



Importance of Mangroves, Seagrass Beds and the Shallow Coral Reef as a Nursery for Important Coral Reef Fishes, Using a Visual Census Technique

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The nursery function of various biotopes for coral reef fishes was investigated on Bonaire, Netherlands Antilles. Length and abundance of 16 commercially important reef fish species were determined by means of visual censuses during the day in six different biotopes: mangrove prop-roots (*Rhizophora mangle*) and seagrass beds (*Thalassia testudinum*) in Lac Bay, and four depth zones on the coral reef (0 to 3 m, 3 to 5 m, 10 to 15 m and 15 to 20 m). The mangroves, seagrass beds and shallow coral reef (0 to 3 m) appeared to be the main nursery biotopes for the juveniles of the selected species. Mutual comparison between biotopes showed that the seagrass beds were the most important nursery biotope for juvenile *Haemulon flavolineatum*, *H. sciurus*, *Ocyurus chrysurus*, *Acanthurus chirurgus* and *Sparisoma viride*, the mangroves for juvenile *Lutjanus apodus*, *L. griseus*, *Sphyraena barracuda* and *Chaetodon capistratus*, and the shallow coral reef for juvenile *H. chrysargyreum*, *L. mahogoni*, *A. bahianus* and *Abudefduf saxatilis*. Juvenile *Acanthurus coeruleus* utilized all six biotopes, while juvenile *H. carbonarium* and *Anisotremus surinamensis* were not observed in any of the six biotopes. Although fishes showed a clear preference for a specific nursery biotope, most fish species utilized multiple nursery biotopes simultaneously. The almost complete absence of juveniles on the deeper reef zones indicates the high dependence of juveniles on the shallow water biotopes as a nursery. For most fish species an (partial) ontogenetic shift was observed at a particular life stage from their (shallow) nursery biotopes to the (deeper) coral reef. Cluster analyses showed that closely related species within the families Haemulidae, Lutjanidae and Acanthuridae, and the different size classes within species in most cases had a spatial separation in biotope utilization.

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Introduction

Many studies in various parts of the world have recognized the importance of mangroves and seagrass beds as habitats for fishes. Mangroves and seagrass beds have been shown to contain a high diversity and abundance of estuarine and/or coral reef fishes in the Caribbean (e.g. Springer & McErlean, 1962; Austin, 1971; Weinstein & Heck, 1979; Thayer *et al.*, 1987; Baelde, 1990; Sedberry & Carter, 1993), in the Indian Ocean (e.g. Little *et al.*, 1988; van der Velde *et al.*, 1995; Pinto & Punchihewa, 1996), and in the Pacific Ocean (e.g. Blaber, 1980; Bell *et al.*, 1984; Robertson & Duke, 1987; Blaber & Milton, 1990; Morton, 1990; Tzeng & Wang, 1992).

Several hypotheses have been proposed to explain the high abundance of (juvenile) fishes in mangroves

and seagrass beds. The hypotheses are based on avoidance of predators, the abundance of food and the interception of fish larvae: (a) the structural complexity of these biotopes provide excellent shelter against predators (Parrish, 1989; Robertson & Blaber, 1992), (b) 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), (c) the relatively turbid water of the bays and estuaries decrease the foraging efficiency of predators (Blaber & Blaber, 1980; Robertson & Blaber, 1992), (d) these biotopes provide a great abundance of food for fishes (Odum & Heald, 1972; Carr & Adams, 1973; Ogden & Zieman, 1977) and (e) these biotopes often cover extensive areas and may intercept planktonic fish larvae more effectively than the coral reef (Parrish, 1989).

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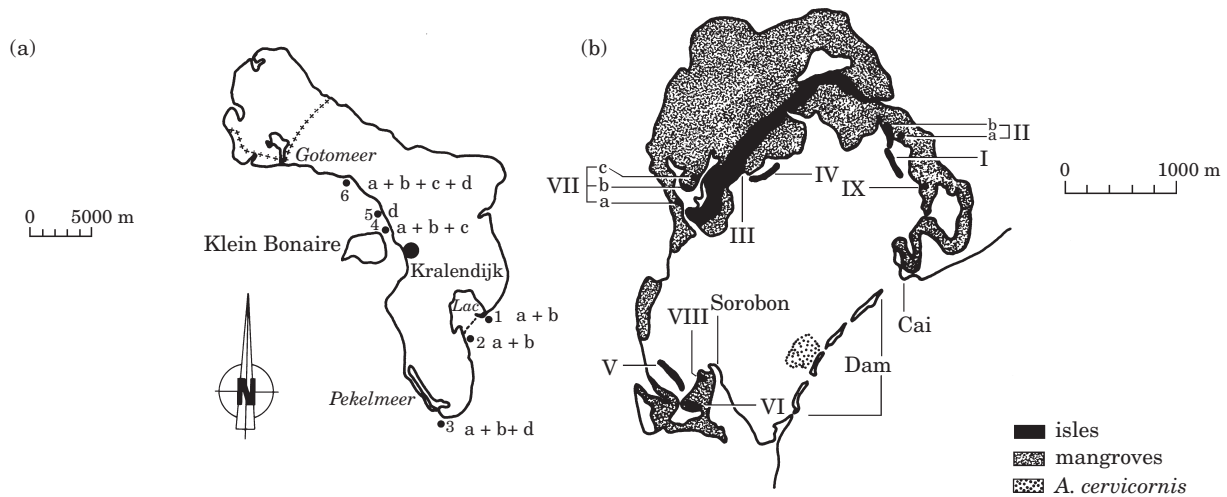


FIGURE 1. (a) Map of Bonaire showing the different coral reef study sites. a=20 to 25 m, b=10 to 15 m, c=3 to 5 m, d=0 to 3 m. (b) Map of Lac Bay showing the different mangrove (II, IV, VI, VII, VIII, IX) and seagrass bed (I, III, V) study sites. *A. cervicornis*=*Acropora cervicornis*.

Studies on fish community structure in Caribbean lagoons, bays and estuaries containing mangroves or seagrass beds often mention high densities of juvenile fish and state that these biotopes function as nursery areas for various coral reef fish species (e.g. Austin, 1971; Weinstein & Heck, 1979; Baelde, 1990; Sedberry & Carter, 1993). In the Indo-Pacific, however, the nursery function of these biotopes is apparent only in some regions (Blaber, 1980; Bell *et al.*, 1984; Little *et al.*, 1988; Tzeng & Wang, 1992), whereas in other regions these biotopes do not appear to be important (Quinn & Kojis, 1985; Thollot & Kulbicki, 1988; Blaber & Milton, 1990; Thollot, 1992).

Most studies describing the nursery function of mangroves and seagrass beds were based on qualitative observations, made no distinction between abundances of juvenile and adult fishes, and did not provide quantitative data on fish size. The few studies which did provide size data for separate species only mentioned the full size range of all fish caught (Springer & McErlean, 1962; Austin, 1971). Hence, size-frequency data of juvenile and adult reef fish are largely lacking for these biotopes. Furthermore, many fish species show ontogenetic shifts in habitat utilization and migrate from their nursery grounds to an intermediate life stage habitat or to the coral reef (Ogden & Ehrlich, 1977; Weinstein & Heck, 1979; McFarland, 1980; Rooker & Dennis, 1991). The size range and the biotopes where these shifts occur have also not been described accurately for many fish species.

