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CONNECTIVITY BETWEEN COASTAL HABITATS OF TWO OCEANIC CARIBBEAN ISLANDS AS INFERRED FROM ONTOGENETIC SHIFTS BY CORAL REEF FISHES

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ABSTRACT Mangroves and seagrass beds are considered important nursery habitats for juveniles of coral reef fishes. Studies have mostly focused on the fish community of just one habitat, so the connectivity between different coastal habitats is often unclear. In this study, density and size of reef fish were determined using a single sampling technique in four non-estuarine bay habitats and four reef zones in Curaçao and Bonaire (Netherlands Antilles). The data indicate that of the complete reef fish community at least 21 species show ontogenetic cross-shelf shifts in habitat utilization. The 21 species mainly utilized shallow-water habitats (mangroves, seagrass beds, channel and shallow reef) as nursery habitats and the deeper coral reef zones (> 5 m depth) as adult life-stage habitats. Fish species utilized 1–3 different nursery habitats simultaneously, but habitat utilization clearly differed between species. Previous studies showed that the dependence on these nursery habitats is very high, based on reduced density or absence of adults on coral reefs where these habitats were absent. The strong connectivity between several coastal habitats during the ontogeny of various commercially important reef fish species is evidence for the inclusion of bay habitats within boundaries of fishery reserves or marine protected areas.

INTRODUCTION

Many coastal ecosystems are impoverished and in decline world-wide as a result of anthropogenic disturbances. Estimates suggest that 30-60% of the world's mangroves have already been lost and seagrasses are declining at similar rates (Shepherd et al. 1989, Spalding 1998). The importance of mangroves and seagrass beds as nurseries for the juveniles of fishes which live as adults on the coral reef has been recognized by many studies in various parts of the world (see reviews by Parrish 1989, Robertson and Blaber 1992). The importance of these habitats is particularly evident in the Caribbean, but in some parts of the Pacific it has been questioned whether these habitats play an important nursery role (Blaber and Milton 1990, Thollot 1992).

In general, mangroves and seagrass beds form ideal nurseries for juvenile fishes because of the high abundance of food and shelter, and a reduced predation pressure (Parrish 1989, Laegdsgaard and Johnson 2001). Mangroves and seagrass beds apparently provide more advantages as a nursery habitat than other habitats for some species, but the question remains whether fishes can utilize alternative habitats or whether the dependence on mangroves and seagrass beds is obligate. Nagelkerken et al. (2000b) made a distinction between nursery, reef and bay species. Nursery species were defined as species whose juveniles utilize bay habitats as a nursery and the adults occur on the coral reef, reef species were defined as species which generally complete their entire benthic life-cycle on the coral reef, and

bay species were defined as species which are abundant in bays as juveniles and adults, and are not present or occur in low abundances on the coral reef. Studies showed that juveniles of 17 nursery species are highly associated with mangrove/seagrass dominated bays (Nagelkerken et al. 2000b, Nagelkerken and van der Velde 2002), but are largely absent in bays lacking these nursery habitats (Nagelkerken et al. 2001a). Furthermore, these species are rarely found as juveniles on the coral reef (Nagelkerken et al. 2000b). In addition, Nagelkerken et al. (2002) demonstrated that 10 out of the 17 nursery species show absence or highly reduced densities of adults on reefs of islands completely lacking mangroves and seagrass beds. This suggests a high dependence of these nursery species on mangroves and seagrass beds, and implies that their density on the reef is a function of the presence of these habitats.

Previous studies have shown that in mangrove/seagrass dominated bays juvenile fish can also utilize additional nursery habitats (Nagelkerken et al. 2000b, Nagelkerken and van der Velde 2002). Since presence of habitats can vary between bays and many fish species show ontogenetic shifts between habitats (Appeldoorn et al. 1997, Nagelkerken et al. 2000c, Cocheret de la Morinière et al. 2002), fine-scale studies on the distribution of fishes in coastal habitats are needed for a better understanding of the transitions between habitats and their role in regulating the extent of fish movement and survival (Appeldoorn et al. 1997). So far, very few studies have provided detailed size-frequency distributions of Caribbean fish in coastal habitats which could

TABLE 1

Number of transects sampled, and range in water depth, temperature, salinity and visibility (horizontal Secchi disk distance) of the selected bay and reef habitats in Curaçao (Spanish Water Bay) and Bonaire (Lac Bay). nd = no data. ¹Data from van Moorsel and Meyer (1993).

	Submerged							
	Channel Curaçao	mud flat Curaçao	Seagrass bed		Mangrove		Coral reef	
			Curaçao	Bonaire	Curaçao	Bonaire	Curaçao	Bonaire
Water depth (m)	5–6	1–5	0.4–2.0	0.4–1.4	0.4–1.1	0.3–1.2	0–18	0–25
Temperature (°C)	nd	nd	27.0–31.4	28.6–33.4	nd	28.5–34.0	26.2–29.7	26.8–29.8
Salinity (‰)	34–36	34–36	34–36	37–44	34–36	39–44	34–35	nd
Visibility (m)	nd	nd	2.7–14.6	4.6–21.6 ¹	nd	nd	10.1–24.7	nd
No. of transects sampled	32	89	87	84	85	196	108	372

indicate ontogenetic habitat shifts. The majority of studies on fish communities of coastal habitats did not distinguish between size classes or only studied one or two habitats. Lindeman et al. (2000) made a first attempt to provide such data by determining for a wide variety of reef fishes the shelf depth (3 depth ranges) and habitat (3 types) that juveniles and adults were associated with, and by inferring ontogenetic cross-shelf migrations from these data.

Overfishing has led to a decline in reef fish stocks world-wide (Russ 1991). Marine protected areas (MPAs), which have to prevent habitat loss or degradation, and marine fishery reserves, which are closed to all types of fishing, are becoming an increasingly popular tool to protect and manage coastal habitats and sustain reef fish populations. Several studies have shown that over time, reef areas protected from fishing show a significant increase in fish density and size, and even a spillover of fish to adjacent reef areas (see reviews by Roberts and Polunin 1991, 1993, Russ 1991, Roberts et al. 2001). As stated earlier, most of the 17 nursery species, which include several highly commercially important fish species (Dalzell 1996), show a high dependence on mangroves and seagrass beds. As a result of the spatial separation of juveniles and adults, it seems necessary to include these bay nursery habitats within MPA boundaries to sustain fish stocks on coral reefs.

In the present study, we investigated in detail (i.e. for size classes of 5 cm) the distribution of reef fishes in 8 different coastal habitats of two oceanic Caribbean islands to evaluate the importance of each of these habitats as nurseries and adult life-stage habitats, the type of possible ontogenetic cross-shelf migrations, and the degree of connectivity between these habitats. The

results are presented only for those species for which the data indicate a cross-shelf shift in habitat utilization, and are compared between the two islands.

MATERIALS AND METHODS

In Curaçao and Bonaire (Netherlands Antilles), fish densities were determined in several non-estuarine bay habitats and reef zones in size classes of 5 cm, by conducting visual counts along belt transects. This technique is rapid, non-destructive and inexpensive. It can be used for all selected habitats, the same areas can be resurveyed over time, and the results can be compared with those of many other studies (English et al. 1994). Disadvantages are interobserver differences in the accuracy with which fish abundance is estimated, and the fact that fish may be attracted to or scared off by the observers. Therefore, species identification and quantification of fish abundance and size were first thoroughly practiced by the three observers together, which served to reduce interobserver differences in abundance estimations. Cryptic and pelagic species were not included in the studies.

The two bays had relatively clear water (Table 1). The water temperature in all habitats ranged between 26.2 and 34.0° C. In Curaçao, water salinity was similar in the bay habitats and the coral reef, but in Bonaire salinity was clearly higher in the bay habitats. The mean daily tidal range in Curaçao and Bonaire is about 30 cm (de Haan and Zaneveld 1959).

