangrove habitats as a nursery.

Data on the reef fish community structure were collected by visual census in quadrats using SCUBA and a stationary point-count method (Polunin and Roberts, 1993) by two independent observers. Square quadrats of 10 × 10 m were surveyed at four depth zones: shallow

Table 1
Main shallow-water habitats of the eight largest bays along the southwestern coastline of Curaçao, and the abundance of nursery species

	Total bay area (m ²)	Bay area covered by seagrass beds (%)	Bay area consisting of muddy/sandy seabeds (%)	Length of inundated mangroves along shoreline (m)	Value as nursery	<i>Lutjanus analis</i>	<i>Lutjanus apodus</i>	<i>Lutjanus griseus</i>	<i>Lutjanus mahogoni</i>	<i>Gerres cinereus</i>	<i>Chaetodon capistratus</i>	<i>Haemulon flavolineatum</i>	<i>Haemulon sciurus</i>	<i>Haemulon parra</i>	<i>Ocyurus chrysurus</i>	<i>Scarus iserti</i>	<i>Sparisoma chrysopteron</i>	<i>Sphyræna barracuda</i>
Sta. Martha Bay	569,238	—	100	—	Low	**	*	*	—	***	—	—	—	—	*	—	—	***
San Juan Bay	159,060	—	100	60	Low	*	*	*	—	**	—	—	—	—	—	—	—	—
St. Michiel Bay	193,640	—	100	—	Very low	—	*	—	—	***	—	—	—	—	—	—	—	*
Piscadera Bay	726,168	2	98	3964	High	***	***	***	—	**	*	***	**	—	*	***	***	***
Zakito Bay	140,151	—	100	2267	Very low	—	—	—	—	*	—	—	—	—	—	—	—	—
St. Anna Bay	4,190,000	—	100	—	Very low	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Spanish Water Bay	2,846,511	15	82	8702	High	— ^a	*	*	— ^a	*	***	***	***	— ^a	***	— ^a	— ^a	***
Fuik Bay	687,556	3	97	3200	High	*	*	—	***	*	**	*	*	—	*	*	*	*

The presence of 13 nursery species is based on Nagelkerken et al. (2001) and unpublished data (Nagelkerken) for which the bays were sampled using a beach seine net. Based on estimated total standing stocks of juveniles on seagrass beds and muddy/sandy seabeds, presence of species is expressed as absent (—), low (*), high (**) or very high (***). Classes are distinguished per species by dividing the highest total standing stock by three. Based on mean abundance and mean species richness of nursery species in the main nursery habitats of the bays, Nagelkerken (unpubl. data) classified the nursery function of the bays as high, low or very low. No data are available for St. Anna Bay, but its nursery function is assumed to be very low (see text). nd, no data.

^a Presence in seagrass/mangrove habitats demonstrated by means of visual census (Nagelkerken et al., 2000b).

Table 2

Size classes (cm) used to define juveniles for each nursery species, based upon half the length of the smallest maturation sizes obtained from FishBase World Wide Web (Froese and Pauly, 2002) and Munro (1983) (for *Lutjanus analis*, the maturation size of *Ocyurus chrysurus* was used to distinguish the juveniles (see text))

Species	Juveniles	Species	Juveniles
<i>Acanthurus chirurgus</i>	0–10	<i>Lutjanus griseus</i>	0–10
<i>Chaetodon capistratus</i>	0–5	<i>Lutjanus mahogoni</i>	0–12.5
<i>Gerres cinereus</i>	0–10	<i>Ocyurus chrysurus</i>	0–12.5
<i>Haemulon flavolineatum</i>	0–5	<i>Scarus coeruleus</i>	0–15
<i>Haemulon parra</i>	0–12.5	<i>Scarus guacamaia</i>	no data
<i>Haemulon plumieri</i>	0–10	<i>Scarus iserti</i>	0–10
<i>Haemulon sciurus</i>	0–10	<i>Sparisoma chrysotermum</i>	0–12.5
<i>Lutjanus analis</i>	0–12.5	<i>Sphyraena barracuda</i>	0–30
<i>Lutjanus apodus</i>	0–12.5		

reef flat (2.5 m), reef flat (5 m), drop-off (10 m) and reef slope (15 m). A single 10 m line was used as a reference for the size of a complete quadrat. At each site, ten quadrats (placed in a direction parallel to the coastline) per depth zone were surveyed, to a total of 40 quadrats per site. These 40 quadrats were surveyed during three visual census rounds: 16 quadrats at each site in December 1999, 16 quadrats in January 2000 and 8 quadrats in February 2000. After placing the quadrat line, the observer waited for 5 min to minimise fish disturbance. All nursery species within or passing through the quadrat were then counted over a period of 10 min. During fish counting the observer was at the edge of the quadrat for 8 min. After 8 min, the observer moved through the quadrats to search for and/or estimate sizes of possible small juvenile fish hiding behind or between coral boulders. Care was taken to ensure that fishes that regularly moved in and out of the quadrat were not counted twice. Fishes were classified into size classes of 2.5 cm. Each reef site was visited by the two observers simultaneously and each observer collected a total number of 20 quadrats. The location on the reef, within a reef site, where an observer would place the quadrats was randomly allocated to each of the observers during each census round, making sure not to recount the same area of reef. Species identification and quantification were first thoroughly and simultaneously practised by the two observers. Estimation of size classes was trained by repeatedly estimating the sizes of 40 pieces of electrical wires of known length (range 2.5–50 cm, in classes of 2.5 cm) under water. Training was continued until differences in size-estimation were minimal (maximum difference of one size class of 2.5 cm for wire sizes <15 cm and two size classes for sizes >15 cm) between the two observers. Training in fish species identification was continued until it was the same between the observers. The training procedure started two weeks before the census and was repeated before each census round (three census rounds over a period of three months).

