

SPACE USE OF *LUTJANUS APODUS* INCLUDING MOVEMENT BETWEEN A PUTATIVE NURSERY AND A CORAL REEF

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ABSTRACT

To study space use of snappers in a putative nursery area (a Caribbean embayment with mangroves and seagrass beds) and their movement to the presumed adult habitat (a coral reef), 59 sub-adult schoolmaster snappers *Lutjanus apodus* (Walbaum, 1792) were caught in the embayment, tagged individually, and surveyed from 17 to 90 d. Most fishes ($n = 48$) were resighted only inside the embayment: 94% of all resightings were located along the structurally complex rocky bay shoreline. The maximum linear distance between resightings was small within days (median distance moved = 5 m), and larger across days (median distance = 34 m). Fishes showed high fidelity to daytime shelter sites: 80% of all resightings were within a 10 m radius around a 2 m wide core area of presence. Four of the largest *L. apodus* (size range 17.8–20.0 cm) were resighted 1–30 times (over 31 d) on the adjacent coral reef, and they showed larger maximum distances between resightings across days (median distance = 217 m) than *L. apodus* that were only resighted in the embayment (median distance = 28 m). This is the first study providing direct evidence of connectivity between a putative nursery area in a tropical non-estuarine embayment and the adult coral reef habitat, based on observations of tagged fishes.

Ontogenetic migration of coral reef fish species that use putative nursery habitats such as mangroves and seagrass beds when juvenile, and the coral reef when reaching maturity, remains to be directly quantified. Such “nursery species” seem to use different habitat types during different life-stages in order to minimize mortality and maximize growth (Dahlgren and Eggleston, 2000; Adams et al., 2006). Up to now, the presumed nursery function and ontogenetic habitat shifts are mostly inferred from (1) different size-frequency distributions of fish in the various juvenile and adult habitat types (e.g., Appeldoorn et al., 1997; Nagelkerken et al., 2000b; Nakamura and Sano, 2004), (2) the distribution of fish along coastal coral reefs near and far away from the presumed nursery habitats in embayments (Dorenbosch et al., 2004a; 2005; 2007), and (3) the absence or low densities of adults of so-called nursery species on coral reefs of islands where these habitats are not present or very scarce (Nagelkerken et al., 2002; Mumby et al., 2004; Dorenbosch et al., 2005). Despite all this indirect evidence, actual ontogenetic migration by individual fishes from the nurseries to the coral reef has never been demonstrated, although such information is very important for the conservation of interlinked habitat types that function as complete ecosystems (Beck et al., 2001; Gillanders et al., 2003).

Recent technological developments hold great promise for elucidating such migration patterns by the use of markers or tracers such as stable C and N isotopes (Fry et al., 1999; Rubenstein and Hobson, 2004) and trace elements in otoliths (Chittaro et al., 2004). In tropical non-estuarine regions, however, these methods may lack discriminative power, due to the relatively small spatial scales involved (Chittaro et al., 2005), and due to absence of freshwater input giving distinct signatures to coastal regions. For instance, a recent otolith microchemistry study of the schoolmaster

snapper *Lutjanus apodus* (Walbaum, 1792) showed that there was too much overlap in elemental signatures between reef and mangrove habitats separated by 1–54 km to indicate movement between them (Chittaro et al., 2006). Therefore, observing movements of artificially tagged fishes may be a more reliable and direct method when studying movements between nurseries and the coral reef.

Among the so-called “nursery species” are many snappers (Lutjanidae). Studies on movements of young snappers have focused on their daily migrations during twilight between daytime resting habitats in mangroves and nighttime feeding habitats in soft bottom substrates, such as seagrass beds. These studies, however, only infer movement and habitat connectivity by comparing daytime and nighttime fish abundances (Rooker and Dennis, 1991; Nagelkerken et al., 2000c). Other than these migrations, virtually nothing is known about other types of movement and site fidelity in back-reef habitats. Only two short (< 2 wks) studies report on site fidelity of tagged juvenile snappers in Caribbean seagrass beds [*Ocyrurus chrysurus* (Bloch, 1791): Watson et al., 2002] and in Indo-Pacific rocky shoreline structures [*Lutjanus fulviflamma* (Forsskål, 1775): Dorenbosch et al., 2004b].