Surveys in Curaçao

The study was carried out in Spanish Water Bay and on the coral reef in front and down-current of the bay

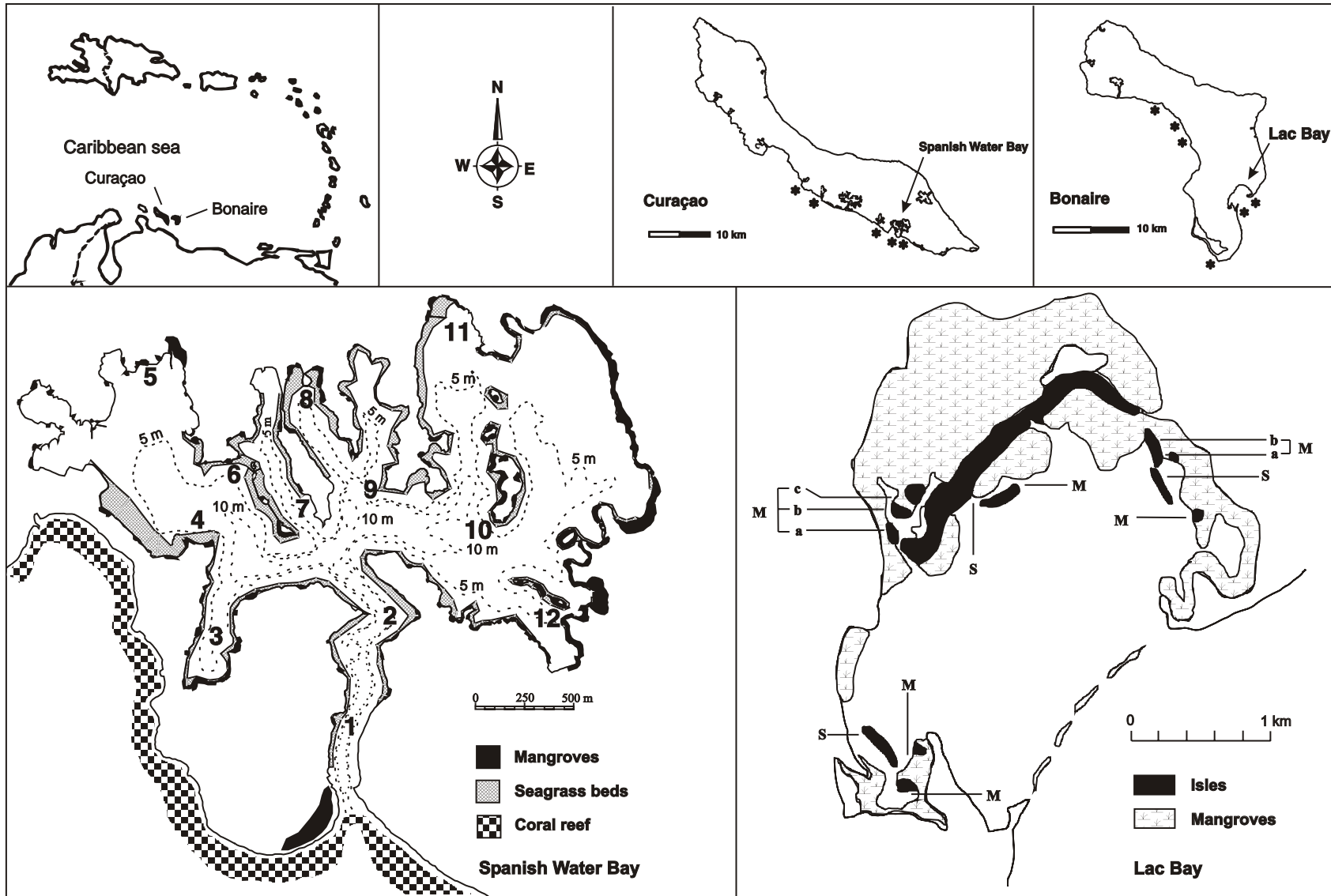


Figure 1. Map of Curaçao and Bonaire showing the study sites in the various habitats. * indicates location of reef sites. Spanish Water Bay: numbers 1–12 show the study sites in the bay; the 10 m isobath shows the location of the channel; the submerged mud flats are located between the seagrass beds and the channel. Lac Bay: M = mangrove sites; S = seagrass sites.

(Figure 1). The bay is connected to the sea by a relatively long (1 km) and deep (11–18 m) channel, which continues into the central part of the bay. Apart from the channel, the bay is relatively shallow (< 6 m depth). Four main habitats were selected in the bay: mangroves, seagrass beds, submerged mud flats and the channel (Figure 1). All habitats remained submerged during low tide. On the adjacent coral reef, depth zones of 0–3 m, 3–5 m, 10–15 m, and 15–25 m were studied. Differences in structural reef complexity were not recorded. All bay habitats had a muddy substratum, whereas the substratum on the reef was sandy.

Rhizophora mangle (red mangrove) was found along a large part of the shoreline of the bay. The mangrove stands studied were on average 27 ± 11 m long (i.e., distance along the shore) and 1.4 ± 0.5 m wide (i.e., from the outer mangrove fringe to the shoreline). The shoreline areas of the shallow parts of the bay were dominated by turtle grass, *Thalassia testudinum*. This seagrass species was found at a depth of 0.4–3 m, but in the turbid areas of the bay it extended only to a depth of about 1.5 m. Mean seagrass cover was $81 \pm 12\%$. The height of the seagrass was 22 ± 8 cm, at a density of 143 ± 66 seagrass shoots m^{-2} . At depths of 2–6 m, where light levels were low, *T. testudinum* was absent and submerged mud flats occurred with some growth of macroalgal species such as *Halimeda opuntia*, *H. incrassata*, *Cladophora* sp. and *Caulerpa verticillata* (Kuenen and Debrot 1995). The density, areal cover and height of the algal canopy were very low (cover mostly < 20%; height < 10 cm). The muddy slopes of the channel were scattered with fossil reef rocks (10–100 cm in size), which were almost completely overgrown by filamentous algae. The soft bottom of the channel was almost completely devoid of vegetation. The fringing coral reef extended continuously along the entire south-western coast of the island. From the shore, a submarine terrace (shelf) gradually sloped to a ‘drop-off’ at a depth of about 6–8 m, where the reef sloped off steeply.

Twelve study sites in Spanish Water Bay (Figure 1), and five reef sites on a 12-km long tract of the coral reef beyond the bay were selected. For each bay habitat, four replicate transects were randomly selected at each of the study sites (Table 1). All transects in all habitats were surveyed during the daytime: once in the period November 1997–March 1998 and once in August 1998. The transects on the seagrass beds, submerged mud flats and coral reef measured 3 x 50 m, while those in the channel measured 3 x 25 m because of the smaller area of this habitat. Isolated stands of mangrove were selected and

surveyed completely. The band of mangroves fringing the shoreline was narrow (up to 2 m), permitting a complete census. Because the mud flats were distributed over a relatively wide depth range, for a representative sample of the fish community, the transects were surveyed close to shore at 2-m depth as well as in the deeper parts of the bay at 5-m depth. Snorkeling gear was used for the surveys in the mangroves, seagrass beds and mud flats at 2-m depth, whereas SCUBA gear was used on the mud flats at 5-m depth, in the channel and on the coral reef. The transects were marked by a thin rope, placed at least 30 minutes before the survey began, in order to minimize disturbance effects. In Curaçao, the complete fish fauna was surveyed, but size-frequency diagrams are only shown for those species for which the data indicate a cross-shelf ontogenetic shift in habitat utilization, and for which sufficient data within the size classes are available. For data on the other fish species see Nagelkerken and van der Velde (2002).