For each species, data were also analysed separately for juveniles, based upon their maturation size (Table 2). Maturation sizes were obtained from FishBase World Wide Web (Froese and Pauly, 2002) and Munro (1983). If this database gave maturation size as a range, the smallest observed maturation size was used. Juveniles were defined as individuals smaller than half the maturation size (i.e., maturation size divided by two) to be able to distinguish them from larger subadults. Maturation size for *Lutjanus analis* was 37.5 cm, which is much larger than that of the other Lutjanidae studied (i.e., 17.5–22.5 cm). This value was based on only one study (quoted in FishBase World Wide Web), and may therefore not be very reliable. The same maturation size for *L. analis* as for *Ocyurus chrysurus* was therefore used. This was based on the fact that *O. chrysurus* and *L. analis* have almost the same maximum length, and because for *O. chrysurus* a large number of studies have determined the maturation size (quoted in FishBase World Wide Web).

Since fish densities are often correlated to the degree of coral cover (Luckhurst and Luckhurst, 1978; Hixon and Beets, 1993; Grigg, 1994) the total hard coral cover (both living and dead corals) at each site for each depth zone was visually quantified. To estimate coral cover of the quadrat, the 10 × 10 m quadrat was divided into four quarters of 5 × 5 m. For each quarter, coral cover was estimated separately and was averaged for the whole quadrat afterwards. The 10 m quadrat line was marked with a red label in the middle to visually estimate the size of each quarter. Because the number of quadrats for which the cover was estimated was not constant for each site (between 6 and 10 estimations per depth zone per site), cover was averaged for quadrats and expressed as mean hard coral cover per depth zone per site.

2.3. Statistical analysis

Principal Component Analysis (PCA) was used to study the spatial distribution pattern of nursery species along the gradient of reef sites. PCA was carried out on log¹⁰-transformed mean fish densities (with all size classes pooled) per reef site, using the Canoco 4.0 ordination program (ter Braak and Smilauer, 1998). Default options were used for the analysis: scaling was focused on inter-species correlations (to focus more on the relationships between species), species scores were divided by the standard deviation (to reduce the influence of species with a large variance in density), and the data were centred by species (used for ordinary PCA, where each species is weighted by its variance).

To test the influence of coral cover on fish density, separate linear regressions were run for each species at each depth zone. Since *Haemulon parra* occurred only at one reef site, no regression analysis could be performed

for this species. For each species, mean fish density (with all size classes pooled) at each site ($N = 11$) was used as the dependent variable and mean hard coral cover was used as the regression. Regression analyses were performed using SPSS version 11.5.

The influence of the presence of a bay nursery habitat on the occurrence of nursery species on the reef was tested using generalized linear models. Because the data consisted of counts, a model based on a Poisson distribution was used. For each quadrat, visual census counts of all size classes were pooled. Because the 10 quadrats of a depth zone were laid out in a line parallel to those in other depth zones, counts of quadrats distributed over the four depth zones were pooled to one count. Therefore, data for each site consisted of 10 counts (i.e., each a sum of counts over four depth zones). These fish counts were used as the dependent variable in the model. The factor 'reef category' was used as a fixed factor. Because data were collected during three time periods (visual census rounds), a three-level block was added to the model, each level being one visual census round. The log link function and type 3 analysis were used in the model. Post-hoc comparisons between reef categories were made by calculating differences of least squares means. Statistics were performed using the SAS system for Windows V8.

3. Results

3.1. Total fish density

In the present study, 15 of the 17 known nursery species were observed in the quadrats on the reef. *Haemulon plumieri* and *Scarus guacamaia* were not observed.

Of the 56 linear regressions between fish density and coral cover, only three were significant: *Haemulon sciurus* in the 15 m zone ($P < 0.01$; $R^2 = 0.63$; $Y = 0.91 - 1.20X$), *Scarus coeruleus* in the 5 m zone ($P < 0.01$; $R^2 = 0.65$; $Y = 0.60 + 1.57X$) and *Lutjanus mahogoni* in the 5 m zone ($P < 0.05$; $R^2 = 0.37$; $Y = -2.63 + 11.08X$).

