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# ARE NON-ESTUARINE MANGROVES CONNECTED TO CORAL REEFS THROUGH FISH MIGRATION?

*Ivan Nagelkerken*

## ABSTRACT

Mangroves are an important fish habitat, but little is known of their nursery function and connectivity to other habitats such as coral reefs. Here, the present status of knowledge on connectivity between non-estuarine mangroves and coral reefs by postlarval coral reef fishes is reviewed. Only since the year 2000 has more indirect evidence been obtained for such connectivity, largely based on studies: (1) quantifying juvenile/adult fish abundances in these habitats to deduce ontogenetic migrations, (2) investigating the effect of absence of mangroves on reef fish assemblages, (3) investigating the effect of mangrove forest size on reef fish abundances, and (4) investigating the effect of distance from mangroves on reef fish abundances. Almost all studies have been done in the Caribbean, and they are practically absent for the much larger Indo-Pacific region. So far, it appears that coral reef fish species do not show an obligate dependence on mangroves as a juvenile habitat, except perhaps for the vulnerable Caribbean parrotfish species *Scarus guacamaia* Cuvier, 1829. Six Caribbean species of Haemulidae and Lutjanidae show high dependence on mangroves/seagrass beds as juvenile habitats, and may be the most vulnerable to loss of these habitats. A study on otolith microchemistry has provided some evidence for one species that mangroves may indeed contribute to coral reef fish populations.

Mangroves are among the few terrestrial tropical plant species which can withstand continuous contact with seawater. Not all mangrove species grow along the shoreline, and a clear zonation of species from the shore inwards is often present. Species typically present along the shoreline and growing in direct contact with seawater or subject to daily tidal influences of marine water are mostly *Rhizophora mangle* Linnaeus, 1753 and sometimes *Avicennia germinans* (Linnaeus) Stearn, 1958 in the Caribbean, and *Sonneratia alba* J. Smith 1819, *Rhizophora mucronata* Lamarck, 1804 and *Avicennia marina* (Forsskål) Vierhapper, 1907 in the Indo-Pacific. The mangrove surface area subject to (periodic) salt water influence can range from a few square meters (in fringing mangroves) to several hectares (in large estuarine areas).

Mangroves can harbor a variety of fish species, depending on their setting within the coastal landscape and the influence of marine waters and rivers (i.e., influence of salinity). Species include freshwater, estuarine, and marine species, which visit the mangroves for spawning, foraging, shelter, or as a nursery habitat (Blaber, 2000). Mangroves are ideal habitats for many fish species because they provide a high abundance of food, and shelter against predation (Nagelkerken et al., 2000a; Laegdsgaard and Johnson, 2001; Cocheret de la Morinière et al., 2004; Verweij et al., 2006). The latter is the result of the high structural complexity of the mangrove prop-roots which can be used as shelter, the often high turbidity of the water, the dark mangrove environment which makes predation on fish less successful, and the distance away from coral reefs or offshore areas where densities of the largest fish predators are often highest (Shulman, 1985; Parrish, 1989; Manson et al., 2005).

The high abundance of juvenile fish (and prawns) in mangroves has been used for several decades as an argument that mangroves serve as important nursery areas. However, hardly any proof exists of true migration from mangrove nurseries to the

Table 1. Search results (on “topic”) from ISI Web of Science® (Thomson Corporation™) (15 March 2006). Asterisk (\*) denotes a wildcard to specify zero or more alphanumeric characters (e.g., “fish\*” includes the search terms “fish,” “fishes,” “fisheries,” etc.).

Search term	# hits
Reef* and Fish*	4,860
Mangrove* and Fish*	609
Mangrove* and Reef* and Fish*	147
Mangrove* and Reef* and Fish* and Link*	16
Mangrove* and Reef* and Fish* and Connect*	10

adult habitats on coral reefs or offshore areas, and mangroves may merely function as sinks for juvenile fish. According to Beck et al. (2001), habitats only serve as true nurseries when their contribution to adult fish populations is larger, on average, than that of other juvenile habitats. This should be supported by a higher density, growth, or survival of animals in the nursery habitat, and by ontogenetic migration between the nursery habitat and the adult habitat (Beck et al., 2001). By far the majority of studies have focused on fish densities in a variety of shallowwater habitats, whereas studies on growth, survival, and movement are largely lacking (Beck et al., 2001; Heck et al., 2003; Sheridan and Hays, 2003; Faunce and Serafy, 2006).

