Habitat selection during settlement of three Caribbean coral reef fishes: Indications for directed settlement to seagrass beds and mangroves

Abstract—We studied the settlement patterns of three Caribbean coral reef fishes in three different habitat types: mangroves, seagrass beds, and coral reefs. The settlement patterns of the three species were not random and could best be explained by active habitat selection during settlement. *Acanthurus bahianus* preferentially settled on the shallow reef flat and in adjacent seagrass beds, *Lutjanus apodus* settled exclusively into mangroves, and *Ocyurus chrysurus*, settled into both mangroves and seagrass beds. The settlement patterns of these three species reflect their habitat utilization during later juvenile stages. This study, therefore, suggests that the higher juvenile densities in mangroves and seagrass beds are determined by habitat selection during settlement rather than by post-settlement processes. This habitat selection during settlement is in accordance with the assumed importance of mangroves and seagrass beds as juvenile habitats of coral reef fishes and underlines the pressing need for their conservation.

Most coral reef fishes attain considerable swimming capabilities at the end of their pelagic life stage and possess highly developed visual, auditory, and olfactory senses enabling them to actively locate and navigate toward coastal areas (Leis et al. 2002; Fisher et al. 2005). These capabilities may enable reef fish larvae to locate optimal habitats for settlement (i.e., defined as the transition from the pelagic to the benthic environment) in a heterogeneous coastal landscape encompassing several shallow-water habitats (e.g., shallow coral reefs, algal beds, mud flats, seagrass beds, and mangroves). Seagrass beds and mangroves are assumed to function as important nursery habitats for several species of coral reef fish because of the high availability of shelter and food and the low predation pressure (Beck et al. 2001; Mumby et al. 2004). Caribbean bays with seagrass beds and mangroves often contain higher densities of juveniles (Nagelkerken et al. 2000), and reef sites adjacent to these nursery habitats have significantly larger adult populations as compared to reef sites lacking such nearby nursery habitats (Dorenbosch et al. 2004; Mumby et al. 2004; Dorenbosch et al. 2006).

To reduce mortality rates during their early post-settlement life stage, it would be advantageous for coral reef fish to settle directly into habitats that offer optimal survival rates (Adams and Ebersole 2004). We hypothesized that species that use mangroves and seagrass beds as nursery habitats differ in their settlement pattern from species that do not use these habitats during their juvenile stage. However, little is known about the active habitat selection of pelagic larvae during their settlement. The settlement of reef fish larvae into mangroves and seagrass beds has been documented previously, but few studies have monitored settlement simultaneously in different nursery

habitats as well as on adjacent coral reefs (Adams and Ebersole 2004). Hence, the extent to which spatial variation in juvenile densities between nursery habitats and adjacent reef sites are a function of active habitat selection during settlement, as opposed to post-settlement processes such as post-settlement migration, predation, and competition (Carr and Hixon 1995; Steele and Forrester 2002), remains unclear.

To test our hypothesis, we analyzed the settlement patterns of three coral reef fish species in three different habitat types—mangroves, seagrass beds, and shallow coral reefs—in a tropical Caribbean lagoon. The Schoolmaster (*Lutjanus apodus*, Lutjanidae) is highly associated with mangroves during its juvenile life stage, the Yellowtail snapper (*Ocyurus chrysurus*, Lutjanidae) with both seagrass beds and mangroves, and the Ocean surgeonfish (*Acanthurus bahianus*, Acanthuridae) mainly with shallow coral reefs (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002). We hypothesized that settlement patterns of these species would reflect their juvenile habitat utilization, with *A. bahianus* settling predominantly into shallow reef areas, *L. apodus* into mangroves, and *O. chrysurus* into both mangroves and seagrass beds.