PCA allowed the reef sites to be divided into four clusters (Fig. 2). One cluster was formed by the three reef sites adjacent to sg–mg bays and was characterised by nine nursery species. Compared with the other reef sites, the mean densities of seven of these species were highest on reefs adjacent to sg–mg bays (Table 3). A second cluster was formed by the reefs between sg–mg bays and was characterised by high densities of *Chaetodon capistratus*. A third cluster was formed by two reefs adjacent to mud/sand bays and one reef at great distance from sg–mg bays, and harboured five species. Two reefs located at great distance from sg–mg bays and one reef adjacent to a mud/sand bay formed

a fourth cluster, in which none of the species had their highest densities.

Generalized linear models were significant for 14 species (Table 3). Post-hoc comparisons showed significantly higher counts of *Ocyurus chrysurus*, *Lutjanus apodus*, *Haemulon sciurus* and *Scarus coeruleus* in the category reefs adjacent to sg–mg bays than in the other three categories (Fig. 3a, Table 3). *Ocyurus chrysurus* had decreasing counts on reefs located at increasing distances from sg–mg bays. *Lutjanus mahogoni* and *Lutjanus analis* also had their highest densities in the category reefs adjacent to sg–mg bays (Fig. 3a). For these two species, fish counts in the category reefs adjacent to sg–mg bays differed significantly from those in the categories reefs between sg–mg bays and reefs adjacent to mud/sand bays, but not from reefs at great distance from sg–mg bays. *Sphyraena barracuda* had its highest density in the category reefs adjacent to sg–mg bays, but a significant difference between counts was only found between reefs adjacent to sg–mg bays and reefs at great distance from sg–mg bays.

Of the other eight nursery species, two had their highest density in the category reefs between sg–mg bays (*Chaetodon capistratus* and *Sparisoma chrysopteron*) and two in the category reefs adjacent to mud/sand bays (*Haemulon flavolineatum* and *Scarus iserti*) (Table 3). Three species had their highest densities in the category reefs at great distance from sg–mg bays (*Gerres cinereus*, *Lutjanus griseus*, and *Haemulon parra*). Densities of *Acanthurus chirurgus* were highest on reefs adjacent to sg–mg bays and on reefs adjacent to mud/sand bays.

Pooled densities of the seven nursery species occurring in higher densities on reefs adjacent to sg–mg bays were higher at all reef sites adjacent to sg–mg bays than at other reef sites (Fig. 1a). This pattern was not found for the other eight nursery species observed on the reef (Fig. 1b). Non-nursery congeners of species with higher densities on reefs adjacent to sg–mg bays, had their highest densities on reef sites in the southwestern part of the gradient along the coast of the island, at great distance from bays with sg–mg (Fig. 1a). Non-nursery congeners of species without higher densities on reefs adjacent to sg–mg bays did not show higher densities in any particular part of the gradient of reef sites examined (Fig. 1b).

3.2. Juvenile fish density

For the seven nursery species which had their highest densities (for the entire size range) on reefs adjacent to sg–mg bays, juveniles were also observed on the coral reef (Fig. 3b). An exception was *Lutjanus analis*, for which only adults were observed on the reef. Juveniles of *Haemulon sciurus* were only observed on reefs adjacent to sg–mg bays, and those of *Sphyraena barracuda* only