Studies referring to the nursery function of lagoons, bays and estuaries in the Caribbean have mostly

focused on either mangroves or seagrass beds, and usually with a different sampling method. This makes a comparison between studies and biotopes difficult. Only a few studies have sampled both biotopes simultaneously (Thayer *et al.*, 1987; Sedberry & Carter, 1993), and even fewer have included censuses on the adjacent or off-shore coral reef (e.g. van der Velde *et al.*, 1992). Hence, quantitative data describing the ecological links of fish faunas between mangroves, seagrass beds and coral reefs are largely lacking (Ogden & Gladfelter, 1983; Birkeland, 1985; Parrish, 1989).

To provide a better insight into the importance of mangroves, seagrass beds and depth zones of the coral reef as nursery biotopes and their interrelationship in fish fauna, size frequency data were collected for 16 commercially important reef fish species in each biotope, using a visual census technique. The objectives of the present study were to answer the following four questions: (1) Which biotopes are used as a nursery by the selected fish species? (2) Which biotope is preferred by a fish species in case multiple nursery biotopes are used? (3) Do fish species show an ontogenetic shift from their nursery biotopes to other biotopes when reaching a larger size? (4) Do closely related fish species show a spatial separation in biotope utilization?

Materials and methods

Lac Bay is the largest bay of Bonaire with an area of approximately 8 km² and is situated on the exposed eastern side of the island [Figure 1(a)]. The bay

TABLE 1. Depth, temperature and salinity of the seawater in the six different biotopes

	Depth (m)	Temperature (°C)	Salinity
Seagrass bed	0.4–1.4	28.6–33.4	37–44
Mangroves	0.3–1.2	28.5–34.0	39–44
Coral reef	0–3	29.0–29.8	n.d.
Coral reef	3–5	27.1–29.3	n.d.
Coral reef	10–15	27.1–29.8	n.d.
Coral reef	20–25	26.8–29.5	n.d.

n.d. = no data.

consists of a shallow basin (0 to 3 m deep) and is protected from wave exposure by a shallow barrier of dead and living corals [Figure 1(b)]. The bay is connected to the sea by a narrow channel which is about 8 m deep. The soft-bottom flora of the bay is dominated by the seagrass *Thalassia testudinum* and the calcareous alga *Halimeda opuntia*. Other common vegetation consists of the seagrass *Syringodium filiforme* and the alga *Avrainvillea nigricans*. The bay is bordered almost completely by the mangrove *Rhizophora mangle*. In front of the bay the coral reef is situated, which runs around the island. The reef consists of a shallow reef terrace which sharply drops off at an angle of 45 to 60° at a depth of 8 to 12 m.

The maximum tidal range on Bonaire is 30 cm (van Moorsel & Meijer, 1993). The seagrass beds and mangrove prop-roots at the study sites were not exposed at low tide and ranged in depth from 0.3 to 1.4 m (Table 1). The temperature, measured during the entire study period, ranged from 28.5 to 34.0 °C in the bay, and was on average higher than on of the coral reef where it ranged from 26.8 to 29.8 °C. The salinity, measured at the beginning and at the end of the study period, ranged from 37 to 44 in the seagrass beds and from 39 to 44 in the mangroves. The water of the bay is quite clear and horizontal Secchi visibility ranges from 4.6 to 21.6 m in the central parts of the bay (van Moorsel & Meijer, 1993).

Sixteen reef fish species were selected in the present study. Species were selected which were abundant, not too shy, easy to identify in the field and had a non-cryptic life style. Further selection was on basis of their economic value (i.e. reef fisheries, aquarium fisheries, attraction for diving industry). The 16 species consisted of five species of grunts (Haemulidae): French grunt *Haemulon flavolineatum*, bluestriped grunt *H. sciurus*, smallmouth grunt *H. chrysargyreum*, Caesar grunt *H. carbonarium*, and black margate *Anisotremus surinamensis*; four species of

snappers (Lutjanidae): yellowtail snapper *Ocyurus chrysurus*, mahogany snapper *Lutjanus mahogoni*, schoolmaster *L. apodus*, and gray snapper *L. griseus*; three species of surgeonfishes (Acanthuridae): doctorfish *Acanthurus chirurgus*, ocean surgeon *A. bahianus*, and blue tang *A. coeruleus*; one species of barracuda (Sphyraenidae): great barracuda *Sphyraena barracuda*; one species of parrotfish (Scaridae): stoplight parrotfish *Sparisoma viride*; one species of damselfish (Pomacentridae): sergeant major *Abudefduf saxatilis*; and one species of butterflyfish (Chaetodontidae): four-eye butterflyfish *Chaetodon capistratus*.

The selected fish species were studied using a visual census technique in six different biotopes, viz. mangrove prop-roots and seagrass beds, and the coral reef of 0 to 3 m, 3 to 5 m, 10 to 15 m and 15 to 20 m [Figure 1(a,b)]. Water clarity for visual censuses was good in all six biotopes, even in the mangroves. The visual census technique was based on best estimation by eye of abundance and body length of the selected fish species in permanent belt transects in all six biotopes. Size classes of 5 cm were used for the estimation of body length (TL). The usage of smaller size classes was avoided to reduce differences in size class estimation between observers. For the large-sized *Sphyraena barracuda* size classes of 15 cm were used. Length estimation was practiced prior to the censuses on objects with known length lying on the sea bottom. In addition, the underwater slates for data recording were marked with a ruler for guidance in size estimation. Visual census estimations of fish abundance were compared with catches at two seagrass sites using the drop net quadrat method (Hellier, 1958). At sites VIII and IX [see Figure 1(b)] a drop net of 10 × 10 m was installed on the seagrass bed. During the morning (09.00–10.00h) the net was lowered onto the sea bottom and all fishes within the net were caught, identified and counted. A total of seven drop net catches were made at the two seagrass sites during August to December 1981. In addition, differences in estimation of abundance was statistically tested (*t*-test) between the two observers for each species in each biotope (96 cases).

Advantages of visual censuses are that they are rapid, non-destructive, inexpensive, can be used for all selected biotopes of this study, the same areas can be resurveyed through time, and the results can be compared with many other studies (English *et al.*, 1994). Disadvantages are the differences in accuracy in estimation of numbers and sizes by the observers, and fishes may be attracted or scared off by the observers (English *et al.*, 1994; Cheal & Thompson, 1997; Thompson & Mapstone, 1997).