Material and methods—The study was carried out in the mangroves and seagrass beds of Spanish Water Bay and on the adjacent coral reef on the Caribbean island of Curaçao, Netherlands Antilles (Fig. 1). This secluded bay is situated on the leeward coast of Curaçao and is connected to the sea by a relatively long (1 km) and narrow (35–70 m) entrance channel. The bay (3 km²) is relatively shallow (largely <6-m deep), harboring extensive monospecific seagrass beds (*Thalassia testudinum*) and fringing mangrove stands (*Rhizophora mangle*). The coral reef is located directly adjacent to the entrance channel. Underwater visibility was high in all sites, with mean (±SD) secchi disk visibility of 6.4 (±1.9) m in the bay and 21.3 (±5.4) m on the coral reef. During the period 04 May to 03 September 1998, settlement was monitored twice a week (except during 18–31 May and 15–28 June 1998) by means of underwater visual census surveys of 35 permanent belt transects in seven study sites located in Spanish Water Bay and on the adjacent coral reef (Fig. 1). In each seagrass site, three 3 m × 50 m belt transects were placed (N_{tot} = 18 transects; Table 1), and in each mangrove site, one to three mangrove transects of various sizes were selected, depending on the sizes of the mangrove stands (N_{tot} = 8 transects; *see* Table 1 for transect sizes). On the coral reef, three different depth zones of 5, 10, and 15 m were investigated. At each depth, three 3 m × 50 m belt transects were placed running parallel to the shoreline (N_{tot} = 9 transects; Table 1). Visual census surveys were performed using snorkeling gear
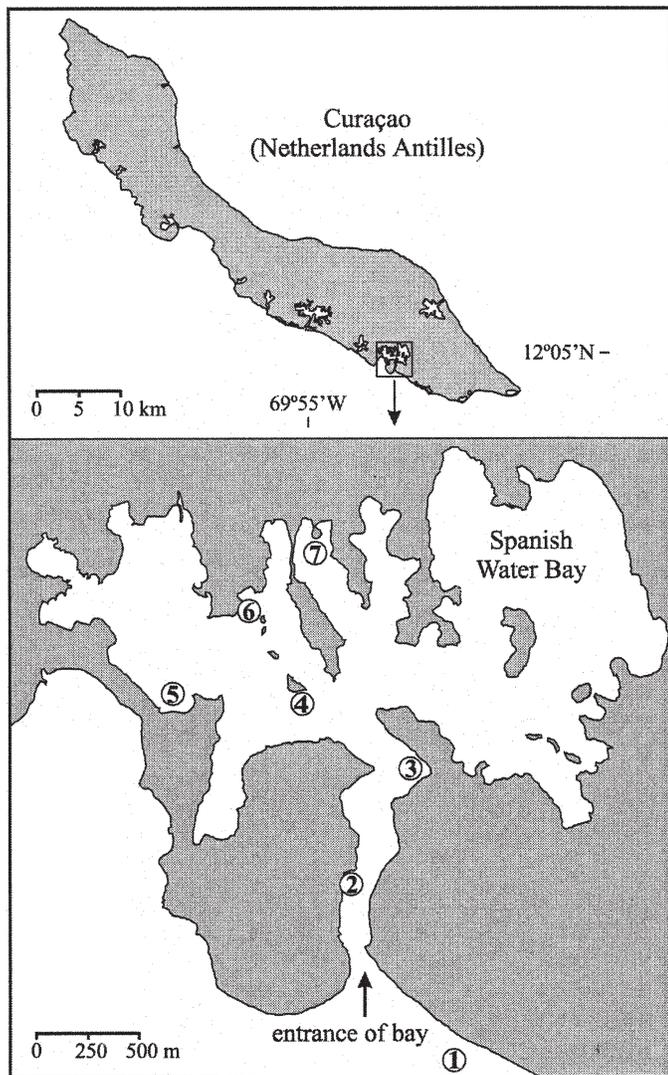
Fig. 1. Map of Spanish Water Bay showing the locations of the study sites on the coral reef (site 1), in the channel (sites 2 and 3), and in the bay (sites 4 to 7).

in the mangrove and seagrass sites (sites 2–7), and using SCUBA on the coral reef (site 1). Because studies have shown that the standard length at settlement of these three species ranges between 1.5 cm and 3.5 cm (Robertson 1988; Watson et al. 2002; Fisher et al. 2005), all individuals smaller than 5 cm were recorded. To estimate the sizes at settlement for each species, a number of newly settled individuals were captured, and their standard length measured. New settlers of all three species could easily be identified to the species level during the visual surveys.