We studied the movement patterns of snappers in a putative nursery area (a shallow Caribbean embayment with mangroves and seagrass beds) and movement to the presumed adult habitat (the coral reef). We tagged sub-adult *L. apodus* caught along the eroded fossilized coral shoreline of this embayment, located adjacent to a living coral reef. We surveyed these fishes over 17–90 d and examined: (1) daytime activity radii (linear distances moved), (2) fidelity to diurnal resting sites, and (3) the extent of movement among rocky shoreline structures, mangrove patches, a bay channel, and the adjacent coral reef.

METHODS

STUDY AREA.—Our study was conducted in Spanish Water Bay (surface area ~3 km², depth of most areas < 6 m) on the southwestern coast of Curaçao, Netherlands Antilles (Fig. 1). The bay entrance is narrow and shallow (70–100 m wide, 5–8 m deep) and a relatively long (1.1 km) and deep (11–18 m) channel connects the inland embayment to an adjacent continuous fringing reef that extends westward and eastward outside of the bay and follows the coastline of the island. The bay shoreline is formed by a fossil coral reef terrace with shaded notches, crevices, and boulders (de Buissonjé and Zonneveld, 1960), which we refer to as “rocky shoreline”. Part of this bay shoreline is fringed by *Rhizophora mangle* (Linnaeus, 1753), of which the roots are permanently inundated (mean tidal range is ca. 30 cm; de Haan and Zaneveld, 1959). The bay also harbors seagrass beds, predominantly *Thalassia testudinum* (Bank ex König, 1805).

The selected study area included: the west side of (a) the channel-shaped bay area, (b) the bay mouth and start of the coral reef (0.5–5.0 m deep), and (c) the fringing coral reef extending outwards from the bay (Fig. 1). In the western channel-shaped bay area, the four fringing mangrove stands and rocky shoreline were marked by a 540 m long nylon twine line attached to the substratum (depth 0.2–1.0 m) and following the contours of the shoreline at a distance of approx. 3 m from the high tide waterline (Fig. 1). To demark the channel habitat, a 200 m long nylon line was placed which followed the channel drop-off at a depth of 3–4 m (Fig. 1). Both bay transects were divided into 2 m sections. The reef transect was 225 m long, followed the drop-off at a depth of 3–4 m (Fig. 1), and was marked every 8–10 m. Bay transects were 4 m wide, while the reef transect was 20 m wide.

CATCHING AND TAGGING OF FISHES.—*Lutjanus apodus* were caught during the daytime and nighttime, using Antillean fish traps baited with squid. Fishes were caught at eight loca-