Although mangrove fish communities have been studied for several decades, little is known of their nursery function and their connectivity with surrounding habitats (Table 1). This is firstly the result of many studies focusing on only the mangrove habitat (e.g., prop-root system, creeks, channels) and not on other habitats as well. Secondly, in cases where multiple habitats have been surveyed, the fish communities of mangroves and their adjoining habitats mostly have been studied with different methods, making comparisons difficult. Thirdly, in very few cases did studies of (juvenile) mangrove fish communities include the adult fish habitat (i.e., offshore areas or coral reefs). Fourthly, in most cases only total densities of species are reported, without distinguishing between juvenile and adult fish so as to determine the distribution of size classes in different habitats. As a result, relatively little is known about connectivity between mangroves and other habitats, and only 12 studies could be used to investigate ontogenetic habitat utilization of juvenile and adult fish in mangroves and coral reefs (Table 2).

The focus of this review is on the present status of knowledge on connectivity between non-estuarine mangroves and coral reefs for postlarval coral reef fishes. The reason for this selection is based on the fact that most studies of mangrove fish communities have been done in estuaries. This is probably because many of the largest mangrove ecosystems are located there, many of which within a reasonable distance of marine laboratories. However, there are probably hundreds to thousands of (fairly isolated) islands around the world which harbor marine mangrove systems (i.e., not influenced by rivers) close to coral reefs. Very little is known of these systems, and although the size of the mostly small fringing mangrove stands on these islands is not comparable to the large mangrove forests in estuaries, on a local scale they possibly serve as important nursery or juvenile habitats that sustain and/or enhance the islands’ coral reef fish populations.

This review will not deal directly with the nursery function of mangroves, since several reviews on the potential mechanisms of the nursery function of (estuarine) mangroves and other habitats already exist (e.g., Parrish, 1989; Sheridan and Hays,

Table 2. Overview of studies including at least the mangrove and coral reef habitat, and distinguishing between juvenile and adult densities (or between size-classes), so as to deduce ontogenetic migration between habitats at species level (first section), followed by other studies related to mangrove–reef connectivity. M = mangroves, S = seagrass beds, SB = soft bottom, HB = hard bottom, N = subtidal notches in fossil coral reef terrace, C = channel, CR = coral reefs.

Reference	Habitats studied	Location	Geographic area
<b>Mangrove-reef ontogenetic studies</b>			
Thollot, 1992	M, CR	New Caledonia	Indo-Pacific
Rooker, 1995	M, CR	Puerto Rico	Caribbean
Nagelkerken et al., 2000b	M, S, SB, C, CR	Curaçao	Caribbean
Nagelkerken et al., 2000c	M, S, CR	Bonaire	Caribbean
Cocheret de la Morinière et al., 2002	M, S, CR	Curaçao	Caribbean
Nagelkerken and van der Velde, 2002	M, S, SB, C, CR	Curaçao	Caribbean
Christensen et al., 2003	M, S, CR	Puerto Rico	Caribbean
Nagelkerken and van der Velde, 2003	M, S, SB, C, CR	Bonaire/Curaçao	Caribbean
Serafy et al., 2003	M, CR	Florida, USA	Caribbean
Eggleston et al., 2004	M, S, HB, C, CR	Florida, USA	Caribbean
Mumby et al., 2004	M, S, CR	Belize/Mexico	Caribbean
Dorenbosch et al., 2006	M, S, N, CR	Aruba	Caribbean
<b>Mangrove-absence studies</b>			
Ogden et al., 1985	CR	Sombrero Island	Caribbean
Miller and Gerstner, 2002	CR	Navassa Island	Caribbean
Mumby et al., 2004	CR	Belize/Mexico	Caribbean
Dennis et al., 2005	CR	Mona Island	Caribbean
Dorenbosch et al., 2005	CR	Tanzania	Indo-Pacific
<b>Distance-to-mangrove studies</b>			
Thollot, 1992	CR	New Caledonia	Indo-Pacific
Nagelkerken et al., 2000b	CR	Curaçao	Caribbean
Appeldoorn et al., 2003	CR	Old Providence/ Santa Catalina	Caribbean
Halpern, 2004	CR	Virgin Islands	Caribbean
Dorenbosch et al., 2004	CR	Curaçao	Caribbean
Dorenbosch et al., 2005	CR	Tanzania	Indo-Pacific
Dorenbosch et al., 2006	CR	Aruba	Caribbean
Dorenbosch et al., 2007	CR	Aruba	Caribbean
<b>Mangrove-size studies</b>			
Halpern, 2004	CR	Virgin Islands	Caribbean
Mumby et al., 2004	CR	Belize/Mexico	Caribbean
<b>Otolith studies</b>			
Chittaro et al., 2004	M, CR	Belize	Caribbean