Results and discussion—Inferences of habitat selection by larvae during settlement are difficult because of the impact of post-settlement processes, which may significantly alter the initial spatial distribution of newly settled individuals within a period of a few weeks (Carr and Hixon 1995; Steele and Forrester 2002). To exclude possible effects of post-settlement processes, only data from the first days at the peak of the settlement were used to determine the spatial distribution of newly settled individuals. For all three species, settlement occurred in distinct peaks. For *A. bahianus*, settlement was first observed on 02 June, whereas settlement of *O. chrysurus* and *Lutjanus apodus* was first observed on 17 August (Fig. 2). New settlers ranged in standard length between 2.5 cm and 3.5 cm for *A. bahianus* and 1.5 cm to 2.5 cm for *O. chrysurus* and *L. apodus*, which is comparable to settlement sizes reported from other studies in the Caribbean (Robertson 1988; Watson et al. 2002; Fisher et al. 2005).

A pronounced difference in spatial patterns of settlement was observed between the three coral reef fish species. Settlement of *A. bahianus* was observed predominantly on the shallow coral reef (at 5 m; densities ranging from 298 fish 150 m^{-2} to 344 fish 150 m^{-2}) and, to some extent, in the nearby seagrass beds located in the channel entrance (sites 2 and 3; densities ranging from 0 fish 150 m^{-2} to 31 fish 150 m^{-2}; Fig. 3). The settlement of *O. chrysurus* was observed in both the seagrass beds (densities ranging from 0 fish 150 m^{-2} to 500 fish 150 m^{-2}) and mangroves (ranging from 0 fish 150 m^{-2} to 640 fish 150 m^{-2}), located

Table 1. Surveyed habitat types, site numbers, number of transects, transect sizes, number of surveys, and total surveyed areas per site in Spanish Water Bay and the adjacent coral reef (Curaçao, the Netherlands Antilles) during 04 May–03 September 1998 (Site numbers correspond to locations indicated in Fig. 1).

|	Site	Habitat type	No. of transects	Transect size (m^2)	No. of surveys	Total surveyed area (m^2)
Reef	1	Reef 15 m	3	150	25	11,250
		Reef 10 m	3	150	25	11,250
		Reef 5 m	3	150	25	11,250
Channel	2	Seagrass beds	3	150	29	13,050
	3	Seagrass beds	3	150	29	13,050
		Mangroves	2	46.8/50.0	27	2,613.6
Bay	4	Seagrass beds	3	150	28	12,600
		Mangroves	1	80.3	27	2,168.1
	5	Seagrass beds	3	150	28	12,600
		Mangroves	2	60.2/13.0	27	1,976.4
	6	Seagrass beds	3	150	28	12,600
	7	Seagrass beds	3	150	28	12,600
		Mangroves	3	79.8/53.6/45.0	29	5,173.6
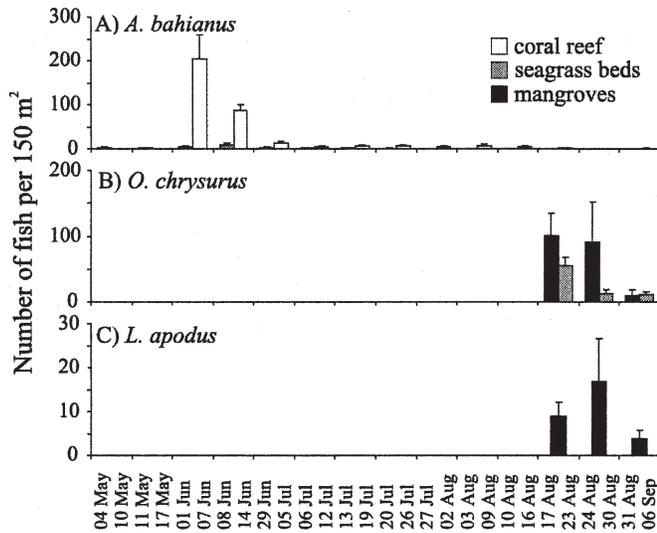
Fig. 2. Weekly mean (±SE) densities per 150 m² of newly settled individuals in different habitat types in Spanish Water Bay and on the adjacent coral reef (Curaçao, Netherlands Antilles) for (A) *A. bahianus*, (B) *O. chrysurus*, and (C) *L. apodus*, during 04 May–03 September 1998.