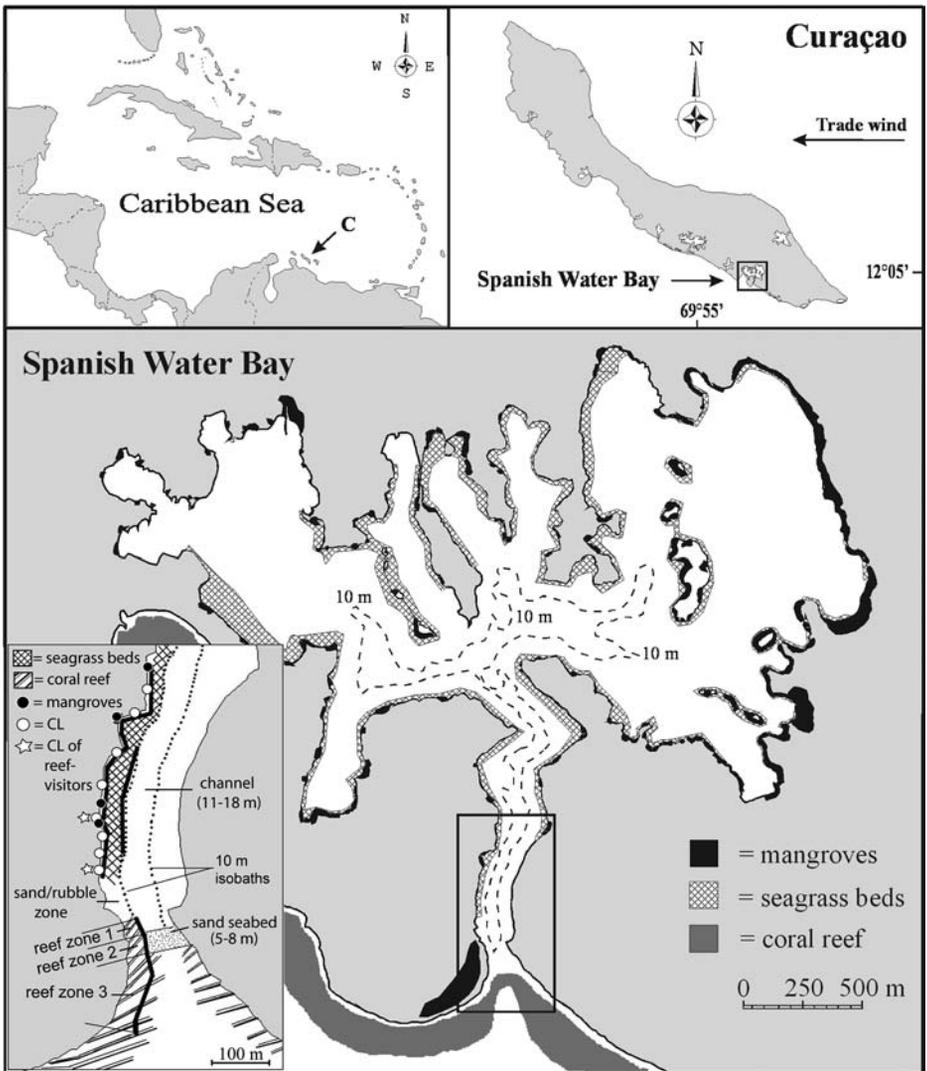


Figure 1. Map of Spanish Water Bay on Curaçao ("C") and the selected study area. Grey areas represent land masses, white areas represent water masses. The middle of the bay is dominated by macro-algal flats (Kuenen and Debrot, 1995). Bold lines are survey and transect routes along the rocky shoreline, the channel, and coral reef drop-off. Black circles indicate locations of mangrove stands (4–20 m long and 2–4 m wide). "CL" = catch location, "reef visitors" = *Lutjanus apodus* resighted on the reef. Depth given in meters (m). Three reef zones could be distinguished: (1) reef in bay mouth, adjacent to channel; (2) reef in bay mouth, adjacent to sand bar; (3) reef extending outside of the bay.

tions at the rocky shoreline (Fig. 1). Captured fishes ($n = 59$) were kept briefly in an underwater net and were tagged with markers consisting either of monofilament line and colored beads (line diameter 0.18–0.25 mm, bead diameter 1.5–2.6 mm), or of colored plastic plates (fingerling tags, 3.2×6.4 mm and vinyl stretchable thread, *Floytag*). Before tagging, fish fork length (FL) was measured to the nearest mm, and the fishes were wrapped in a wet cloth. Tags were inserted into the muscle tissue just under the anterior or the central part of the dorsal fin base, using a hollow injection needle (0.50 mm diameter for monofilament line, 1.10 mm diameter for vinyl thread). The skin was pierced at a downward angle of about 60° to the fishes'

body, so that scales were not torn off. On the thread protruding from the other side of the fish, a single bead (in case of fingerling tags), or the mirror image of the series of beads (maximum of two) was attached. The tag was fastened at the end with a knot. The number and combination of colored beads or plates was unique to each fish so that each individual could be recognized underwater. Tagged fishes were released at their catch location and upon release all fishes swam away vigorously. The tagging procedure took < 1 min and needles were cleaned with diluted ethanol before tagging the next fish.

SURVEYS.—The study period lasted from 22 March to 28 June 2005 (99 d). Fishes were tagged on 24 different days between day 1 and day 60, and surveys took place on 47 d between day 4 and day 99. Surveys were conducted by four observers using snorkelling gear between 1000–1200 and/or 1530–1730. When a tagged individual was resighted, the tag code, time, and location were recorded. Bay transects (width 4 m) were surveyed once within a time-interval, while the much wider reef transect (width 20 m) had to be surveyed twice to cover the entire width (i.e., surveying two 10 m wide transects). If an individual was resighted more than once during the same time interval, only the first resighting was used.

During some surveys, areas outside the marked line transects were also searched, including the seagrass beds between the bay shoreline and channel transect, the transition-zone between the rocky bay shoreline and the coral reef habitat (the “sand-rubble zone”: 115 m long, up to 2 m deep, 40–45 m wide), a 100–300 m extension of the reef transect away from the bay, and a 100 m extension of the rocky shoreline transect deeper into the bay (Fig. 1). Additionally, channel and reef zones deeper than 3 m were surveyed by two SCUBA divers (once in the channel, thrice on the reef).

To determine whether fishes had moved away from their daytime sites at night, surveys were conducted by four snorkelling observers holding flashlights between 2000–2130 on days 53 and 58. These surveys were carried out in the same areas as the daytime surveys, including all unmarked areas described above, except for channel and reef zones > 3 m deep.