2003; Manson et al., 2005; Adams et al., 2006), while studies are still lacking which directly test the factors related to nursery function as proposed by Beck et al. (2001). Instead, studies providing (indirect) evidence for the existence of any connectivity between non-estuarine mangroves and coral reefs by fishes will be reviewed, whether or not the mangroves serve as true nurseries.

## MANGROVE-REEF CONNECTIVITY BASED ON SIZE-FREQUENCY DATA

Non-estuarine mangroves mostly co-occur with seagrass beds; hence, there are few studies which have been done in seascapes where only mangroves and adjacent coral reefs are present. The presence of seagrass beds in this seascape makes the habitat interactions more complex, since ontogenetic migrations can occur between mangroves and seagrass beds before fish potentially move to the coral reef (e.g., Rooker and Dennis, 1991; Nagelkerken et al., 2000c). Also, the combined presence of mangroves and seagrass beds may cause differences (i.e., enhancement) in fish density, species richness, and species presence (Robertson and Blaber, 1992; Nagelkerken et al., 2001). As a result, relatively little is known of the connectivity between solely mangroves and coral reefs.

In situations where seagrasses are absent, some indirect evidence has been obtained for mangrove-reef connectivity. In New Caledonia, Thollot and Kulbicki (1988) found an overlap of 13 species between the two habitats, and suggested that *Epinephelus caeruleopunctatus* (Bloch, 1790) and *Epinephelus howlandi* (Günther, 1873) utilize the mangroves as a nursery habitat. However, due to the lack of density and size-frequency data in the study, this conclusion is difficult to evaluate. In a more detailed study in the same bay, Thollot (1992) found an overlap of 43 species between the two habitat types, of which 13 species were found as juveniles in the mangroves and as adults on the coral reefs. These included species of Lutjanidae (*Lutjanus argentimaculatus* (Forsskål, 1775), *Lutjanus fulvivflamma* (Forsskål, 1775), *Lutjanus fulvus* (Forester in Bloch and Schneider, 1801), *Lutjanus russelli* (Bleeker, 1849)), Acanthuridae (*Acanthurus blochii* Valenciennes, 1835, *Acanthurus dussumieri* Valenciennes, 1835), Carangidae (*Caranx ignobilis* (Forsskål, 1775), *Caranx melampygus* (Cuvier, 1833), *Caranx papuensis* Alleyne and MacLeay, 1877), and species from four other families (*Hyporhamphus dussumieri* (Valenciennes, 1846), *Lethrinus harak* (Forsskål, 1775), *Parupeneus indicus* (Shaw, 1803), *Siganus lineatus* Valenciennes, 1835). However, juveniles of several of the above species were also found in other habitats (i.e., soft bottom, seagrass beds, and coral reefs), and the adults of these species also occurred in areas lacking extensive mangrove habitats (Table 3), suggesting that for most species mangroves are not obligate juvenile habitats of New Caledonia. In Papua New Guinea, coral reefs located adjacent to mangroves did not show a higher density of adult fish than isolated coral reefs, suggesting that the mangroves did not contribute significantly to the adult reef fish population (Birkeland and Amesbury, 1988). However, only total fish density for all species pooled was provided, masking possible effects at the species level.