in the channel and the bay areas (sites 2–7; Fig. 3). Observed densities in the seagrass beds were much higher than those reported by Watson et al. (2002), who found mean abundances at peak settlement of 3–11 fish per 150 m² in *Thalassia testudinum* beds of the British Virgin Islands (Caribbean). The settlement of *L. apodus* was observed exclusively in the mangroves in the bay area (i.e., sites 5 and 7; Fig. 3). During the entire survey period not a single settler of *O. chrysurus* or *L. apodus* was observed on the coral reef, whereas settlers of *A. bahianus* were not observed in the bay area (Fig. 3).

These results show clear differences in settlement habitat between the three species: mangroves for *L. apodus*, mangroves and seagrass beds for *O. chrysurus*, and shallow coral reefs (and to some extent seagrass beds in close proximity to the shallow reefs) for *A. bahianus*. It is highly unlikely that these spatial patterns have arisen from passive dispersal by oceanographic currents. Spanish Water Bay is a fairly secluded bay devoid of strong currents and with a very small tidal range (average daily tidal range is approximately 30 cm). Moreover, the different habitat types in Spanish Water Bay are located very close to each other, making passive dispersal by means of different oceanographic currents as a cause for the observed patterns unlikely. If spatial variation in settlement was solely caused by oceanographic currents, then *O. chrysurus* and *L. apodus*, which arrived simultaneously to Spanish Water Bay, would have shown a similar settlement pattern. The observed differences in settlement patterns are best explained by active habitat selection of the larvae during their settlement. It is known that the late pelagic stages of Lutjanidae and Acanthuridae are among the strongest swimming reef fish larvae, capable of swimming against relatively strong currents (Fisher et al. 2005). Wilson and
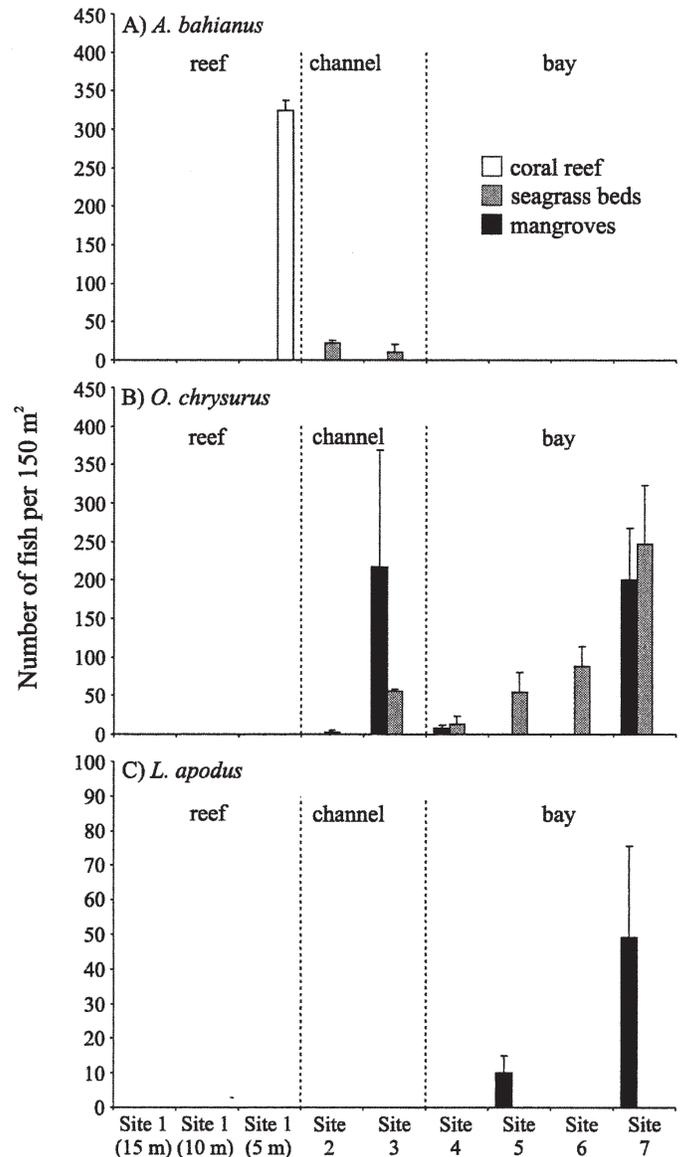