TABLE 2. Mean density (1000 m⁻²) of the 16 fish species in the six different biotopes surveyed by visual census, and mean density on the seagrass beds based on drop net catches

	Seagrass bed		Mangroves	Coral reef 0–3 m	Coral reef 3–5 m	Coral reef 10–15 m	Coral reef 20–25 m
	drop net	visual census					
<i>Haemulon flavolineatum</i>	782.5	115.3	59.9	52.4	37.4	12.4	2.9
<i>H. sciurus</i>	12.7	5.5	4.3	0.4	0.4	9.6	0.5
<i>H. chrysargyreum</i>	0.0	0.01	0.0	64.7	53.9	0.0	0.0
<i>H. carbonarium</i>	0.0	0.0	0.0	0.0	0.0	5.4	0.1
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.8	0.1
<i>Ocyurus chrysurus</i>	20.6	16.4	1.2	0.0	1.1	24.7	11.8
<i>Lutjanus mahogoni</i>	0.0	1.1	0.0	9.6	1.7	12.6	2.3
<i>L. apodus</i>	30.2	8.1	65.8	0.5	0.0	9.7	3.4
<i>L. griseus</i>	4.8	8.7	29.9	0.0	0.0	0.0	0.04
<i>Acanthurus chirurgus</i>	0.0	9.2	0.8	5.6	0.1	0.6	0.8
<i>A. bahianus</i>	27.0	3.3	0.2	86.6	19.3	5.6	4.4
<i>A. coeruleus</i>	0.0	1.1	2.6	10.2	21.8	7.7	4.5
<i>Sphyraena barracuda</i>	6.3	0.9	5.1	0.0	0.0	0.1	0.2
<i>Sparisoma viride</i>	60.3	26.1	1.4	11.1	34.6	11.4	6.3
<i>Abudefduf saxatilis</i>	0.0	0.2	3.9	65.2	0.3	16.8	0.1
<i>Chaetodon capistratus</i>	12.7	4.9	16.7	2.7	14.4	23.1	9.6

In each of the six biotopes, permanently marked belt transects were established. In the seagrass beds, a transect of 300 × 3 m was established at three different sites. In the mangroves, nine transects were established of 3 m wide and 25 to 100 m long. On the coral reef, six sites were selected and at each site, transects of 3 × 100 m were established at two to four depth zones [Figure 1(a)]. During May to November 1981, visual censuses were done by two trained observers together in the morning (09.00–11.00h) and in the afternoon (14.00–16.00h) by means of snorkelling or SCUBA diving. The census in each transect was repeated at monthly intervals. The fish counts in transects at the different sites, of the morning and afternoon survey, and of all seven months were pooled and averaged per area. They are expressed as the average fish density per 1000 m² for each size class of each species in each biotope.

Cluster analyses were carried out using the computer programme CLUSTAN1C2 (Wishart, 1978). The average-linkage method (Sokal & Michener, 1958) was used in combination with the Bray-Curtis coefficient. Separate analyses were carried out for closely related species belonging to a single family (Haemulidae, Lutjanidae, Acanthuridae) using log-transformed data of the densities in the different size classes and biotopes. Cluster analysis of all species together was carried out on data in which densities per size class for each biotope were transformed to percentages of total composition of a particular species. This was done to compare biotope utilization

between species without the data being affected by differences in total fish densities.

Results

Drop net catches vs visual census

Catches with the drop net showed higher abundances for some fish species than estimations with the visual census technique (Table 2), especially for *H. flavolineatum*. On the other hand, visual estimations of abundance of *A. chirurgus* were much higher than with the drop net quadrat method. For the visual censuses, only in 8 out of 61 cases a significant difference ($P < 0.05$, *t*-test) was found in estimation of abundance between the two observers (for 35 cases insufficient data were available for statistical testing).

Biotope utilization of Haemulidae

Juveniles of Haemulidae were restricted to shallow water biotopes (i.e. seagrass beds, mangroves and reef of 0 to 3 m), whereas adults were found on the deeper reef (>3 m) (Figure 2, Table 3). An exception was formed by adult *Haemulon chrysargyreum* which were also found on the reef of 0 to 3 m. Large juveniles of *H. sciurus* utilized the mangroves as an intermediate life stage biotope, in their ontogenetic shift from the seagrass beds to the coral reef. *Haemulon flavolineatum* showed significant temporal differences in total density in the seagrass beds (Friedman's test,