Off southeastern Florida, Serafy et al. (2003) found juvenile as well as adult *Haemulon sciurus* (Shaw, 1803), *Haemulon parra* (Desmarest, 1823), *Lutjanus apodus* (Walbaum, 1792), *Lutjanus griseus* (Linnaeus, 1758), and *Sphyraena barracuda* (Walbaum, 1792) in mangroves and on adjacent coral reefs showing that mangroves are not exclusively juvenile habitats. For two species (*L. apodus* and *S. barracuda*) a clear mangrove-to-reef ontogenetic migration was inferred from length-frequency data, suggesting enhancement of local reefs. This is supported by Mumby et al. (2004), who found a significant increase in fish biomass (*Haemulon flavolineatum* (Desmarest, 1823), *Haemulon plumierii* (Lacépède, 1801), *H. sciurus*, *L. apodus*, *Ocyurus chrysurus* (Bloch, 1791), *Scarus iserti* Bloch, 1790) on shallow fore-reefs and deeper *Montastrea* spp. reefs located close to mangroves compared to reefs isolated

Table 3. Habitat utilization by juvenile fishes for species observed in non-estuarine mangroves, indicated for each study separately (+ = species common: density > 10% of highest density in any habitat, P = present (no density data provided), L = low density (< 10% of highest density in any habitat), - = absent). For the Indo-Pacific (New Caledonia, Tanzania) data are from: Thollot (1992) and Dorenbosch et al. (2005); for the Caribbean (Aruba, Bahamas, Belize, Bonaire, Curaçao, Florida, Mexico, Puerto Rico) data are from: Rooper (1995), Nagelkerken et al. (2000b,c), Cocheret de la Morinière et al. (2002), Nagelkerken and van der Velde (2002), Serafy et al. (2003), Eggleston et al. (2004), Mumby et al. (2004), Chittaro et al. (2005) and Dorenbosch et al. (2006). For habitat abbreviations see Table 2. EA = early juvenile habitat (< 5 cm FL, habitat contribution > 20% of total density of all habitats), ? = unknown; data are from Nagelkerken et al. (2000b) and Nagelkerken and van der Velde (2003). Isolot. = occurrence of adult fish on isolated reefs far away from mangroves/seagrass beds (P = species present–no density data provided, = = similar fish density as reefs close to mangroves/seagrass beds, R = reduced fish density compared to reefs close to mangroves/seagrass beds, - = absent); data are from Ogden et al. (1985), Nagelkerken et al. (2002), Miller and Gerstner (2002), Mumby et al. (2004), and Dennis et al. (2005). Dist. = decrease of reef fish density with distance from mangrove/seagrass beds (+ = decrease present, ± = potential decrease, - = decrease absent); data are from Thollot (1992), Nagelkerken et al. (2000b), Halpern (2004), and Dorenbosch et al. (2004, 2005, 2007).

Species	Juvenile habitat							Isolat.	Dist.
	EA	M	S	SB	HB	C	CR		
Indo-Pacific									
<i>Acanthurus blochii</i>		P					P	P	±
<i>Acanthurus dussumieri</i>		P					P		±
<i>Caranx ignobilis</i>		P						P	-
<i>Caranx melampygus</i>		P						P	-
<i>Caranx papuensis</i>		P						P	-
<i>Hyporhamphus dussumieri</i>		P						P	+
<i>Lethrinus harak</i>		P	P					R	+-
<i>Lutjanus argentimaculatus</i>		P						-	+±
<i>Lutjanus fulviflamma</i>		P	P					R	+-
<i>Lutjanus fulvus</i>		P	P					P	-
<i>Lutjanus russelli</i>		P							-
<i>Parupeneus indicus</i>		P		P				-	+-
<i>Siganus lineatus</i>		P							-
Caribbean									
<i>Acanthurus chirurgus</i>	S, CR	++L	+++	-		+	++L	=P-	+-
<i>Chaetodon capistratus</i>	M, S, C	++	++	L		+	+-	=P-	+-
<i>Gerres cinereus</i>	M	++	LL	L		L-	--	R--	-
<i>Haemulon chrysargyreum</i>	C, CR	+-	--	-		+	+-	R--	-
<i>Haemulon flavolineatum</i>	M, S, CR	++++	++++	L		L	++LL	=PR--	--
<i>Haemulon parra</i>	M	++	L	-		-	+-	---	
<i>Haemulon plumierii</i>	S	+	+	-		+	-	R----	
<i>Haemulon sciurus</i>	M, S	++++++	+++++L	L	L	L-	+LLLL--	RRR--	+-
<i>Hypoplectrus unicolor</i>	?	+	L	-		+	-	R-	
<i>Lutjanus apodus</i>	M	++++++	+LLL	L		LL	++LLL	PRRR	+++
<i>Lutjanus griseus</i>	M	+++++	+LLL	L	+	+L	+LL--	R--	
<i>Lutjanus mahogoni</i>	S, CR	++-	LL-	-		L	+L-	=P-	++-
<i>Mulloidichthys martinicus</i>	?	+	L	-		-	+	PP	-
<i>Ocyurus chrysurus</i>	S, C	+++L	++++	L		+	++++	RRRR-	+++
<i>Scarus guacamaia</i>	?	+++	L--	L		-	---	R---	-
<i>Scarus iserti</i>	S, C	+++	+++	L		+	+++	PPRR	--
<i>Sparisoma chrysopteron</i>	C	+	+	-		+	+	=PP	+-
<i>Sparisoma viride</i>	S, CR	+L	+L	-		+	++	PP	-
<i>Sphyraena barracuda</i>	M	++++	+LL	L		L-	+LL-	PR-	+-