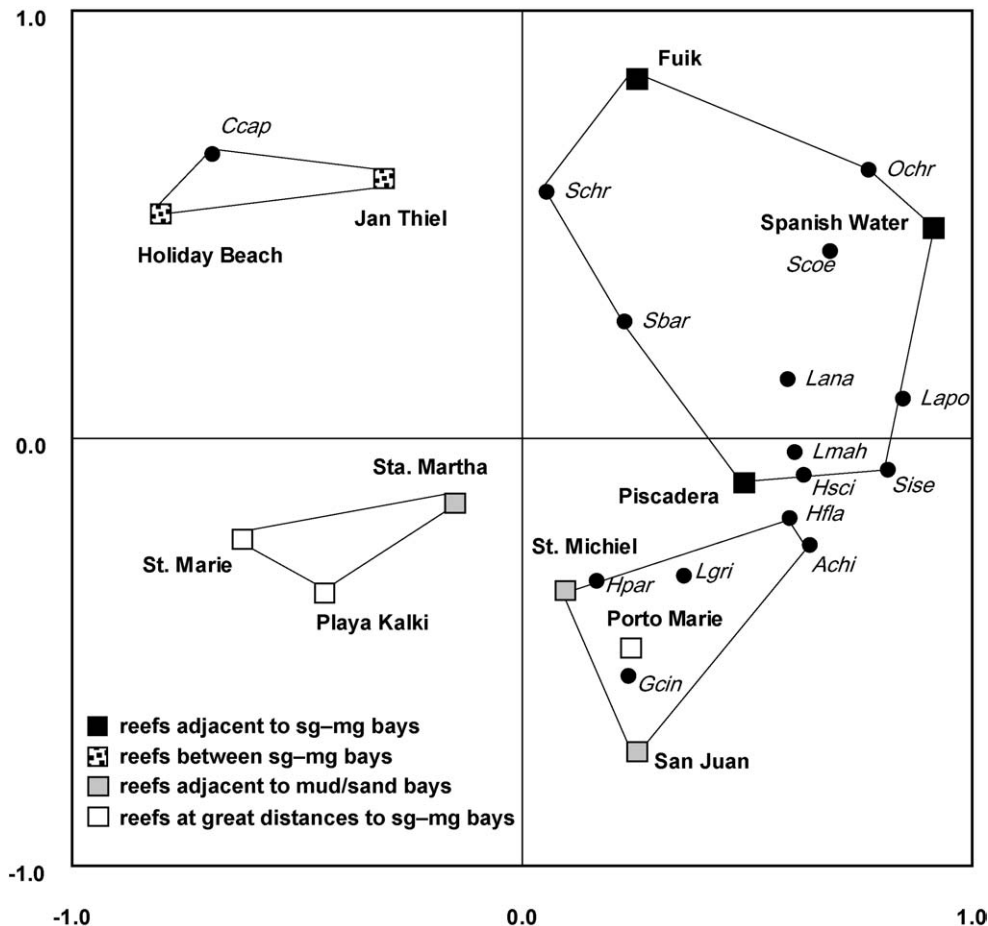


Fig. 2. Principal Component Analysis (PCA) of mean densities of the 15 nursery species at various reef sites. The horizontal axis represents the first PCA axis, the vertical axis the second PCA axis. The first two axes accounted for 67.9% of the total variance. Abbreviations: sg–mg bays: bays with seagrass beds and mangroves; mud/sand bays: bays dominated by muddy/sandy seabeds; Achi: *Acanthurus chirurgus*; Ccap: *Chaetodon capistratus*; Gcin: *Gerres cinereus*; Hfla: *Haemulon flavolineatum*; Hpar: *Haemulon parra*; Hsci: *Haemulon sciurus*; Lana: *Lutjanus analis*; Lapo: *Lutjanus apodus*; Lgri: *Lutjanus griseus*; Lmah: *Lutjanus mahogoni*; Ochr: *Ocyurus chrysurus*; Scoe: *Scarus coeruleus*; Sise: *Scarus iserti*; Schr: *Sparisoma chrysotum*; Sbar: *Sphyrna barracuda*. On the basis of sites and species which showed the highest similarity in composition and density distribution (using PCA), four clusters of sites and species were identified and bordered by lines.

on reefs between sg–mg bays. Despite the presence of juveniles of six of these seven nursery species on the coral reef, densities of their juveniles were much higher in seagrass beds and mangroves than on the reef (Fig. 3b). An exception was *Scarus coeruleus*, for which juvenile densities on the coral reef and those in seagrass beds in Spanish Water Bay were similar.

For the eight nursery species which did not show highest densities (for the entire size range) on reefs adjacent to sg–mg bays, juveniles were also found on the coral reef, except *Lutjanus griseus* and *Haemulon parra* (Fig. 4a). The eight species can be divided into two groups. Densities of juveniles of *Chaetodon capistratus*, *Haemulon flavolineatum*, *Gerres cinereus*, *L. griseus*, and *H. parra* were considerably higher in seagrass beds or mangroves in Spanish Water Bay than on the reef (Fig. 4a) whereas juveniles of *Sparisoma chrysotum*, *Scarus iserti*, and *Acanthurus chirurgus* showed similar

densities in seagrass/mangrove habitats and in reef habitats (Fig. 4b).

4. Discussion

The present study showed significantly higher densities of four nursery species on reefs adjacent to sg–mg bays than in all three other reef categories, whereas three other nursery species showed significantly higher densities at reefs adjacent to sg–mg bays than in two of the three other reef categories. This is probably caused by the very high densities in the bays (summarised in Table 1) of juveniles, which migrate to the adjacent reef when reaching adulthood. This connectivity between nursery habitats in a bay and the reef adjacent to a bay has been indicated before for Spanish Water Bay (Nagelkerken et al., 2000b; Nagelkerken and van der Velde, 2002;

Table 3

Results of the generalized linear models with reef category as fixed factor and survey time as random block