DATA ANALYSIS.—Fish movement was characterized in terms of (1) daytime activity radius, (2) site fidelity, and (3) between-habitat movement. We refrained from using the term “home range” because we only examined daytime space use and believe that “home range” should include both daytime and nighttime activity spaces.

Because all fishes were exclusively resighted along longitudinal transects during daytime, their activity radius was expressed as the linear distance between the two most extreme resighting locations (following Zeller, 1997; Chapman and Kramer, 2000). This is the minimal distance a fish has traversed. When an individual was resighted in the same transect section only, the activity radius was assumed to be 2 m (i.e., the length of transect sections between markers in the channel-shaped bay area). The daytime activity radius was calculated for two time-scales: (1) “within days”, for individuals resighted during the two different time intervals on the same day, and (2) “across days” over a period of 17–90 d, using the first resightings of all time intervals of the entire study period.

Site fidelity was calculated by measuring the linear distance of all resightings to the 2 m wide transect section where an individual was resighted most frequently, i.e., the “core area of presence”. Because site fidelity is a process covering relatively long time periods, it was only calculated for the time-scale “across days”. To assess the relationship between the use of the core area of presence and time, we calculated the linear distance to this core area for each chronological resighting. Then, we performed a linear regression (SPSS 14.0) between this distance (dependent variable) and the consecutive resightings (independent variable).

Home range parameters and activity radii may be influenced by the number of resightings (Odum and Kuenzler, 1955; Laundré and Keller, 1984; Samietz and Berger, 1997), and interpreting data from individuals with too few resightings may lead to an underestimation of the actual activity radius. Therefore, we calculated movement patterns across days only for those fishes of which the activity radius reached a horizontal asymptote (thus did not increase any further) with an increasing number of resightings (following Zeller, 1997). To find out which fishes met this criterion, we created area observation curves for each separate individual. We

calculated the maximal linear distance between all previous and every consecutive resighting and plotted this against the number of resightings. Fishes showed no increasing activity radius after 9 resightings, so we calculated activity radii and site fidelity across days only for individuals resighted at least 10 times.

Besides the number of resightings, fish size may also influence their space use, because as fishes grow larger their home range may increase if the provision of resources requires a larger area (Grant, 1997; Jones, 2005). Even though all fishes in our study were sub-adults (see Discussion), individual size-related changes in movement patterns may occur while nearing sexual maturity. Therefore, relationships between the number of resightings and fish size (independent variables) and the linear activity radius and the percentage of resightings at the core area of presence (dependent variables) were tested using linear regressions (SPSS 14.0). When testing the activity radius within days the effect of fish size was tested using simple linear regression. When testing the activity radius and site fidelity across days, the total number of resightings was also added as an independent variable to the linear regression (i.e., multiple linear regression). Multicollinearity was not present, as no correlation could be demonstrated between fish size and the total number of resightings.

RESULTS

RESIGHTINGS.—The size of the 59 tagged fishes ranged from 13.2–21.0 cm FL. Fifty-two of the 59 tagged *L. apodus* (88%) were resighted at least once. Fishes with 10 resightings or more ($n = 21$) were resighted 17 times on average (range 10–33 times) across an average period of 39 d (range 17–90 d). After about 6 wks most fishes had either lost the tag or the tag colors were no longer recognizable due to algal fouling.

Tagged fishes were never resighted in the bay channel during daytime, or in unmarked seagrass beds or deeper zones of the channel and reef. During the complete study period most fishes ($n = 48$) were only resighted inside the embayment. Of all *L. apodus* resightings, 94% were concentrated at the rocky shoreline. Exceptions were three *L. apodus* that were also resighted occasionally in the mangroves (1% of all resightings) and four *L. apodus* that were resighted on the coral reef (“reef-visitors”: 5% of all resightings).

During nighttime observations 12 *L. apodus* were resighted: six of them were resighted at the rocky shoreline, while the other six were resighted in seagrass beds. The median distance that these fishes had moved away from the location where they had been resighted during the late afternoon on the same day was 11 m (range = 2–176 m) and the median distance away from their daytime core area of presence was 7 m (range = 2–230 m).