from mangroves. However, these species were not completely absent on isolated reefs, possibly due to the presence of extensive seagrass beds that could have been used as an alternative juvenile habitat (e.g., Nagelkerken et al., 2000b). In the Caribbean area, therefore, it seems that mangroves alone are not obligate nursery habitats for juveniles of most reef fish species. The only exception may be the parrotfish *Scarus guacamaia* Cuvier, 1829, which is listed as a vulnerable species on the IUCN Red List of Threatened Species (International Union for Conservation of Nature and Natural Resources, 2007). Juveniles of these species are only found in mangroves (Nagelkerken and van der Velde, 2002; Mumby et al., 2004; Dorenbosch et al., 2006), and adults are (largely) absent on reefs isolated from mangroves (Nagelkerken et al., 2002; Mumby et al., 2004).

#### MANGROVE/SEAGRASS-REEF CONNECTIVITY BASED ON SIZE-FREQUENCY DATA

Studies related to mangrove-reef connectivity have mostly been conducted in seascapes with ample presence of seagrass beds. In this case it is difficult to distinguish the specific role of mangroves. Nevertheless, the results of these studies are reviewed here because at many oceanic islands, mangroves co-occur with seagrass beds in lagoons, embayments, or back-reef areas.

In the Indo-Pacific, very few studies have reported juvenile and adult densities in non-estuarine mangroves, seagrass beds, and coral reefs. Dorenbosch et al. (2005) examined 76 reef fish species in Tanzania and identified eight species for which the juveniles were predominantly (> 70% of total juvenile density) found in mangroves and/or seagrass beds, and adults predominantly on coral reefs. Of these, six species (*Cheilinus undulatus* Rüppell, 1835, *Hipposcarus harid* (Forsskål, 1775), *Lutjanus monostigma* (Cuvier, 1828), *Monodactylus argenteus* (Linnaeus, 1758), *Plectorhinchus flavomaculatus* (Cuvier, 1830), and *Scolopsis ghanam* (Forsskål, 1775) showed complete absence or a much lower adult density on coral reefs of an island (Grande Comoros) completely lacking mangroves/seagrass beds compared to reefs adjacent to bays harbouring mangroves/seagrass beds (Dorenbosch et al., 2005). Also some other species, which were only to some degree (< 70% of total juvenile density) associated with mangroves/seagrass beds during their juvenile stage, showed reduced densities on reefs isolated from these two habitats, possibly as a result of their partial dependence on mangroves/seagrass beds.