Surveys in Bonaire

The study was carried out in Lac Bay, which is the largest bay in Bonaire with an area of approximately 8 km² (Figure 1). The bay consists of a shallow basin (0–3 m deep) and is protected from wave exposure by a shallow barrier of dead and living corals. The bay is connected to the sea by a short, narrow channel which is about 5–7 m deep. Two main habitats were selected in the bay: mangroves and seagrass beds (Figure 1). On the coral reef, depth zones of 0–3 m, 3–5 m, 10–15 m and 20–25 m were studied. The soft-bottom flora of the bay was dominated by the seagrass *T. testudinum* and the calcareous alga *H. opuntia*. Other common vegetation consisted of the seagrass *Syringodium filiforme* and the alga *Avrainvillea nigricans*. The bay was bordered almost completely by extensive stands of the mangrove *R. mangle*. The coral reef was situated in front of the bay and continued around the entire southern and western shore of the island.

In contrast to Curaçao, a selection of only fourteen reef fish species was studied in Bonaire. The selection was based on their abundance, economic importance and non-cryptic behavior (Nagelkerken et al. 2000c): *Haemulon flavolineatum*, *H. sciurus*, *H. chrysargyreum*, *Ocyurus chrysurus*, *Lutjanus mahogoni*, *L. apodus*, *L. griseus*, *Acanthurus chirurgus*, *A. bahianus*, *A. coeruleus*, *Sparisoma viride*, *Sphyraena barracuda*, *Chaetodon capistratus* and *Abudefduf saxatilis*.

In each of the six habitats, permanently marked belt transects were established (Table 1). In the seagrass

beds, a transect of 300 x 3 m was established at three different sites. In the mangroves, nine transects were established of 3 m wide and 25–100 m length. On the coral reef, six sites were selected and, at each site, transects of 3 x 100 m were established at four depth zones (Figure 1). During May–November 1981, visual censuses were done by two trained observers together in the morning (9:00–11:00 hrs) and in the afternoon (14:00–16:00 hrs) by means of snorkeling or SCUBA diving. The census in each transect was repeated at monthly intervals.

RESULTS

In Curaçao, a total of 114 species were encountered in the various bay and reef habitats. Of these species, at least 20 showed a difference in habitat utilization between small/juvenile fish and large/adult fish (Table 2). Of the 14 selected species in Bonaire, which were the same species (except *Sparisoma viride*) as the group of 20 species in Curaçao, 13 species showed a difference in habitat utilization between small/juvenile fish and large/adult fish. In general, at both islands the small size classes of these species were only observed in shallow-water habitats (i.e. mangroves, seagrass beds, channel, coral reef of 0–3 m), whereas the large size classes were observed on the coral reef. The families which were best represented among the 21 pooled species of both islands showing a differential habitat utilization between young and old fishes, were Lutjanidae (5 species), Scaridae (5 species), Haemulidae (4 species) and Acanthuridae (3 species). The juveniles of these species belong to either of two feeding guilds: zoobenthivores or herbivores (Table 2).

Haemulidae

Juvenile *Haemulon flavolineatum*, *H. sciurus* and *H. plumieri* were mainly observed in the mangroves and seagrass beds (some *H. flavolineatum* also occurred on the shallow reef of Bonaire), whereas the adults were observed on the (deeper) coral reef (Figure 2). In Curaçao, juveniles of the former two species were most abundant in the mangroves, whereas in Bonaire they were most abundant in the seagrass beds. The mangroves formed an intermediate habitat for *H. sciurus* in Bonaire. Juvenile *H. plumieri* also utilized the channel as a nursery habitat. The pattern for *H. chrysargyreum* clearly differed between the two islands. In Curaçao the channel was the most important nursery habitat, whereas in Bonaire it was the shallow reef. Furthermore, in Bonaire

the adults were also common in the juvenile habitat. Not shown is the size-frequency distribution of *H. parra* in Curaçao, because large individuals were not encountered in any of the habitats. Juveniles of 1–15 cm were observed in the mangroves and observations from another survey in Curaçao (Dorenbosch, van Riel, Nagelkerken and van der Velde unpubl. data) showed that larger specimens reside on the coral reef, although in very low densities, suggesting that this species also shows an ontogenetic cross-shelf migration.

Lutjanidae

In Curaçao, *Ocyurus chrysurus* utilized three different nursery habitats (primarily the channel, and also mangroves and seagrass beds), while in Bonaire the seagrass beds formed the main nursery habitat (Figure 3). Juvenile *Lutjanus mahogoni* were most abundant in the seagrass/mangroves in Curaçao, and in the seagrass beds and on the reef of 0–3 m and 3–5 m in Bonaire. The deeper reef was the main habitat for adult *O. chrysurus*, *L. mahogoni* and *L. apodus*. For *Lutjanus apodus* and *L. griseus* the mangroves were the main nursery habitat. The channel formed an important intermediate and adult life-stage habitat for *L. griseus* in Curaçao. On both islands, adult *L. griseus* were mainly observed in bay habitats (mangroves or channel) but also occurred on the coral reef; in Curaçao large specimens on the reef were only observed outside the reef transects. Juveniles of *L. analis* were equally abundant in the mangroves and seagrass beds; larger specimens utilized the submerged mud flats as an intermediate life-stage habitat. Very large individuals were not very abundant on the coral reef and were more often observed in the channel.

Acanthuridae

Juvenile *Acanthurus chirurgus* utilized a wide range of nursery habitats: mangroves, seagrass beds and the shallow coral reef at both islands, and in Curaçao also the channel (Figure 4). Large specimens were observed on the deeper coral reef, but in Curaçao they were also abundant in the channel. For *A. bahianus*, the main nursery habitat was the shallow coral reef. The utilization of the deeper reef by adults was more obvious in Curaçao than in Bonaire, where some adults were still observed in the juvenile habitat. The pattern of *A. coeruleus* in Curaçao was similar to that of *A. bahianus*. In Bonaire, *A. coeruleus* utilized a much wider range of nursery habitats than in Curaçao: the mangroves, seagrass beds, the reef of 0–3 m and reef of 3–5 m.

Table 2

Habitats containing highest densities of small and large specimens of different fish species in various bay and reef habitats of Curaçao (Spanish Water Bay) and Bonaire (Lac Bay). Gray areas indicate most important habitats (abundance > 40% within any size class). + = important habitats (abundance 20–40% within any size class).

	Species group ¹	Feeding guild ² (juveniles)	Maximum size (cm) ³	Smallest size classes						Minimum size (cm) ⁴	Largest size classes						Main cross-shelf migration ⁵	Habitat dependence: bays ⁶	Habitat dependence: islands ⁷	
				Mangrove	Seagrass bed	Channel	Reef 0–3 m	Reef 3–5 m	Reef 10–15 m		Reef 15–25 m	Mangrove	Seagrass bed	Channel	Reef 0–3 m	Reef 3–5 m				Reef 10–15 m
<i>Haemulon flavolineatum</i>	N	BI	10							15										
Curaçao				+	+													M→R	M+S	-
Bonaire				+	+		+						+	+	+			S→R		
<i>Haemulon sciurus</i>	N	BI	20							20										
Curaçao				+							+							M→R	S	+
Bonaire				+	+										+			S→M→R		
<i>Haemulon chrysargyreum</i>	R	BI	10							10										
Curaçao				+		+												C→R		
Bonaire							+								+	+		SR→R		
<i>Haemulon plumieri</i>	N	BI	15							15										
Curaçao				+	+	+									+			M/S→R	nd	+
<i>Ocyurus chrysurus</i>	N	PI/BI	15							20										
Curaçao				+	+	+									+	+	+	C/M→R	M+S	+
Bonaire					+											+	+	S→R		
<i>Lutjanus mahogoni</i>	N	BI	10							20										
Curaçao				+	+													M→R	S	-
Bonaire					+		+	+										SR→R		
<i>Lutjanus apodus</i>	N	BI	20							30										
Curaçao				+											+			M→R	S	+
Bonaire				+	+						+							M→R		
<i>Lutjanus griseus</i>	N	BI	15							15										
Curaçao				+		+									+	+	+	M→C→C/R ⁸	S	+
Bonaire				+	+						+							M/S→M/R		
<i>Lutjanus analis</i>	N	BI	15							25										
Curaçao				+	+										+			M/S→SMF →C/R	M+S +SMF	+
<i>Acanthurus chirurgus</i>	N	H	10							15										
Curaçao				+	+	+	+								+			M/S→C→C/R	nd	-
Bonaire					+		+								+	+	+	S/SR→R		
<i>Acanthurus bahianus</i>	R	H	10							15										
Curaçao							+								+	+	+	SR→R		
Bonaire					+		+								+	+	+	SR→R		
<i>Acanthurus coeruleus</i>	R	H	5							5										
Curaçao							+								+	+	+	SR→R		
Bonaire					+		+	+							+	+	+	unclear		