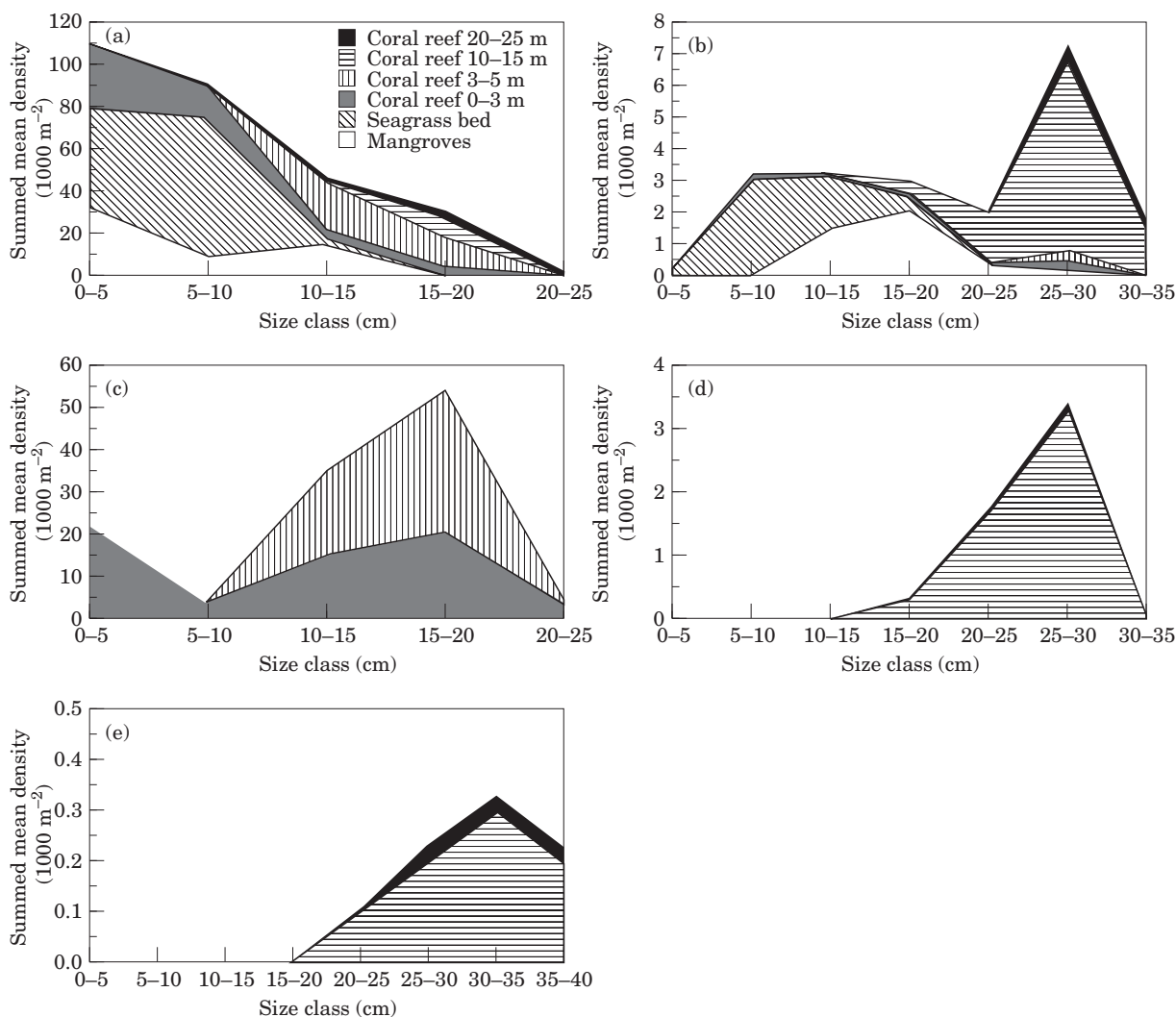


FIGURE 2. Summed mean densities of Haemulidae in different biotopes. (a) *Haemulon flavolineatum*; (b) *H. sciurus*; (c) *H. chrysargyreum*; (d) *H. carbonarium*; (e) *Anisotremus surinamensis*.

$P < 0.05$), increasing from 25.4 per 1000 m² in May to 178.9 per 1000 m² in October.

Cluster analysis of all size classes of all haemulids also showed a spatial separation in biotope utilization among the different size classes and/or species, with juveniles found in the mangroves and seagrass beds, medium-sized individuals on the reef and partly still in the mangroves, and very large individuals on the deep reef (Figure 3). *Haemulon chrysargyreum* formed a separate cluster since adults partly co-occurred with the juveniles in their nursery habitat.

Species of Haemulidae showed a spatial separation in biotope utilization and occurred in different biotope clusters as calculated by cluster analysis (Figure 4). Furthermore, the Haemulidae were not found together in a single cluster with any species belonging to the same feeding guild (Figure 4, Table 3). Only

H. carbonarium and *A. surinamensis* showed some similarity in biotope utilization, but the former was much more abundant than the latter (Figure 2). Considering the entire species size range, *H. flavolineatum* dominated over its related species in the seagrass beds, mangroves and reef of 20 to 25 m, but co-occurred with *H. chrysargyreum* on the reef of 0 to 5 m [Figure 5(a), Table 2]. *Haemulon sciurus* and *H. carbonarium* co-occurred with *H. flavolineatum* on the reef of 10 to 15 m. *Anisotremus surinamensis* was not dominant in any of the biotopes.

Biotope utilization of Lutjanidae

Juveniles of Lutjanidae were restricted to the shallow water biotopes (Figure 6, Table 3). Only juveniles of *L. mahogoni* were also partly found deeper on the reef

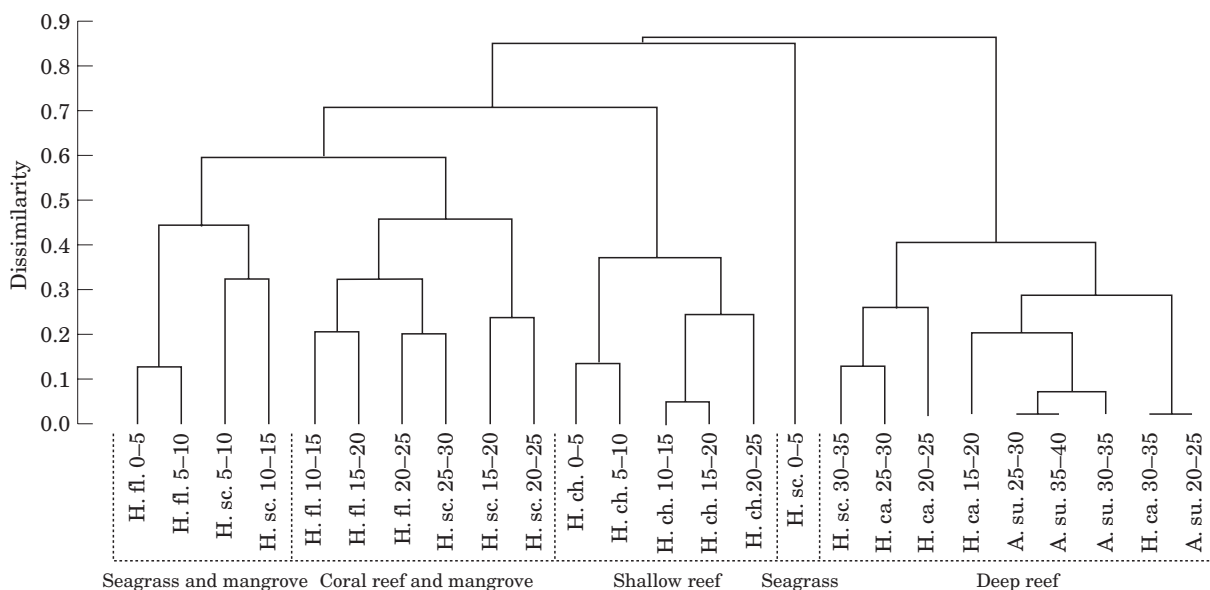


FIGURE 3. Cluster analysis of all size classes of Haemulidae in different biotopes. H. fl.=*Haemulon flavolineatum*, H. sc.=*H. sciurus*, H. ch.=*H. chrysargyreum*, H. ca.=*H. carbonarium*, A. su.=*Anisotremus surinamensis*. The numbers indicate the size classes.

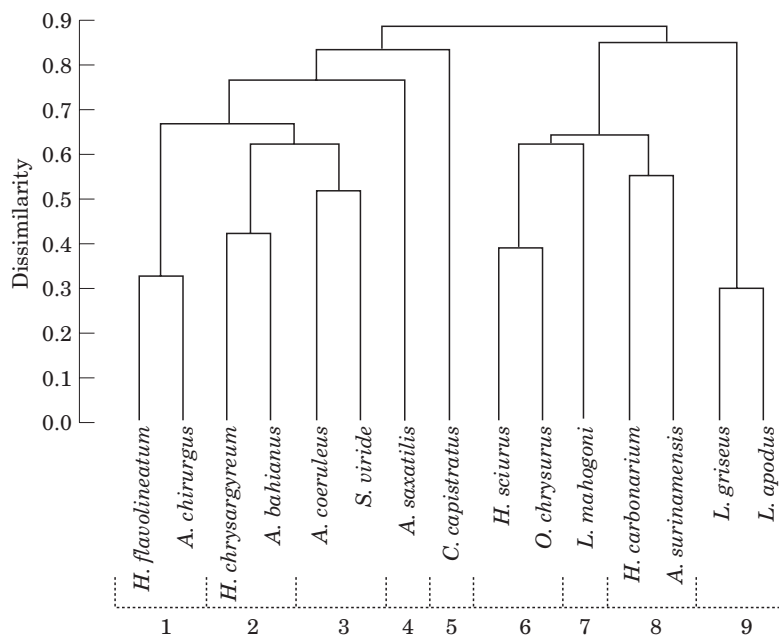


FIGURE 4. Cluster analysis of all 16 fish species based on the abundance of each size class in the different biotopes.

of 3 to 5 m. All species, except *L. griseus*, showed an ontogenetic shift to the (deeper) coral reef. *Lutjanus apodus* and *L. griseus* also occurred as adults in the mangroves. *Lutjanus apodus* showed significant temporal differences in total density (Friedman's test, $P < 0.05$), increasing in the mangroves from 57.7 per 1000 m² in May to 92.3 per 1000 m² in August, and

in the seagrass beds from 0.9 per 1000 m² in May to 17.2 per 1000 m² in October. *Ocyurus chrysurus* increased in density in the seagrass beds from 4.4 per 1000 m² in June to 41.4 per 1000 m² in November.