On Curaçao, Nagelkerken et al. (2000b) found an overlap of 38 species between mangroves and the adjacent coral reef. The most in-depth study on the distribution of juvenile and adult fish species in Caribbean shallow-water habitats, including mangroves and coral reefs, is by Nagelkerken and van der Velde (2002). They investigated habitat utilization of 50 coral reef species in four different bay habitats and at four different depth zones on the coral reef. Their results suggested a strong mangrove-to-reef ontogenetic migration for at least 10 species [*Chaetodon capistratus* Linnaeus, 1758, *H. flavolineatum*, *H. parra*, *H. sciurus*, *L. apodus*, *Lutjanus mahogoni* (Cuvier in Cuvier and Valenciennes, 1828), *S. guacamaia*, *Sparisoma chrysotum* (Bloch and Schneider, 1801), *S. barracuda*, and partially *Gerres cinereus* (Walbaum, 1792)], and a mangrove- and/or channel-to-reef ontogenetic migration for two species (*L. griseus*, *Ocyurus chrysurus*). The latter may also be true for *H. plumierii* (Nagelkerken and van der Velde, 2003). The above results are supported by other studies which were based on a smaller selection of fish species (Rooker, 1995; Nagelkerken et al.,



2000c; Cocheret de la Morinière et al., 2002; Christensen et al., 2003; Eggleston et al., 2004). When interpreting these data, however, the distinction between early and late stage juveniles should be considered. Juveniles may settle in one habitat (e.g., seagrass beds) and move to another habitat (e.g., mangroves) with increasing size, before making a final migration to the coral reef (Rooper and Dennis, 1991; Nagelkerken et al., 2000c; Christensen et al., 2003). The above results for mangrove-to-reef ontogeny are based on the late stage juveniles, but may be different for early stage juveniles. In Curaçao and Bonaire, the main settlement habitat for *H. plumierii*, *L. mahogoni*, and *O. chrysurus* is seagrass (and channel/reef) instead of mangroves, for *C. capistratus*, *H. flavolineatum*, and *H. sciurus*, mangroves as well as seagrass beds are used as settlement habitats, and only *G. cinereus*, *H. parra*, *L. apodus*, *L. griseus*, and *S. barracuda* settle predominantly in mangroves (Table 3). These data also apply to individual species on other islands (Rooper, 1995; Christensen et al., 2003; Eggleston et al., 2004).

On the coral reef, early juveniles of most of the above 13 species are either absent or found in very low densities (except for the occasional late stage juvenile), suggesting that in contrast to mangroves/seagrass beds, the reef is not an important juvenile habitat for these species in terms of fish density (Nagelkerken et al., 2000b; Nagelkerken and van der Velde, 2002). This probably explains why adult densities of these species are enhanced on coral reefs near bays harboring mangroves and seagrass beds (Table 3). In the complete absence of such bays, densities of *H. sciurus*, *L. apodus*, and *O. chrysurus* were highly reduced on the coral reef, while those of *G. cinereus*, *H. plumierii*, *L. griseus*, *S. guacamaia*, and *S. barracuda* were reduced in most cases (Nagelkerken et al., 2002). Furthermore, Miller and Gerstner (2002) found highly reduced densities of *O. chrysurus* and a complete absence of Haemulidae on the reefs of Navassa Island, while Ogden et al. (1985) found complete absence of six of the above eight species (the exceptions were *L. apodus* and *S. barracuda*) on the reefs of Sombrero Island; both islands lack mangroves and seagrass beds. Also on Mona Island with no mangroves and restricted seagrass areas, most of the above species were absent or showed reduced abundances (Dennis et al., 2005). These findings suggest that mangroves/seagrass beds contribute significantly to reef fish populations, although it does not appear that this dependence is obligate (i.e., that the species as such will not persist when these potential nursery habitats are absent). Survival of a few juveniles settling directly on the coral reef may potentially be sufficient to sustain the adult reef populations, merely because the total surface area of coral reefs is often much larger than that of fringing mangroves on small oceanic islands.

Reef fish densities of *C. capistratus*, *H. flavolineatum*, *L. mahogoni*, and *S. chrysotermum* were not reduced on coral reefs when bays harbouring mangroves/seagrass beds were absent, suggesting that these species show little dependence on these two habitats (Nagelkerken et al., 2002). On Mona Island, all four species were present (Dennis et al., 2005), however, three of the four species were absent from two other islands with little or no mangroves/seagrass beds: *H. flavolineatum* was absent from Navassa Island (Miller and Gerstner, 2002), while *C. capistratus*, *H. flavolineatum*, and *L. mahogoni* were absent from Sombrero Island (Ogden et al., 1985). Clearly, there is variability in the possible nursery roles of shallow-water habitats.