Table 2. Continued.

	Species group ¹	Feeding guild ² (juveniles)	Maximum size (cm) ³	Smallest size classes						Minimum size (cm) ⁴	Largest size classes						Main cross-shelf migration ⁵	Habitat dependence: bays ⁶	Habitat dependence: islands ⁷
				Mangrove	Seagrass bed	Channel	Reef 0–3 m	Reef 3–5 m	Reef 10–15 m		Reef 15–25 m	Mangrove	Seagrass bed	Channel	Reef 0–3 m	Reef 3–5 m			
<i>Sparisoma viride</i>	R	H	10																
Curaçao							+	+					+	+	+	+	+	unclear	
Bonaire							+						+	+	+	+		S→R	
<i>Scarus iserti</i>	N	H	10																
Curaçao							+	+					+	+	+	+		C→R	M+S +
<i>Scarus coeruleus</i>	N	H	15																
Curaçao							+	+					+					C/S→R	nd +
<i>Scarus guacamaia</i>	N	H	20																
Curaçao							+	+										M→R	nd +
<i>Sparisoma chrysopterygum</i>	N	H	15																
Curaçao							+	+	+				+	+				C/M→C/R	S -
<i>Sphyrna barracuda</i>	N	P	40																
Curaçao							+											M→M/R	S +
Bonaire							+											M→M/R	
<i>Chaetodon capistratus</i>	N	H	5																
Curaçao							+	+					+					M→R	M+S -
Bonaire							+	+					+	+				M→R	
<i>Abudefduf saxatilis</i>	R	O	10																
Curaçao																			
Bonaire							+											SR→R	
Bonaire							+											SR→R	
<i>Gerres cinereus</i>	N	BI	15																
Curaçao							+											M→M/C/R	none -

¹following Nagelkerken et al. (2000b): N = nursery species, R = reef species (see text for definition)

²feeding guild: BI = benthic invertebrate feeder, PI = planktonic invertebrate feeder, H = herbivore, P = piscivore, O = omnivore

³upper size limit for smallest size classes

⁴lower size limit for largest size classes

⁵main cross-shelf migration is derived from absolute densities: M = mangrove, S = seagrass bed, C = channel, SMF = submerged mud flat, SR = shallow reef, R = reef

⁶shows the obligate habitats in bays for juveniles of nursery species; data derived from Nagelkerken et al. (2001a); nd = no data

⁷shows which nursery species are absent/scarce as adults on the reefs of islands where mangroves/seagrass beds are completely lacking; data from Nagelkerken et al. (2002)

⁸as inferred from fish observed outside of transects

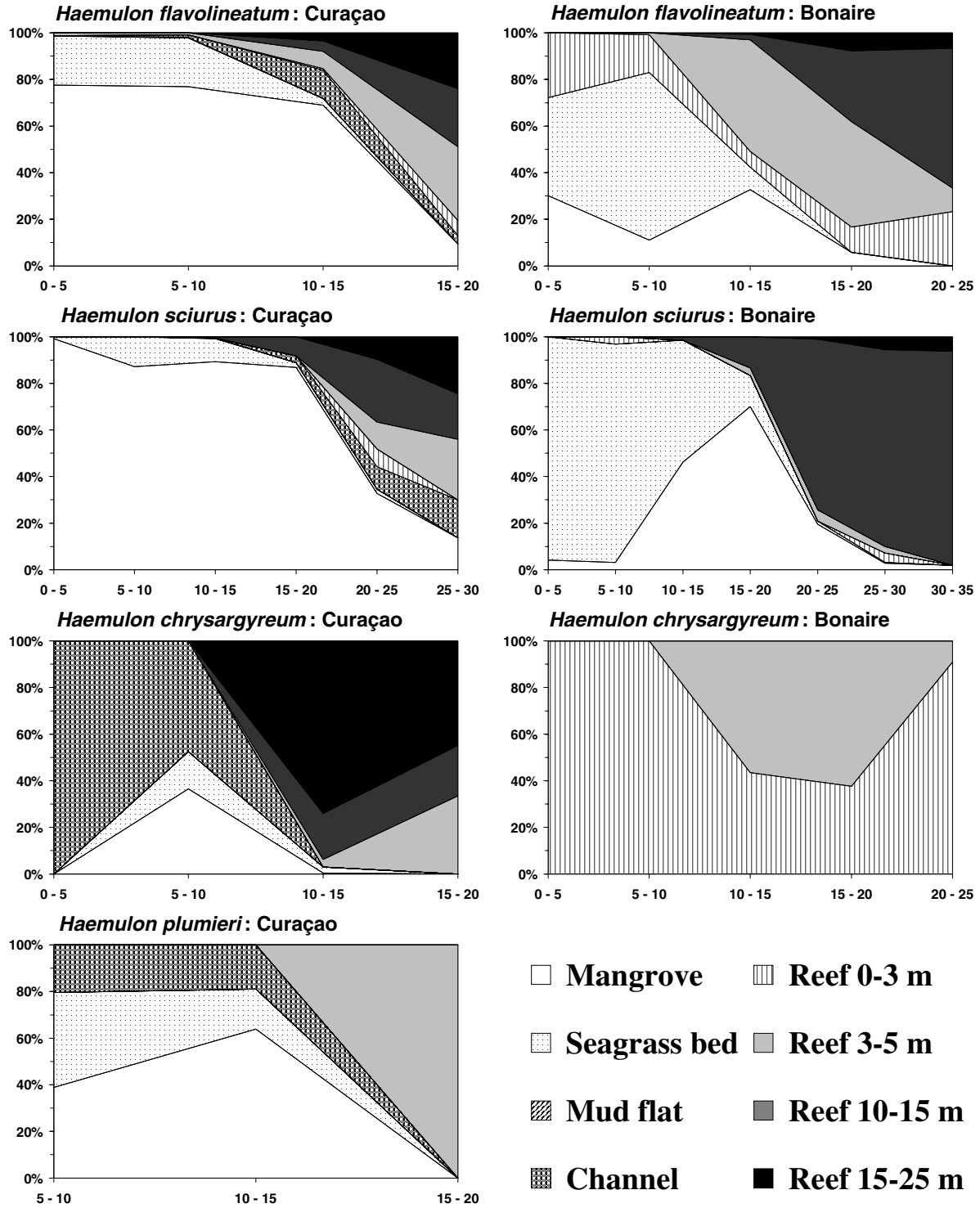


Figure 2. Size-frequency diagrams for species of Haemulidae in various habitats of Curaçao and Bonaire. X-axis shows size classes in cm; Y-axis shows relative density (%). Mud flats refer to the submerged mud flats.