Cluster analysis of all size classes of all lutjanids also revealed a clear separation between adults and large individuals (except *L. griseus*) on the deep reef (10 to

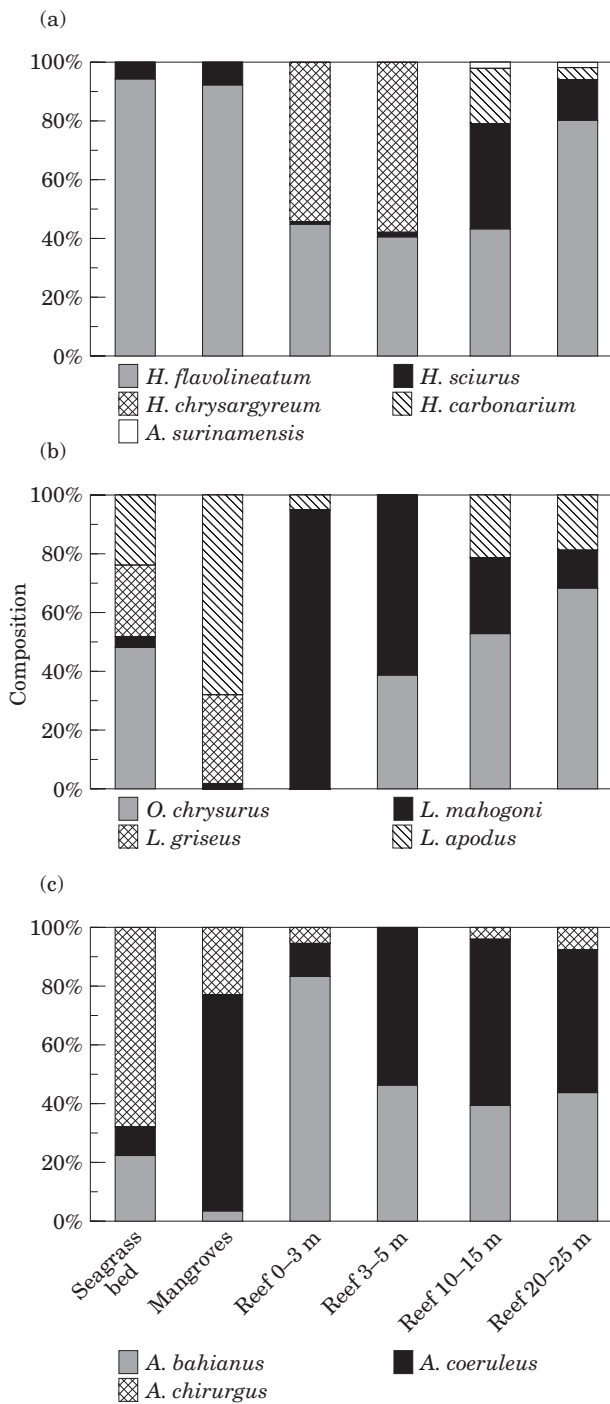


FIGURE 5. Biotope partitioning between closely related species: (a) Haemulidae, (b) Lutjanidae, (c) Acanthuridae. The abundance of each species is expressed as the percentage composition of the total abundance of all related species within a single family for each biotope. The entire size range of a species is pooled per biotope, although preferences may differ among size classes. For the specific differences among size classes see Figures 2, 6 and 8.

25 m), and juveniles in the shallow water biotopes (Figure 7).

Species of Lutjanidae showed a spatial separation in biotope utilization, except *L. griseus* and *L. apodus* which showed some degree of similarity in biotope utilization and also belonged to the same feeding guild (Figure 4, Table 3). Considering the entire species size range, *L. apodus* dominated over its related species in the mangroves, while for *L. mahogoni* and *O. chrysurus* this was the case on the reef of 0 to 3 m and on the reef of 20 to 25 m, respectively [Figure 5(b), Table 2]. In the other three biotopes, lutjanids co-occurred without a single species showing an overall dominance.

Biotope utilization of Acanthuridae

Juveniles of Acanthuridae were restricted to the shallow water biotopes, whereas adults were found on the reef (Figure 8, Table 3). Adults were also found in the juvenile nursery habitat (i.e. reef of 0 to 3 m), however, co-occurring with the juveniles. For larger juveniles of *A. coeruleus* the reef of 3 to 5 m was also of importance. *Acanthurus bahianus* showed significant temporal differences in total density (Friedman's test, $P < 0.05$), with peak abundances in the seagrass beds of around 5 per 1000 m² in July, October, and November. *Acanthurus coeruleus* increased in density on the reef of 3 to 5 m from 5.4 per 1000 m² in May to 47.1 per 1000 m² in September.

Cluster analysis of all size classes of all acanthurids also showed a separation between juveniles in the seagrass beds and mangroves, and medium-sized and larger individuals on the reef (Figure 9).

Species of Acanthuridae showed a spatial separation in biotope utilization and occurred in different biotope clusters (Figure 4). Of the Acanthuridae, only *A. coeruleus* was found with another herbivore species (*S. viride*) in a single cluster, although the dissimilarity in biotope utilization between the two species was still high (Figure 4, Table 3). Considering the entire species size range, each species dominated over its related species in a particular biotope: *A. chirurgus* in the seagrass beds, *A. coeruleus* in the mangroves, and *A. bahianus* on the coral reef of 0 to 3 m [Figure 5(c), Table 2]. In the other reef zones, *A. coeruleus* and *A. bahianus* co-occurred in almost equal densities.