Some other coral reef species are also commonly found as juveniles in the mangroves (*Acanthurus chirurgus* (Bloch, 1787), *Haemulon chrysargyreum* Günther, 1859, *Hypoplectrus unicolor* (Walbaum, 1792), *Mulloidichthys martinicus* (Cuvier,



1829), *S. iserti*, *Sparisoma viride* (Bonnaterre, 1788); Table 3), but their densities are lower there compared to other shallow-water habitats (Nagelkerken and van der Velde, 2003), and mangroves probably play only a minor or negligible role in the life-cycle of these fish species.

Combining all of the above data, it appears that for all studied Caribbean islands at least seven species associated with mangrove/seagrass beds as juveniles are not present or have reduced adult densities on the reef when embayments harboring mangrove/seagrass beds are absent: *G. cinereus*, *H. parra*, *H. plumierii*, *H. sciurus*, *L. griseus*, *O. chrysurus*, and *S. guacamaia* (Table 3). These species may be the most vulnerable to loss of mangrove/seagrass habitats. This is also supported by Nagelkerken et al. (2001), who showed that juveniles of at least *H. parra*, *H. sciurus*, *L. griseus*, and *O. chrysurus* were absent or scarce in embayments lacking mangroves. An exception is *G. cinereus* which can use soft muddy substratum as an alternative habitat in the absence of mangroves (Nagelkerken et al., 2001, 2002). Although other species may depend less on the presence of mangroves/seagrass beds, these habitats could still enhance adult fish densities on adjacent coral reefs. For *H. flavolineatum*, *L. apodus*, *S. iserti*, and *S. barracuda*, the results are contradictory: some studies found absence or reduced adult densities on isolated reefs whereas other studies found no effect (Table 3), indicating a possible variability in habitat dependence of these species based on local difference in some combination of biotic and/or abiotic factors.

#### CONNECTIVITY BASED ON DISTANCE TO MANGROVES/SEAGRASS BEDS

Studies relating adult fish densities on the coral reef to proximity of mangrove/seagrass habitats have produced mixed results (Tables 2, 3). Halpern (2004) did not find a relationship between distance from mangroves and density of *G. cinereus* and *L. apodus* on the reefs of the Virgin Islands. Lack of a relationship with distance to mangroves/seagrass beds was also found off Aruba for 14 of the 15 reef species associated with mangroves/seagrass beds as juveniles (Dorenbosch et al., 2006, 2007), and for *C. capistratus*, *H. flavolineatum*, and *S. iserti* off Curaçao (Nagelkerken et al., 2000b). Other studies in the Caribbean as well as in the Indo-Pacific have reported relationships with distance to embayments or areas harboring a combination of mangroves and seagrass beds. For example, off Curaçao, reef densities of *A. chirurgus*, *L. apodus*, *L. mahogoni*, *O. chrysurus*, *S. chrysopteron*, and *Stegastes dorsopunicans* (Troschel, 1865) decreased exponentially with distance from an embayment (Nagelkerken et al., 2000b), while densities of *H. sciurus*, *L. apodus*, *L. mahogoni*, *O. chrysurus*, *Scarus coeruleus* (Bloch, 1786), and *S. barracuda* were significantly higher on reefs adjacent to embayments harboring mangroves and seagrass beds than on reefs adjacent to embayments without these two habitats and on reefs located away from mangroves/seagrass beds (Dorenbosch et al., 2004). In Old Providence/Santa Catalina, Appeldoorn et al. (2003) found that the biomass of Lutjanidae and Haemulidae was four times greater on patch reefs near mangrove/seagrass areas than on patch reefs farther away (> 9 km) from these areas. In Tanzania, Dorenbosch et al. (2005) showed that adult densities of species which occurred commonly as juveniles in mangrove/seagrass beds (> 70% of total juvenile density from all habitats) were higher on reefs adjacent to an embayment harbouring mangrove/seagrass beds than on reefs located further away (17 km on average) from these two habitats. This was the case for 14 out of 18 species, with significant differences for five (*Cheilio*

*inermis* (Forsskål, 1775), *C. undulatus*, *P. flavomaculatus*, *S. ghanam*, *Scarus ghoban* (Forsskål, 1775). From the data of Thollot (1992) in New Caledonia, it can be deduced that *Hyporhamphus dussumieri* and possibly three other species (*L. argentimaculatus*, *A. blochii*, *A. dussumieri*) show a decrease in density on the reef with distance away from the mangroves.