	Model		Block		Mean density per reef category (# ind. 100 m ⁻²)				P-values of post-hoc comparisons					
	χ^2	P	χ^2	P	1	2	3	4	1–2	1–3	1–4	2–3	2–4	3–4
Species with highest density for reef category 1														
<i>Ocyurus chrysurus</i>	654.50	<0.001	0.95	ns	6.2	1.9	1.3	0.5	<0.001	<0.001	<0.001	0.009	<0.001	<0.001
<i>Lutjanus apodus</i>	245.36	<0.001	1.20	ns	4.0	0.7	1.5	1.7	<0.001	<0.001	<0.001	<0.001	<0.001	ns
<i>Haemulon sciurus</i>	54.66	<0.001	9.39	0.009	0.7	0.1	0.4	0.1	<0.001	0.006	<0.001	0.005	ns	0.001
<i>Scarus coeruleus</i>	55.69	<0.001	13.25	0.001	0.4	0.0	0.2	—	0.001	0.026		0.020		
<i>Lutjanus mahogoni</i>	23.13	<0.001	58.76	<0.001	2.3	1.8	1.3	1.9	0.041	<0.001	ns	0.026	ns	0.004
<i>Lutjanus analis</i>	11.87	0.009	5.94	ns	0.2	0.0	0.0	0.1	0.033	0.011	ns	ns	ns	ns
<i>Sphyaena barracuda</i>	10.47	0.015	9.13	0.010	0.2	0.2	0.1	0.1	ns	ns	0.006	ns	0.045	ns
Other species														
<i>Chaetodon capistratus</i>	501.77	<0.001	3.20	ns	1.8	7.3	1.1	2.2	<0.001	<0.001	0.027	<0.001	<0.001	<0.001
<i>Sparisoma chrysotermum</i>	106.78	<0.001	3.36	ns	1.0	1.7	0.9	0.2	<0.001	ns	<0.001	<0.001	<0.001	<0.001
<i>Haemulon flavolineatum</i>	53.40	<0.001	3.08	ns	6.3	4.7	7.6	5.8	<0.001	0.001	ns	<0.001	0.003	<0.001
<i>Scarus iserti</i>	210.51	<0.001	84.45	<0.001	9.3	6.0	9.9	5.0	<0.001	ns	<0.001	<0.001	0.012	<0.001
<i>Gerres cinereus</i>	31.08	<0.001	0.90	ns	0.2	0.2	0.5	0.6	ns	0.006	<0.001	0.002	<0.001	ns
<i>Lutjanus griseus</i>	22.52	<0.001	5.25	ns	0.1	—	0.1	0.2		ns	ns			ns
<i>Haemulon parra</i>	np				—	—	—	0.1						
<i>Acanthurus chirurgus</i>	28.00	<0.001	91.24	<0.001	1.5	0.9	1.5	0.8	0.001	ns	<0.001	0.002	ns	<0.001
<i>Haemulon plumieri</i>	np				—	—	—	—						
<i>Scarus guacamaia</i>	np				—	—	—	—						

P-values of post-hoc comparisons (differences of least mean squares) between the four types of reef categories are shown. Fish counts were converted into mean fish densities per reef category; highest mean density is printed in bold. Abbreviations and symbols: np: not enough counts to perform the test; ns: non-significant ($P > 0.05$); —: not observed; 1: reefs in front of bays with seagrass beds and mangroves; 2: reefs between bays with seagrass beds and mangroves; 3: reefs in front of bays dominated by bare sediment; 4: reefs at great distances from bays with seagrass beds and mangroves.

Cocheret de la Morinière et al., 2002). The present study suggests that all sg–mg bays along the southwestern coast of the island of Curaçao show this type of connectivity for certain coral reef fish species. A direct interlinkage between these habitats by fish life-cycle migration is difficult to show, but studies using otolith microchemistry (Gillanders, 2002; Gillanders and Kingsford, 1996) have confirmed the existence of these life-cycle migrations between juvenile habitats and adult habitats in temperate marine fish species.

Regarding these seven species with the highest densities on reefs adjacent to sg–mg bays, Nagelkerken et al. (2002) found that densities of *Haemulon sciurus*, *Lutjanus apodus* and *Ocyurus chrysurus* were greatly reduced on coral reefs of islands lacking seagrass and mangrove habitats relative to islands where these habitats were present, indicating that these species are highly dependent on these nursery habitats. For *Lutjanus analis*, *Sphyaena barracuda* and *Scarus coeruleus*, Nagelkerken et al. (2002) found a possible dependence on mangrove and/or seagrass nurseries. The present study suggests that the presence of sg–mg bays strongly influences the distribution pattern of these six species on the coral reef along the coast of a single island. Since mud/sand bays that lack seagrass and mangrove habitats have a limited nursery function (Nagelkerken et al., 2001; Table 1), sg–mg bays are likely to function as the main, and for some species the only, source of

new individuals on the reef, resulting in high densities on reefs adjacent to these bays.

An exception was *Lutjanus mahogoni*, for which density differences between reefs adjacent to sg–mg bays and the other types of reef categories were not as large as those for the other six species. A possible explanation may be found in the ability of this species to spend its juvenile phase on the reef. Based on observations of juveniles on the reef in the present study and by Wilson (2001) and Nagelkerken et al. (2000a), “local recruitment” on the reef may be an important source of new individuals. The higher densities on reefs adjacent to sg–mg bays might be a result of an additional input of individuals from these habitats onto the reef. Comparisons of densities of this species between islands with and without seagrass beds and mangroves did not reveal any differences (Nagelkerken et al., 2002) and are consistent with this hypothesis.

If sg–mg bays function as the main source of new individuals on the reef, the presence of these six species on reefs not adjacent to sg–mg bays may partly result from fish dispersal along the coast. This may explain why the three types of reef located at great distance from sg–mg bays showed much lower densities for six of these nursery species. Studies have shown that fishes are able to migrate along reefs over distances ranging from hundreds of metres to several kilometres (Tulevech and Recksiek, 1994; Kanashiro, 1998; Mazeroll and