Biotope utilization of other species

For the remaining four species, juveniles were also restricted to the shallow water biotopes, whereas adults occurred on the coral reef (Figures 10-13, Table 3). Exceptions were adult *S. barracuda* which

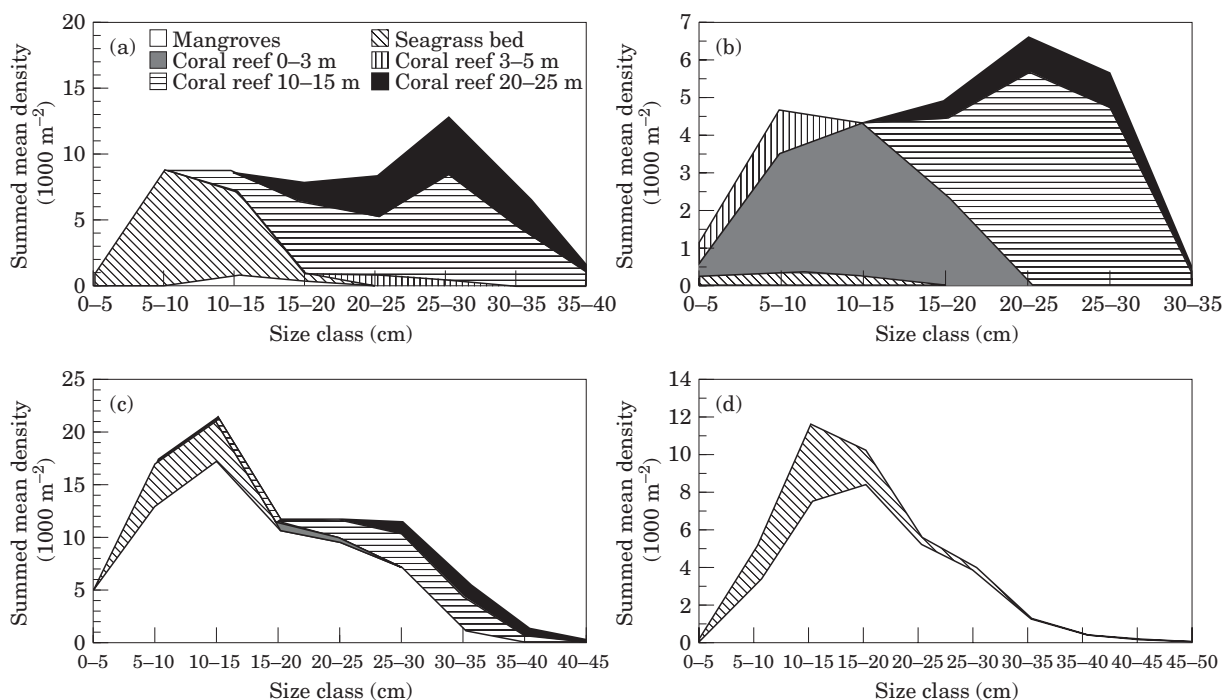


FIGURE 6. Summed mean densities of Lutjanidae in different biotopes. (a) *Ocyurus chrysurus*; (b) *Lutjanus mahogoni*; (c) *L. apodus*; (d) *L. griseus*.

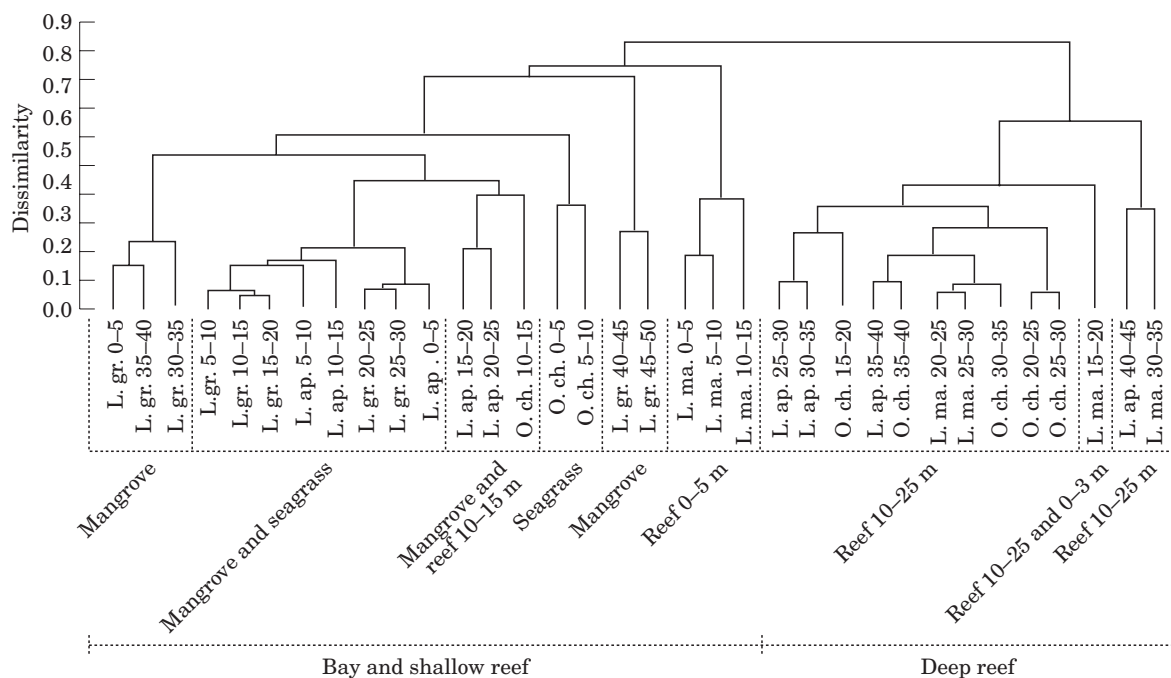


FIGURE 7. Cluster analysis of all size classes of Lutjanidae in different biotopes. L. gr.=*Lutjanus griseus*, L. ap.=*L. apodus*, L. ma.=*L. mahogoni*, O. ch.=*Ocyurus chrysurus*. The numbers indicate the size classes.

also used the seagrass beds and mangroves as a life stage biotope, and juvenile *S. viride* which also used the reef of 3 to 5 m as a nursery biotope. Some adult

A. saxatilis co-occurred with the juveniles on the shallow reef. *Sphyraena barracuda* showed significant temporal differences in total density (Friedman's test,