It is not clear why the above studies obtained different results, but one of the possible explanations is that most species are not obligately dependent on mangroves because they can use seagrass beds as alternative juvenile habitats. In this case, relating fish densities to distance from mangroves may give ambiguous results because presence of nearby seagrass beds is not considered. Secondly, variation in species-specific dispersal of adults on the reefs, and the specific habitat configuration and habitat size within the marine seascape may also interact with this relationship.

#### CONNECTIVITY BASED ON MANGROVE SIZE

Studies of the linkage between fish stocks on the reef and non-estuarine mangrove size are almost non-existent (Table 2). Mumby et al. (2004) found a significant effect of mangrove extent on reef fish community structure, but did not elaborate to species level. Halpern (2004) found a positive relationship for *G. cinereus* between total island mangrove size and reef fish density, but not for *L. apodus*. The latter may have been caused by an interaction with fishing pressure (Halpern, 2004).

#### CONNECTIVITY BASED ON OTOLITH STUDIES

Elements from seawater are continuously incorporated into the otoliths of fishes during their growth, thus otoliths can provide a history of different habitats (with different water quality) in which a fish has lived during its ontogeny (e.g., Gillanders and Kingsford, 2000; Gillanders, 2002). While many studies of otolith microchemistry have been conducted in temperate areas or tropical estuaries, only one published study was done in non-estuarine mangroves and coral reefs. Using otolith microchemistry, Chittaro et al. (2004) determined that 36% of 39 individuals of *H. flavolineatum* from a coral reef had probably passed through a mangrove nursery. If we calculate binomial 95% confidence limits about their percentage (i.e., 23%–52%), the upper limit suggests substantial connectivity, and thus enhancement, of reef fish populations, whereas the lower does not.

#### CONCLUDING REMARKS

This review shows that studies of mangrove-reef connectivity are dominated by those from the Caribbean region. Studies conducted in the much larger Indo-Pacific region are mostly concentrated on estuarine mangroves, which often lack adjacent coral reefs. It is likely that due to the absence of directly adjacent reefs and/or very different environmental variables (e.g., turbidity, salinity) in estuaries compared to non-estuarine lagoons and embayments, studies in the Indo-Pacific have concluded that mangroves play a minor role in this region as a potential nursery habitat for coral reef fishes compared to the Caribbean. Of the very few studies done in non-estuarine mangroves with adjacent reefs in the Indo-Pacific (Thollot, 1992; Dorenbosch et al., 2005), evidence suggests that these two habitats are possibly connected. I argue here

that when more studies are done on Indo-Pacific islands with non-estuarine mangroves and adjacent coral reefs, the importance of mangroves (possibly in combination with seagrass beds) may prove to be greater than assumed thus far.

Most studies have provided indirect evidence of mangrove-reef connectivity based on size-frequency studies. Direct evidence of this connectivity is still lacking (except for a small study by Chittaro et al., 2004). New or advanced techniques such as otolith microchemistry, stable isotope analysis, DNA analysis, and use of internal micro-tags or transponders have recently become more readily available at lower costs, providing new opportunities for investigating the connectivity between tropical coastal habitats by fishes. The present need for studies related to habitat connectivity has already been amply discussed in other reviews (Parrish, 1989; Beck et al., 2001; Gillanders et al., 2003; Heck et al., 2003; Sheridan and Hays, 2003; Manson et al., 2005; Adams et al., 2006; Dahlgren et al., 2006) and applies to the issue of mangrove—reef connectivity. Among the most urgent questions are whether mangroves contribute to coral reef fish populations, the magnitude of the contribution, the distance fish disperse from their nursery areas and the extent of spatio-temporal variability in nursery contribution.

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