CONNECTIVITY BETWEEN COASTAL HABITATS

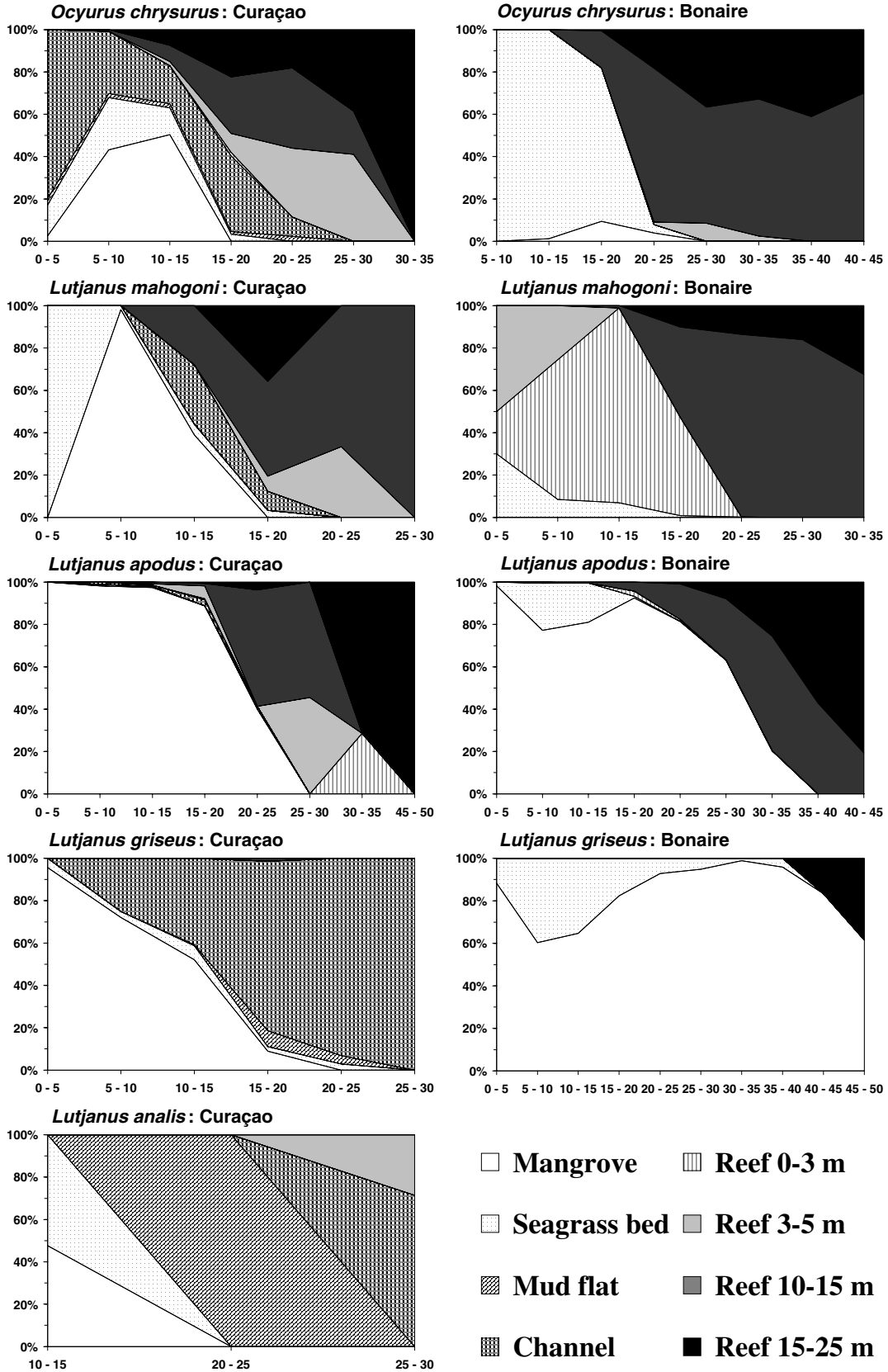


Figure 3. Size-frequency diagrams for species of Lutjanidae in various habitats of Curaçao and Bonaire. For figure legends see Figure 2.

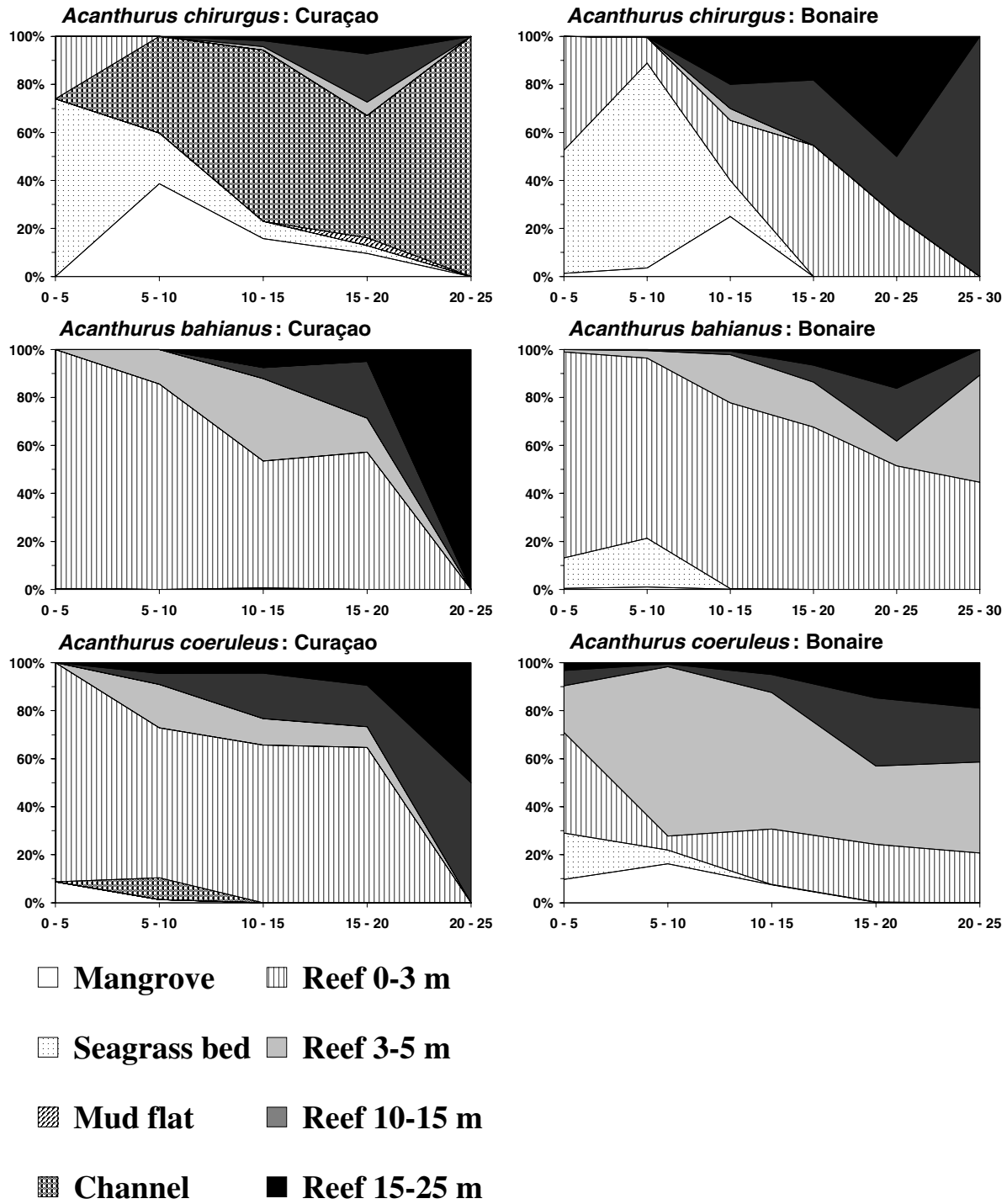


Figure 4. Size-frequency diagrams for species of Acanthuridae in various habitats of Curaçao and Bonaire. For figure legends see Figure 2.