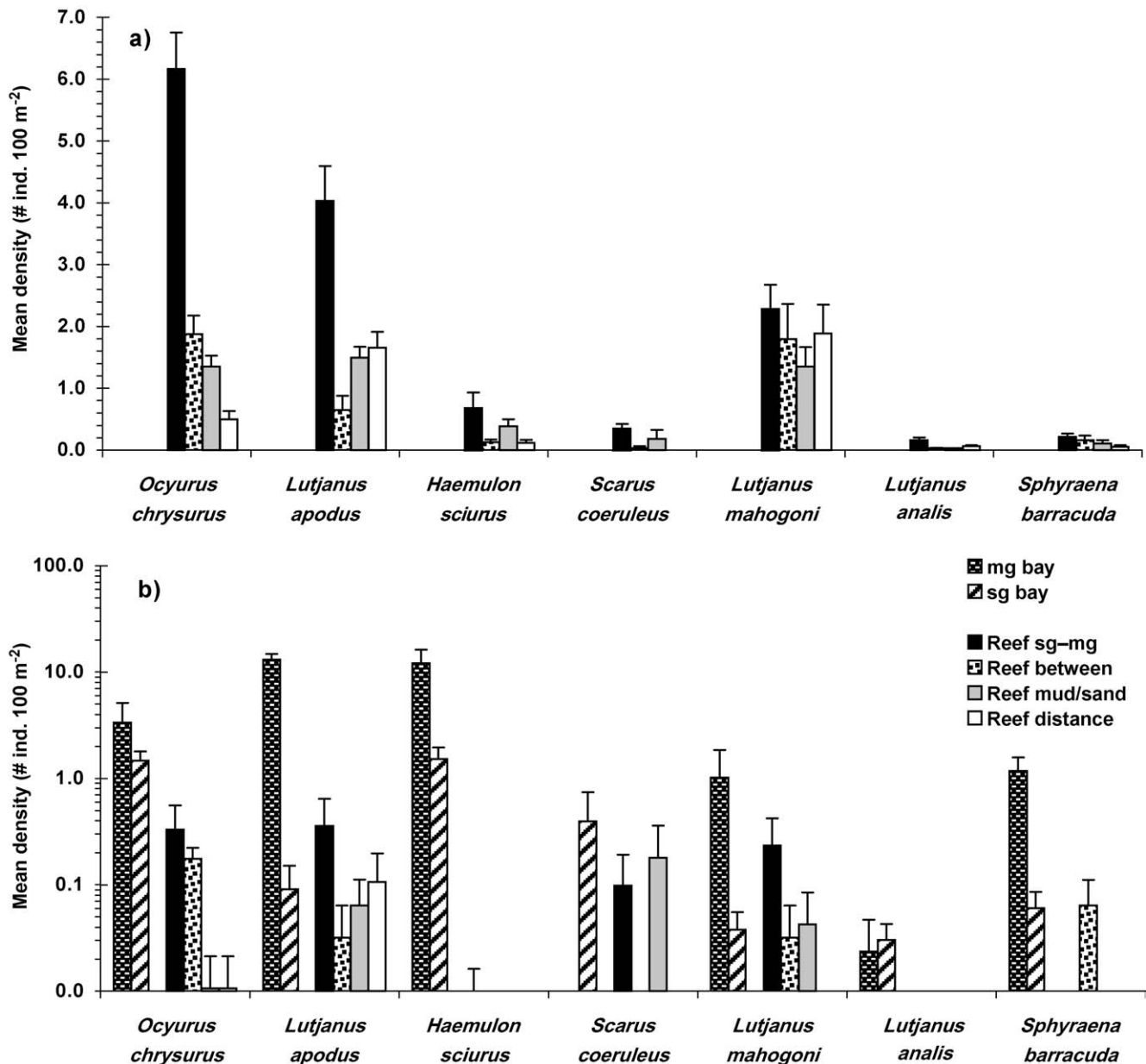


Fig. 3. Mean densities of (a) the entire size range and (b) juveniles of the seven nursery species that had higher densities on reefs adjacent to bays with seagrass beds and mangroves than at other locations (see Table 3). (b) Also shows densities of juveniles in mangroves and seagrass beds in Spanish Water Bay (data recalculated from Nagelkerken and van der Velde, 2002), to allow comparison with densities on the reef. Note that the Y-axis of (b) is on a \log^{10} -scale. Error bars indicate SEM. mg bay: mangrove habitat in Spanish Water Bay; sg bay: seagrass habitat in Spanish Water Bay; Reef sg-mg: reefs adjacent to bays with seagrass beds and mangroves; Reef between: reefs between bays with seagrass beds and mangroves; Reef mud/sand: reefs adjacent to bays dominated by bare sediment; Reef distance: reefs at great distances to bays with seagrass beds and mangroves.

Montgomery, 1998; Zeller, 1998; Chapman and Kramer, 2000). Long-distance dispersal of *Haemulon sciurus*, *Lutjanus analis*, *Lutjanus apodus*, *Ocyurus chrysurus*, and *Sphyraena barracuda* may have contributed to the presence of small fish populations on reefs located at some distance from their main nursery habitats.