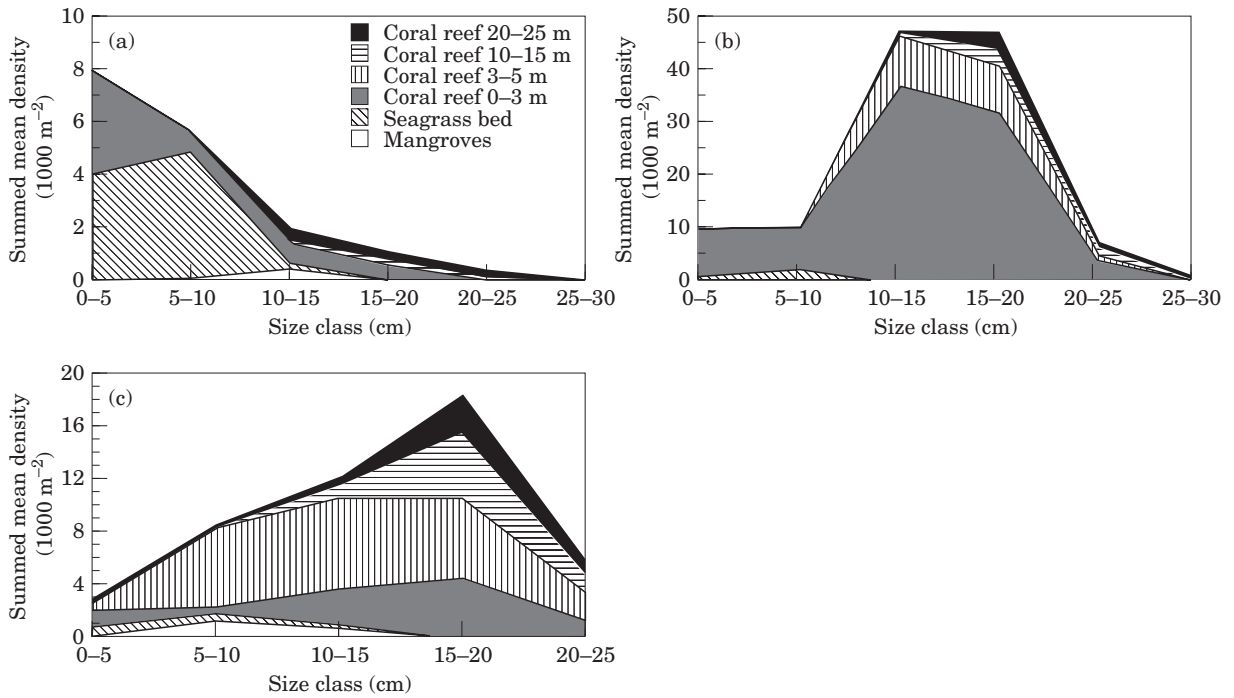


FIGURE 8. Summed mean densities of Acanthuridae in different biotopes. (a) *Acanthurus chirurgus*; (b) *A. bahianus*; (c) *A. coeruleus*.

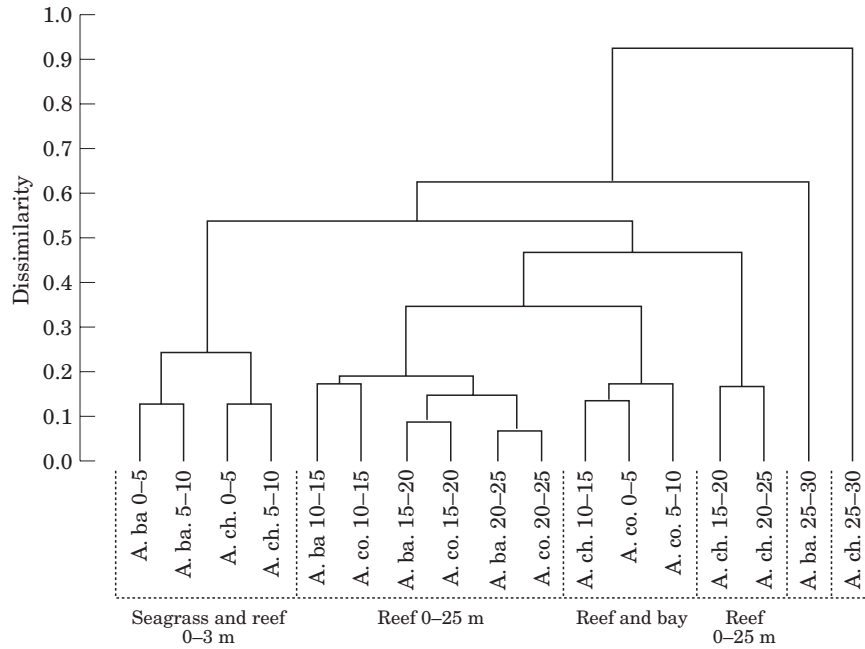


FIGURE 9. Cluster analysis of all size classes of Acanthuridae in different biotopes. A. ba.=*Acanthurus bahianus*, A. ch.=*A. chirurgus*, A. co.=*A. coeruleus*. The numbers indicate the size classes.

$P < 0.05$), with densities in the mangroves about two times higher in August–November than in May–July. *Sparisoma viride* increased in density in the seagrass

beds from 12.7 per 1000 m² in June to 43.1 per 1000 m² in November, and *C. capistratus* from 2.0 per 1000 m² in May to 8.0 per 1000 m² in November.

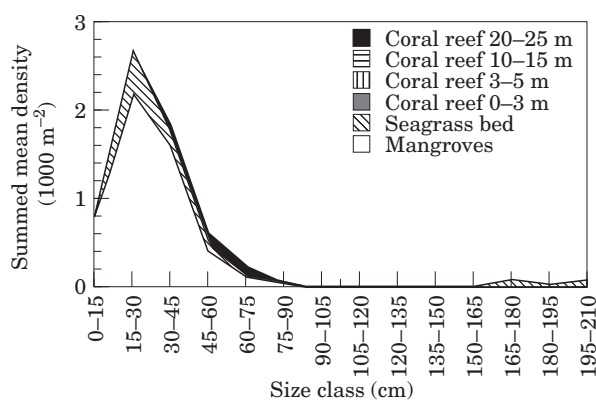


FIGURE 10. Summed mean densities of *Sphyraena barracuda* in different biotopes.

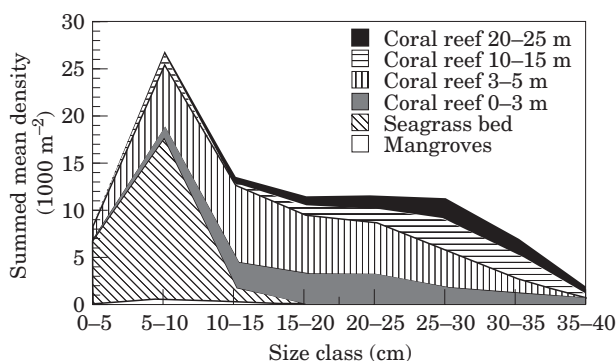


FIGURE 11. Summed mean densities of *Sparisoma viride* in different biotopes.

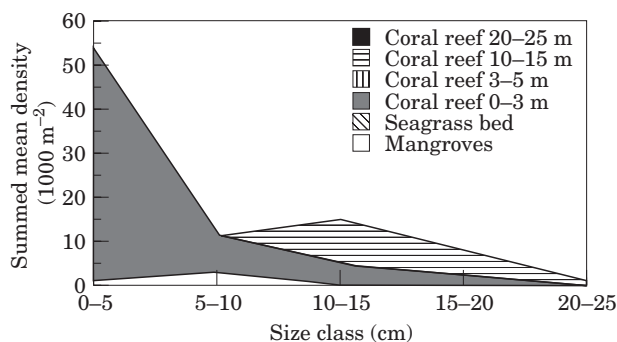


FIGURE 12. Summed mean densities of *Abudedefduf saxatilis* in different biotopes.