Scaridae

In Curaçao, juvenile *Sparisoma viride* utilized almost all habitats as nurseries (Figure 5). Adults were observed on the entire reef, but were absent or rare in the bay habitats. In Bonaire, juveniles mainly utilized the seagrass beds, and adults utilized the coral reef. For *Scarus iserti* in Curaçao the main nursery habitat was the channel, in combination with the mangroves and seagrass beds, while the adults were mainly observed on the coral reef. In Curaçao, juvenile *S. coeruleus* were observed in the channel and seagrass beds, and adults on the shallow coral reef; juvenile *S. guacamaia* were mainly observed in the mangroves, whereas large individuals were observed on the reef of 10–15 m. *Sparisoma chrysopterum* utilized all four shallow-water habitats except the submerged mud flats as a nursery in Curaçao, of which the mangroves and channel were the most important. Adult *S. chrysopterum* showed a partial utilization of the reef, and adult densities remained high in the channel.

Other families

At both islands, *Sphyraena barracuda* utilized the mangroves as the main nursery habitat and the coral reef as well as the mangroves as the adult habitat (Figure 6a). For *Chaetodon capistratus*, the main nursery habitat was the mangroves and the adult habitat the coral reef (Figure 6b). Other important nursery habitats were the channel in Curaçao and the seagrass beds in Bonaire. Juveniles of *Abudefduf saxatilis* were mainly observed on the shallow coral reef whereas the larger individuals utilized the deeper coral reef (Figure 6c). *Gerres cinereus* utilized the mangroves as a nursery habitat and the mangroves, channel and shallow reef as the adult habitat (Figure 6d).

DISCUSSION

Species showing a cross-shelf shift in habitat utilization

Of the total fish community observed, at least 21 species showed a difference in habitat utilization between small/juvenile and large/adult fishes. The strict spatial separation between juveniles and adults indicates an ontogenetic migration across the reef shelf from shallow-water nursery grounds to deep-water lifetime habitats, and implies a high degree of connectivity among these habitats. Previous studies, on single species or a small selection of fish species, have also suggested cross-shelf ontogenetic migrations based on differences in size distribution among habitats on the

shelf (e.g., Starck and Schroeder 1971, Baelde 1990, Sedberry and Carter 1993, Appeldoorn et al. 1997 and references therein, Lawson et al. 1999, Nagelkerken et al. 2000c, Cocheret de la Morinière et al. 2002). Appeldoorn et al. (1997) presented three scenarios for cross-shelf migrations, depending on the width of the shelf and distribution of habitats: 1) presence of suitable adult habitat across the entire (wide) shelf results in a variable adult distribution ranging from near-shore to off-shore, 2) when juvenile and adult habitat are spatially separated across the (wide) shelf, adult migration is clearly directed off-shore and adult migration distances can be much larger than for scenario 1, and 3) at oceanic islands with a narrow shelf adult migration routes will be short and directed off-shore. The present study shows that the ontogenetic shifts suggested for the 21 fish species emphasized in Curaçao and Bonaire all fall under category 3. The data further show that ontogenetic shifts between different juvenile habitats may occur before the actual shift to the adult habitat takes place. This clearly indicates the importance of fine-scale size-frequency data for multiple species over a wide range of habitats for a better understanding of the connectivity among habitats and their utilization.

In a more general study (based on three depth ranges across the shelf) in the region between North Carolina and South Florida, Lindeman et al. (2000) distinguished at least 50 reef species that show some degree of ontogenetic cross-shelf migration (i.e., migrating from areas < 10 m to areas > 30 m depth). These included all species of Lutjanidae and Haemulidae in the present study. The much larger number of species showing ontogenetic shifts than in the present study may be explained by the much wider shelf. In Curaçao and Bonaire, the shelf is just 150–250 m wide. This means that fish do not have much choice of shallow-water habitats other than the narrow shallow reef and the bay habitats. In addition, because of the narrow shelf and the steeply sloping reef on the two islands, depth zones between 5 and 25 m are situated closely to one another. This means that in the present study a shift from 5 or 10 m to 15 m is not considered a real cross-shelf migration, whereas in the case of a less steep and much wider shelf (as in Lindeman et al. 2000) this would be the case.

Two cross-shelf ontogenetic patterns in habitat utilization could be distinguished in the present study (Table 2): 1) for the nursery species group the data mainly indicated an ontogenetic shift from bay habitats to the coral reef; and 2) for the reef species group the data generally indicated an ontogenetic shift from the

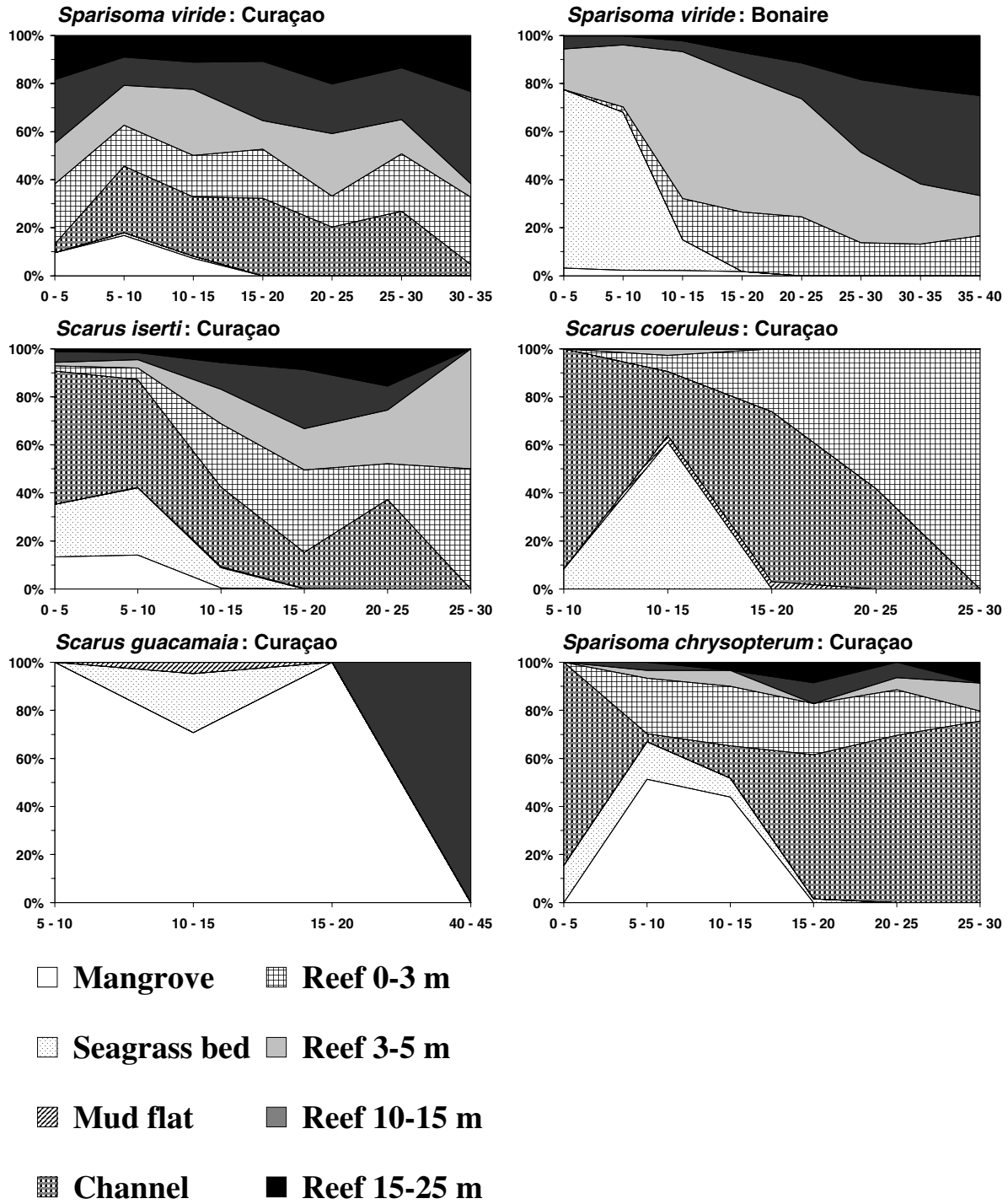


Figure 5. Size-frequency diagrams for species of Scaridae in various habitats of Curaçao and Bonaire. For figure legends see Figure 2.