Fig. 3. Mean (±SE) densities per 150 m² of newly settled individuals in different sites and habitats in Spanish Water Bay and on the adjacent coral reef at peak settlement for (A) 01–02 June for *A. bahianus*, (B) 17–18 August for *O. chrysurus*, and (C) 20–24 August for *L. apodus*.

Meekan (2001) showed that the supply of *L. apodus* larvae to the San Blas Archipelago could not be explained by their model of surface currents, and concluded that active behavior of the larvae, and not oceanographic currents, affected the replenishment at the end of the planktonic stage.

Several studies have shown a strong preference by settling *A. bahianus* for shallow patch-reef and rubble habitats over lagoon habitats (e.g. seagrass beds, algal beds, and sand flats) in St. Croix, U.S. Virgin Islands (Adams and Ebersole 2004). However, to our knowledge, this is the first study that shows a strong active habitat selection during settlement of coral reef fish for nursery habitats (mangroves for *L. apodus* and mangroves and seagrass beds

for *O. chrysurus*) as opposed to coral reefs. These observations are particularly remarkable since *O. chrysurus* and *L. apodus* have to bridge considerable obstacles to reach these preferred nursery habitats. First, the larvae have to pass through a "wall of mouths" (sensu Hamner et al. 1988) that is surrounding the reef face, then swim through the entire channel before reaching the bay area, and subsequently locate and swim to the seagrass beds and mangroves. Such migrations require a considerable amount of energy and are associated with high predation risks, yet offer the potential benefit of reaching habitats that provide a high availability of shelter and food and a low predation pressure (Beck et al. 2001).

The present study shows that settlement patterns are not random, suggesting that different coral reef fish species exhibit different settlement strategies, with nursery species (sensu Nagelkerken et al. 2000) actively selecting seagrass beds and/or mangroves instead of shallow coral reefs. Moreover, differences in habitat utilization during later juvenile life stages of all three species known from literature (Robertson 1988; Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002) correspond closely with the different settlement patterns observed in this study. It is therefore suggested that the higher juvenile densities in mangroves and seagrass beds (found in many studies; Beck et al. 2001; Adams et al. 2006) are mainly determined by habitat selection during settlement, rather than by post-settlement processes. This study, herewith, provides new information to the standing debate on the importance of nursery habitats, such as mangroves and seagrass beds, for adult fish populations on the coral reef (Beck et al. 2001; Mumby et al. 2004; Adams et al. 2006) and underlines the pressing need for their conservation.

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