The presence of adults of species that had their highest densities on reefs adjacent to sg-mg bays in the other reef categories may also be explained by the survival of juveniles that have settled and grown up directly on these

reefs, rather than in seagrass or mangrove habitats. Although it has been shown, for example, that predation pressure results in low survival of Haemulidae on reefs (Beets, 1997), some individuals may survive and contribute to small populations on reefs at some distance from seagrass and mangrove habitats (Shulman and Ogden, 1987). In the specific case of *Scarus coeruleus*, which showed its highest densities on reefs adjacent to sg-mg bays, local recruitment can play a major role because juvenile densities on the reef were comparable to

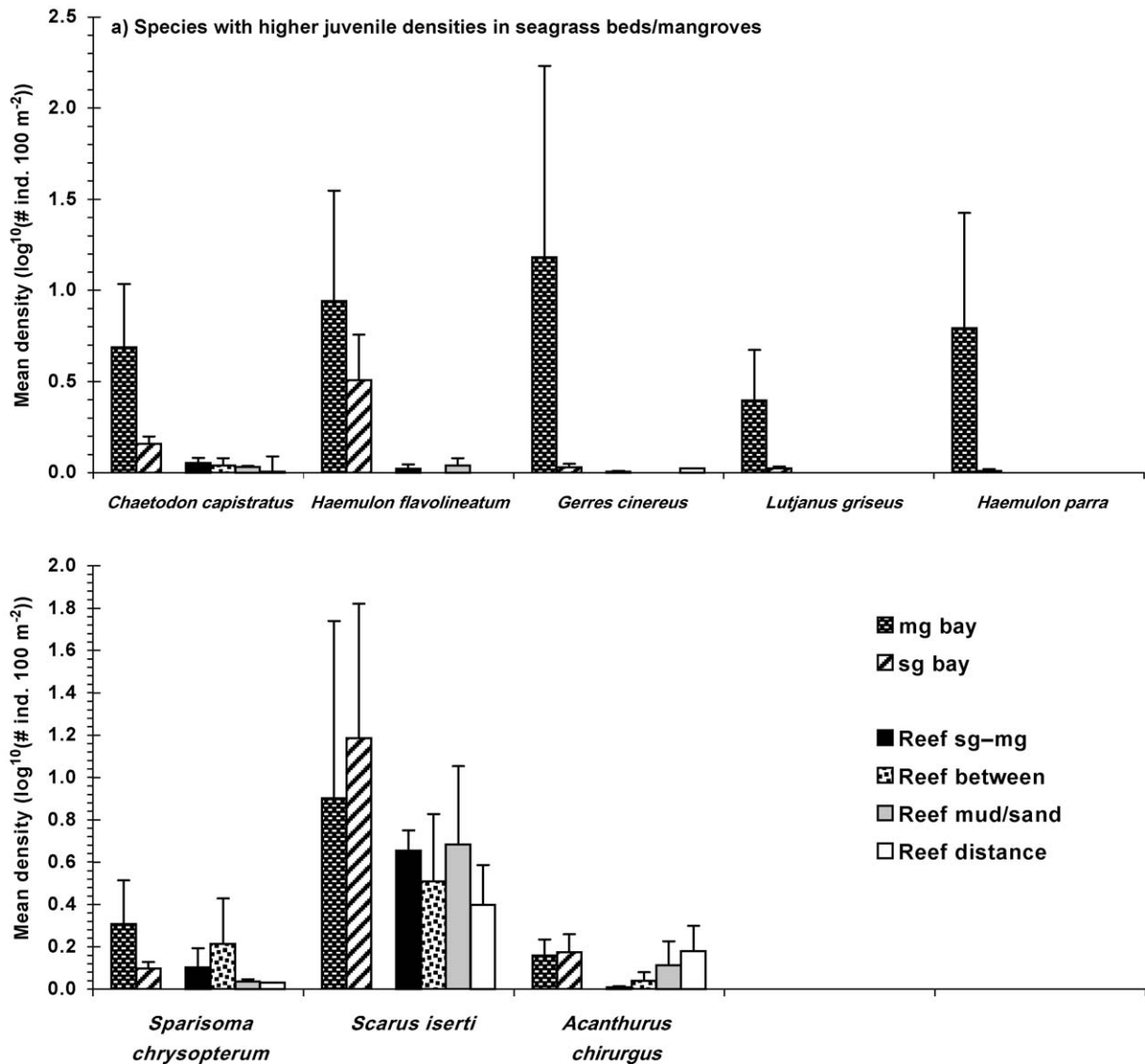


Fig. 4. Mean densities of juveniles of the eight nursery species that did not have higher densities on reefs adjacent to bays with seagrass beds and mangroves than at other locations. Densities are shown on a \log^{10} -scale for the coral reef (this study) and for the mangroves and seagrass beds of Spanish Water Bay (data recalculated from Nagelkerken and van der Velde, 2002). Species with higher juvenile densities in seagrass beds/mangroves than on the reef (a) are distinguished from species with similar densities in seagrass beds/mangroves and on the reef (b). Error bars indicate SEM. For abbreviations see the legend to Fig. 3.

those in seagrass beds. Other studies have also observed juveniles of *S. coeruleus* on patch reefs (Overholtzer and Motta, 1999). These observations suggest that this species can also use the coral reef as a nursery.