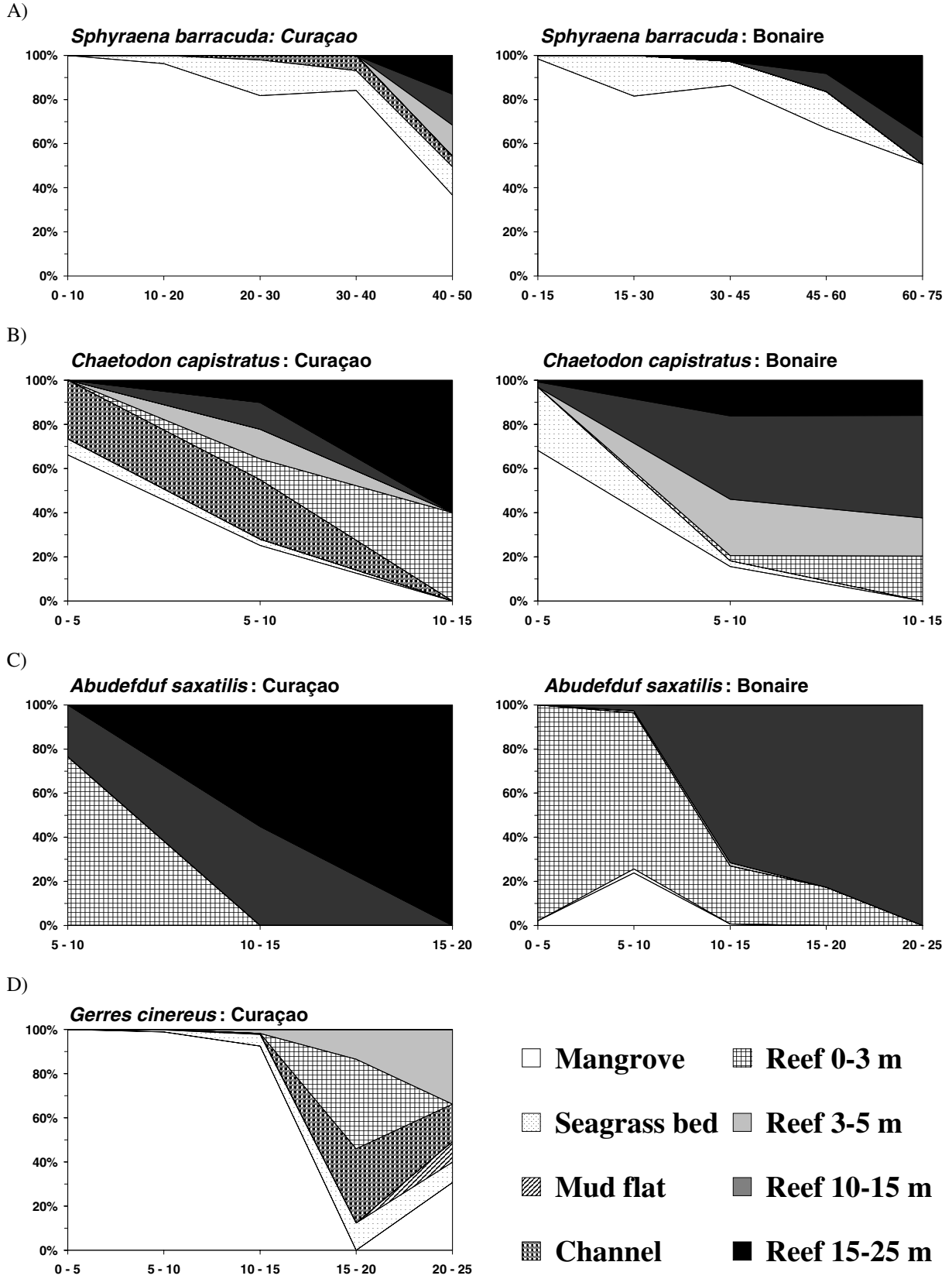


Figure 6. Size-frequency diagram for A) *Sphyraena barracuda*, B) *Chaetodon capistratus*, C) *Abudefduf saxatilis*, and D) *Gerres cinereus* in various habitats of Curaçao and Bonaire. For figure legends see Figure 2.

shallow coral reef (sometimes in combination with bay habitats) towards the deeper coral reef. For both species groups, several congeneric species (i.e., other than the 21 species discussed) did not show a cross-shelf ontogenetic migration and were present on the coral reef throughout their benthic life cycle (Nagelkerken and van der Velde 2002, Nagelkerken et al. unpubl. data). Several common fish families thus consist of species which appear to show an ontogenetic shift from bay habitats or the shallow reef to the (deeper) coral reef and species where no cross-shelf shift occurs at all. These different strategies in habitat utilization by juvenile fish may have the advantage that they temporarily alleviate competition for food and space between life stages within species and between congeneric species (Sedberry and Carter 1993, Cocheret de la Morinière et al. 2002).

Importance of shallow-water habitats

All species for which the data indicated a cross-shelf ontogenetic shift in habitat utilization utilized shallow-water habitats as nurseries. Lindeman et al. (2000) observed that at least 80% of juvenile Lutjanidae and Haemulidae settle in the depth range of 0–10 m. Shallow-water habitats are advantageous to the juveniles because they are frequented less often by predators from the coral reef (Shulman 1985). A second advantage of shallow-water habitats, in particular bay habitats, is that they often contain a much higher abundance of food than the coral reef (Parrish 1989, Nagelkerken et al. 2000a). The latter advantage may explain the dominance of zoobenthivoric or herbivoric species in the bay habitats; abundance of benthic invertebrates and submerged aquatic vegetation is higher in these habitats than on the reef (Nagelkerken et al. 2001b). A third important aspect is the degree of shelter (Parrish 1989). The data show that the mangroves are the most widely used day-time nursery habitat (Table 2), while the submerged mud flats are hardly utilized by small fishes. The greater utilization of mangroves is most likely explained by a higher structural complexity (Nagelkerken et al. 2000b), and not by a higher food abundance, since the submerged mud flats contain much higher food densities than the mangroves (Nagelkerken et al. 2000a). However, this shelter function is only present during day-time. At night the mangrove shelter is left and fish migrate to the more open seagrass beds and submerged mud flats to feed (Nagelkerken et al. 2000a).