Discussion

For several fish species in the seagrass beds the visual census technique showed lower densities than the catches with the drop net quadrat method. Especially *H. flavolineatum* was underestimated in the visual censuses. The formation of large schools in this and other species and the continuous movement of the fishes caused a reduced accuracy in the estimation

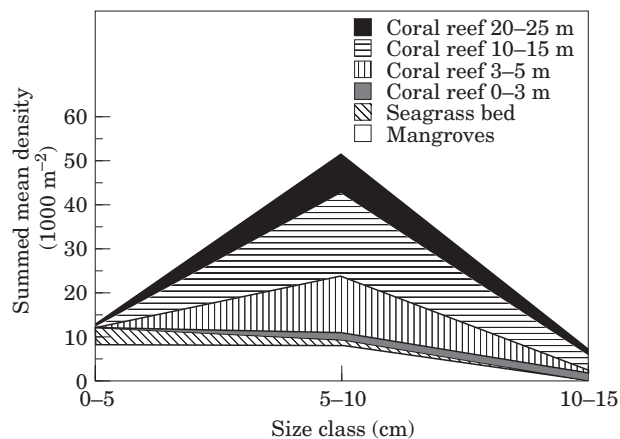


FIGURE 13. Summed mean densities of *Chaetodon capistratus* in different biotopes.

of fish abundance. This variation is assumed to be comparable for the different biotopes, making a comparison among the biotopes possible. Differences in estimation of abundance between observers were present, but not consistent. Although density estimations in seagrass beds are more accurate with the drop net quadrat method, the total surface area sampled (100 m^2) was much smaller than with the visual censuses (900 m^2), resulting in large variations among the transects and a restricted sampling of the biotope studied.

The present study shows the importance of different shallow water biotopes as a nursery for economically important reef fish species. All 14 species for which juveniles were observed used either the mangroves, seagrass beds or the shallow reef of 0 to 3 m, or a combination of these biotopes, as a nursery. The high dependence of juveniles on these biotopes can be deduced from the fact that juveniles were exclusively present or highly dominant in these biotopes and not on the deeper reef (i.e. $>3 \text{ m}$).

The data show that not only mangroves and seagrass beds are important nursery biotopes for juvenile fishes (e.g. Austin, 1971; Weinstein & Heck, 1979; Baelde, 1990; Sedberry & Carter, 1993) but also the shallow coral reef. Two reasons why mangroves and seagrass beds may contain high densities of juvenile fish is their structural complexity which provides a hiding place against predators (Bell & Westoby, 1986; Robertson & Blaber, 1992), and because they are often located at a distance from the coral reef and are therefore less frequented by predators (Shulman, 1985; Parrish, 1989). These two factors also apply to the shallow coral reef of Bonaire, which mostly consists of living and dead colonies of *Acropora palmata*, *Millepora complanata* and other

corals. The dead and living corals provide an ideal hiding space and can house relatively high densities of (juvenile) fish (Nagelkerken, 1974). Furthermore, the shallow reef is separated from the main coral reef and its predators by a shallow reef terrace of about 75 to 125 m in width (van Duyl, 1985). Shulman (1985) showed that at just 20 m from the main reef, in an exposed sandy location, predation on juvenile haemulids was considerably lower than at the edge of the main reef.

Biotope utilization appears to be very specific for the different species and their size classes, each having a different niche. A clear spatial separation in biotope utilization was found among closely related species and among different size groups within species, suggesting avoidance of competition. Biotope partitioning was observed for only a small size range of mostly one or two related species. Likewise, fish species belonging to the same feeding guild showed differences in biotope utilization. Spatial variation across different biotopes often occurs among sympatric fish species (Lewis & Wainwright, 1985; McAfee & Morgan, 1996). Comparable to the present study, Lewis and Wainwright (1985) found a differential biotope utilization for the three species of Acanthuridae and suggested this to be determined by complex interactions of several factors, such as density of competitors, food availability, proximity to shelter, and predator abundance. Munro (1983) stated that interspecific competition for food is probably small for Haemulidae since the different species each favour a certain type of food (Randall, 1967). Nagelkerken *et al.* (2000), however, found *H. flavolineatum* and *H. sciurus* to have similar diets on seagrass beds, which may explain the separation in biotope utilization of the different size classes. Lutjanidae show a high overlap in diet, with exception of *Ocyurus chrysurus* (Randall, 1967; Nagelkerken *et al.*, 2000). As biotope utilization differed only slightly between *Lutjanus mahogoni* and *L. griseus*, which both occurred in similar densities, a high degree of competition may be present between these two species.

When fishes become too large for optimal protection by the seagrass shoots and mangrove prop-roots they often migrate to the coral reef. This migration pattern has largely been described qualitatively for only few species (e.g. Ogden & Ehrlich, 1977; Weinstein & Heck, 1979; McFarland, 1980; Rooker & Dennis, 1991). The present study shows that most of the selected species use the shallow water biotopes as nurseries during their juvenile stage, but migrate permanently to the (deeper) coral reef when reaching a specific size class. An exception was *Lutjanus griseus* of which the entire size range was found in the

mangroves. For some species, the ontogenetic shift to the (deeper) coral reef was partial and a part of the large and adult fish could still be found in their nursery biotope.

The present study shows the importance of Lac Bay for a number of reef fish species. It is not known, however, how much Lac Bay contributes to the reef fish stocks of Bonaire. Effective areas of all biotopes should therefore be measured and the turnover rate of fishes from the bay to the reef be quantified. Furthermore, it should be noted that Lac Bay is not comparable to many other mangrove and seagrass habitats, particularly in the Indo-Pacific. These habitats often have a muddy substratum, are very turbid, and show fluctuating salinities and a greater tidal range. These features influence the nursery function of mangroves and seagrass beds (Blaber, 1997). As the characteristics which are usually associated with these habitats are reduced in Lac Bay, the mechanisms at work responsible for the nursery function of this bay may differ from those in several other bays, lagoons and estuaries which have been studied so far.

Conclusions

The questions asked in this study can be answered as follows. (1) Of all 14 fish species for which juveniles were observed, the mangroves, seagrass beds, shallow reef of 0 to 3 m, or a combination of these biotopes were used as a nursery by the juveniles. (2) The seagrass beds were the most important nursery biotope for juvenile *Haemulon flavolineatum*, *H. sciurus*, *Ocyurus chrysurus*, *Acanthurus chirurgus* and *Sparisoma viride*, the mangroves were the most important biotope for juvenile *Lutjanus apodus*, *L. griseus*, *Sphyraena barracuda* and *Chaetodon capistratus*, the shallow coral reef was the most important biotope for juvenile *H. chrysargyreum*, *L. mahogoni*, *A. bahianus* and *Abudefduf saxatilis*, *Acanthurus coeruleus* did not show a preference for a particular nursery habitat, and for *H. carbonarium* and *Anisotremus surinamensis* it could not be established which biotope was used as a nursery by the juveniles. (3) For most fish species, the juveniles were found in shallow-water biotopes and the large and adult fish on the (deeper) coral reef. (4) Closely related species showed a spatial separation in biotope utilization. This was also observed for different size classes within species.

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