One problem with the interpretation of the present results is that all reefs in front of bays with seagrass bed and mangrove nurseries were located on the southeastern part of the coast, whereas all reefs in front of mud/sand bays and reefs at great distances from bays with mangroves and seagrass beds were located on the northwestern part of the island. Factors other than absence/presence of bays with mangrove and seagrass beds may therefore also influence the reef fish communities at these reef categories. It is argued that even if such factors play

a role, the influence of the presence/absence of nursery bays on the fish community structure of various reef fish species is greater than these other factors. Firstly, and most importantly, if other factors were primarily responsible, then non-nursery congeners of the nursery species would also show significantly elevated densities at reefs in front of nursery bays. This was not the case. Secondly, coral cover at 2, 5, and 10 m depth and overall coral cover did not differ significantly between the southeastern and northwestern reefs ($P > 0.213$, t -test). Only at 15 m depth was the coral cover significantly higher at the latter reefs than at the former ($p = 0.047$, t -test), but the data indicated that with the exception of one fish species no high positive correlation was present

between coral cover and fish densities. Thirdly, *Ocyurus chrysurus*, *Lutjanus apodus* and *Haemulon sciurus* which showed the highest difference in density between the reefs in front of the bays with nursery habitats and the other three reef categories, were three of the four nursery species for which Nagelkerken et al. (2002) indicated that they showed a very high dependence of mangrove/seagrass nurseries at various islands throughout the Caribbean. Environmental factors such as water temperature, salinity and turbidity do not vary in a systematic way at the two parts of the island, partly due to the ocean currents which run straight along the entire southwestern coast of the island. The island does not have any fishing reserves, and fishing takes place along the entire sheltered southwestern coast. It is therefore concluded that the presence of nursery bays is in this case the best possible explanation for the elevated densities of seven nursery species on reefs in front of sg–mg bays.

Among the eight nursery species that did not occur in higher densities as mainly adults on reefs adjacent to sg–mg bays, two groups were distinguished: one including species with higher juvenile densities in seagrass beds/mangroves than on the coral reef, and one including species with similar juvenile densities in seagrass beds/mangroves and on the reef. The first group includes two species (*Chaetodon capistratus* and *Haemulon flavolineatum*) for which local recruitment is probably the main source of adults, because juveniles were found on the entire reef while no higher total density was observed on reefs adjacent to sg–mg bays. Nagelkerken et al. (2000a) also found juveniles of both species on the reef. Nagelkerken et al. (2001) showed a major nursery function of mud/sand bays for *Gerres cinereus* (see Table 1). And since mud/sand bays are present over a large part of the coast, the observations of juveniles of this species at the various reef sites at great distance from sg–mg bays might be explained by the presence of these bays. Juveniles of *Lutjanus griseus* and *Haemulon parra* were predominantly observed in sg–mg bays (Table 1) and not on the coral reef. The presence of these species on reefs at some distance to sg–mg bays might therefore be explained by dispersal along the coast.

For the second group, local recruitment is thought to be the main source of adults on reef sites other than reefs adjacent to sg–mg bays. Nagelkerken et al. (2002) described both *Acanthurus chirurgus* and *Sparisoma chrysopteron* as species that do not depend on mangroves or seagrass beds as nurseries. However, the same study indicated that *Scarus iserti* depends heavily on the presence of seagrass beds and mangroves as nurseries. The results of the present study suggest that around Curaçao, the species is well capable of using the reef as an alternative nursery and is therefore not restricted to seagrass beds and mangroves as nurseries. Small juveniles (0–5 cm) were also frequently observed on most

reef sites. Ontogenetic migrations from sg–mg bays to reefs located much farther away are therefore not likely.

Various studies have demonstrated a close correlation between habitat complexity and total fish density (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984; Grigg, 1994). In the present study, however, the relation between coral cover and fish density was only evident for *Scarus coeruleus*, suggesting that this species favours reefs with a high coral cover. For the two other species which showed a significant relation between density and coral cover, the relation was only significant in one depth zone, and was negative for *Haemulon sciurus*, whereas for *Lutjanus mahogoni* the degree of variation explained by the regression line was very low. Furthermore, the non-nursery congeners of the nursery species showed different distribution patterns among the reef sites than the nursery species. It is therefore likely that in this study coral complexity did not influence the distribution of the sampled nursery species along the coast.

The results of the present study indicate that the distribution of *Haemulon sciurus*, *Lutjanus apodus*, *Ocyurus chrysurus* and *Scarus coeruleus* on the coral reef along the coast of a single island is significantly related to the presence of sg–mg bays. *Lutjanus analis*, *Lutjanus mahogoni* and *Sphyrna barracuda* showed a similar trend but densities at reefs adjacent to sg–mg bays were only significantly higher than those at two of the three reef categories. Six of these seven nursery species showed much higher juvenile densities in seagrass/mangrove habitats than on the reef, but were nevertheless also found as adults on reef locations at some distance from these nursery habitats, suggesting dispersal along the reef. *Acanthurus chirurgus*, *Scarus iserti* and *Sparisoma chrysopteron* showed comparable juvenile densities in seagrass/mangrove habitats and reef habitats, and were also found as adults at various reef sites, suggesting that they can complete their entire life cycle on the reef and are not highly dependent on seagrass beds and mangroves.

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