The majority of the 21 species were observed in one to three different nursery habitats simultaneously during their juvenile life stage. However, various habitats were of varying importance for the various species,

indicating a clearly different habitat preference between species (Table 2). Some species occurred in an intermediate life-stage habitat, before appearing on the coral reef. The most obvious suspected shifts to intermediate habitats were: from seagrass beds to mangroves (*Haemulon sciurus* in Bonaire), from mangroves to the channel (*Lutjanus griseus* in Curaçao) and from seagrass beds/mangroves to the channel (*Acanthurus chirurgus*) or submerged mud flat (*L. analis*) in Curaçao. All these shifts were directed towards habitats which can harbor larger-sized fish, and may be caused by fishes outgrowing the protection of their early juvenile habitat. Other studies have suggested ontogenetic shifts for *H. flavolineatum*, *H. plumieri*, *H. sciurus*, *L. mahogoni* and *Ocyurus chrysurus* from seagrass beds/patch reefs to mangroves (intermediate life stage habitat) to coral reefs or open-water habitats. For *L. apodus*, *L. griseus* and *Sphyraena barracuda* shifts have been observed from the mangroves directly to adult populations (Thayer et al. 1987, Rooker and Dennis 1991, Rooker 1995).

Comparison between islands

Juveniles of several species (*Lutjanus apodus*, *L. griseus*, *Acanthurus chirurgus*, *A. bahianus*, *Sphyraena barracuda*, *Chaetodon capistratus*, *Abudefduf saxatilis*) showed a similar pattern in habitat utilization in Curaçao and Bonaire. In all cases this means a preference for either mangroves or the shallow reef as the main nursery habitat; for *A. chirurgus* an additional preference for seagrass beds was observed. Considering the different structure, size and presence of bay habitats between the two oceanic islands, the similar utilization of the above species for nursery habitats suggests a species-specific preference.

The remaining species (*Haemulon flavolineatum*, *H. sciurus*, *H. chrysargyreum*, *Ocyurus chrysurus*, *L. mahogoni*, *Acanthurus coeruleus*, *Sparisoma viride*) showed a difference in habitat utilization between islands. For the juveniles of all these species, except *A. coeruleus*, the juveniles in Bonaire utilized the seagrass beds or shallow reef as opposed to the mangroves or channel in Curaçao. The utilization of the channel in Curaçao shows that it forms a suitable alternative nursery habitat for several fish species (*H. chrysargyreum*, *O. chrysurus*, *L. griseus*, *A. chirurgus*, *Scarus iserti*, *S. coeruleus*, *Sparisoma chrysopterum*). The reason for the difference in use between mangroves and seagrass beds at the two islands by these species is unclear, but may possibly be related to differences in habitat structure (e.g., prop-root density, seagrass density and height) or environmental variables (e.g., salinity).

In estuaries with large seasonal variation in environmental variables (e.g., salinity, temperature, turbidity) fish community structure is often strongly affected by emigration or immigration of a variety of marine species (e.g., Blaber and Blaber 1980, Yáñez-Arancibia et al. 1988, Laegdsgaard and Johnson 1995). In Curaçao and Bonaire, however, environmental variables did not show large seasonal fluctuations and all 21 species of the present study occurred in the bay habitats throughout the year, although some temporal variation in fish densities was present (Nagelkerken et al. 2000c, Cocheret de la Morinière et al. unpublished data). Patterns in habitat utilization in Spanish Water Bay did not differ for 9 nursery species studied in two subsequent years of sampling, suggesting a stable species-specific pattern in habitat utilization (Cocheret de la Morinière et al. unpublished data). Furthermore, these patterns were strongly correlated to structural complexity of the habitat and food abundance, and not to environmental factors such as temperature, salinity or turbidity. Therefore, the temporal variation in sampling between Curaçao (1997/1998) and Bonaire (1981) may not have had a large effect on the observed patterns of habitat utilization by fishes. The effect on these patterns of a different sampling regime between the two islands is unknown.

Dependence on nursery habitats and importance of MPAs and reserves

Marine protected areas (MPAs) and marine fishery reserves are important tools for conservation of reef fish stocks (Roberts and Polunin 1993, Roberts et al. 2001). Many fishery reserves are located around coral reefs and in such case the only available nursery habitat for the 21 species of the present study would likely be the shallow coral reef. The data show, however, that for 16 out of these 21 species juvenile densities are highest in the mangroves, seagrass beds and channel, as opposed to only 5 species for which juvenile densities are highest on the shallow coral reef but also use bay habitats to a low degree. The question can then be raised: how flexible are these nursery species in adapting to alternative nursery habitats in the absence of their preferred bay habitats? Nagelkerken et al. (2001a) showed that juveniles of all nursery species (except *Gerres cinereus*) were absent or low in density in bays without mangroves and/or seagrass beds (Table 2). Moreover, Nagelkerken et al. (2002) showed absence or low densities of adults of 10 out of 16 nursery species on reefs of islands lacking mangroves and seagrass beds (Table 2). These two studies suggest a high dependence on these habitats. Lindeman et al. (2000), on the other hand, showed that

the newly settled stages of the same nursery species of Lutjanidae and Haemulidae of our study also utilized sediments and hard bottom or coral habitats. It is likely that this is caused by the presence of a wide shelf, where sand flats, hard substrate, patch reefs or coral boulders in shallow water may be used as alternative nursery habitats. Likewise, Lenanton (1982) found that shallow inshore marine environments (i.e., shelf areas with seagrass, rocks and weeds) could function as alternative nursery habitats to those traditionally found in estuaries. We believe that on oceanic islands with narrow shelves where fish do not have much choice of shallow-water habitats on the shelf, mangroves, seagrass beds and possibly channels (either separately or combined) located in bays, lagoons, estuaries or back-reef areas are an important requirement as nurseries for juveniles of several reef fish species.

The observation that various shallow-water bay habitats act as important nursery habitats for at least 10–16 fish species, as opposed to the majority of reef species which do not depend on these habitats and grow up on the coral reef, is not undermining the high importance of these bay habitats for fish communities. These species include some of the most common or commercially important reef fish species. It is hence suggested that the establishment of MPAs and fishery reserves in bay habitats located near coral reefs may enhance the fish stocks of some important reef fish species.

In Bonaire and Curaçao the distribution of mangroves and seagrass beds is restricted to semi-enclosed bays. In Curaçao, significant mangrove and seagrass nursery habitats occur in six inland bays. Total land area of Curaçao is 443 km², of which about 0.55 km² is mangrove (Pors and Nagelkerken 1998) and 0.66 km² is seagrass (60% of which is found in Spanish Water Bay). In Bonaire, significant mangroves and seagrass beds are only found in Lac Bay. Total land area of Bonaire is 288 km², of which roughly 1.8 km² is mangrove and 2.9 km² is seagrass (estimated from map in De Meyer 1998). It is likely that the restricted distribution of bays with nursery habitats on these two islands also results in an uneven along-shore distribution of adult nursery species on the coral reef. Nagelkerken et al. (2000b) found densities of adults of several nursery species to decrease strongly on the reef with increasing distance from the mouth of Spanish Water Bay. The same would be expected near Lac Bay, which would function as the only significant source of juveniles for some fish species. The question remains to what extent the various fish species move away from the coral reef near bays with increasing age or size. This depends, amongst

other things, on the distribution of the habitat, the width of the coastal shelf, and the life stage of the fish (Appeldoorn et al. 1997).

Because of their restricted surface area and distribution, and their high importance as nurseries for fishes, the mangroves and seagrass beds of these islands should have a status as MPAs to prevent loss of important nursery habitat. A large part of Lac Bay is already internationally protected as a RAMSAR site (De Meyer 1998), but in Curaçao the mangroves and seagrass beds are not officially protected. In Curaçao, especially Spanish Water Bay with its relatively large diversity and surface area of various nursery habitats should be designated as a MPA. MPAs need to incorporate a variety of habitats (Carr and Reed 1993, Lindeman et al. 2000), because they all fulfill an important function during different life stages of a fish species. Furthermore, especially the mangrove and seagrass nursery habitats of both islands should be also designated as marine fishery reserves. Benthic mortality of juvenile fish is often high (Shulman and Ogden 1987), and additional human fishing pressure on the juvenile life stage may negatively affect the eventual adult outflow from the bays toward the coral reef.

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