DAYTIME ACTIVITY RADIUS.—Daytime activity radius showed no significant linear relationship with fish size or the number of resightings [within days ($n = 33$): fish size $R^2 = 0.058$, $P = 0.178$, semi-partial correlation “*spc*” fish size = -0.240 ; across days ($n = 21$): $R^2 = 0.038$, $P = 0.704$, *spc* fish size = -0.025 , *spc* resightings = -0.189]. *Lutjanus apodus* only moved short distances within days (median 5 m), regardless of whether they were resighted on the reef or not (Fig. 2). The activity radius across days was larger than within days, and was much larger for fishes resighted on the reef (median 217 m) compared to those resighted in the embayment (median 28 m) (Fig. 2). One individual resighted on the coral reef (not included in Fig. 2: see legend) had an activity radius across days of 262 m, which is within the range of the activity radii across days of the other three reef-visitors (Fig. 2).

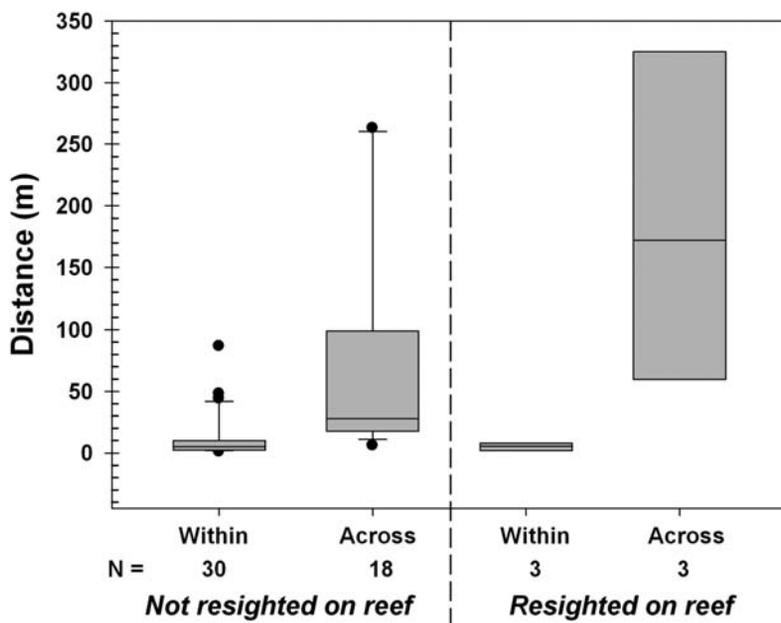


Figure 2. Boxplots of linear distances between the two most extreme resighting locations (day-time activity radii) for *Lutjanus apodus* calculated for the time scales “within days” (for fishes resighted during the two different time intervals on the same day), and “across days” over a period of 17–90 d (for fishes resighted at least 10 times), and calculated separately for fishes not resighted on the reef (left panel) and those resighted on the reef at least once (right panel). A boxplot indicates the median (horizontal line in box), the interquartile range (box height), 10 and 90 percentiles (whiskers), and outliers (dots). N is the number of individual fish (sample size) and differs as a result of the different time scales and criteria. The fourth fish resighted on the coral reef is not included in this figure because it was resighted only six times (see text).

SITE FIDELITY.—The percentage of resightings at the core area of presence showed no linear relationship with fish size or the number of resightings ($n = 21$, $R^2 = 0.135$, $P = 0.272$, spc fish size = 0.327, spc resightings = -0.030). Fishes frequently observed (i.e., > 10 times, $n = 21$) were most likely to be resighted within a 10 m radius around the core area of presence (80% of all resightings) (Fig. 3A). The distance between each chronological resighting and the core area of presence did not change through time ($n = 21$, $R^2 = 0.070$, $P = 0.136$). Sixteen of the 21 fishes shared the area of a 10 m radius around their core area of presence with at least one other tagged individual, while the remaining five fishes showed solitary core areas (Fig. 3B). The core area of presence of two of the four *L. apodus* that were resighted on the reef was located on the reef (Figs. 3B,C).

BETWEEN-HABITAT MOVEMENT.—Four fishes were resighted at least once on the coral reef. They were resighted at locations ranging between distances of 30 and 90 m away from the open-spaced sand/rubble zone (Figs. 1, 3C), and were resighted at an average depth of 3.1 m (range 0.5–5.0 m). One of these individuals (Ind 1: Fig. 3C) was resighted only once on the reef (fourth resighting) and its other resightings (# 1–3 and # 5–10) were at the rocky shoreline in the channel-shaped bay area. The last resightings of the other three individuals were all on the reef. Individual 2 was resighted a total of six times: the first three resightings were at the rocky bay shoreline,

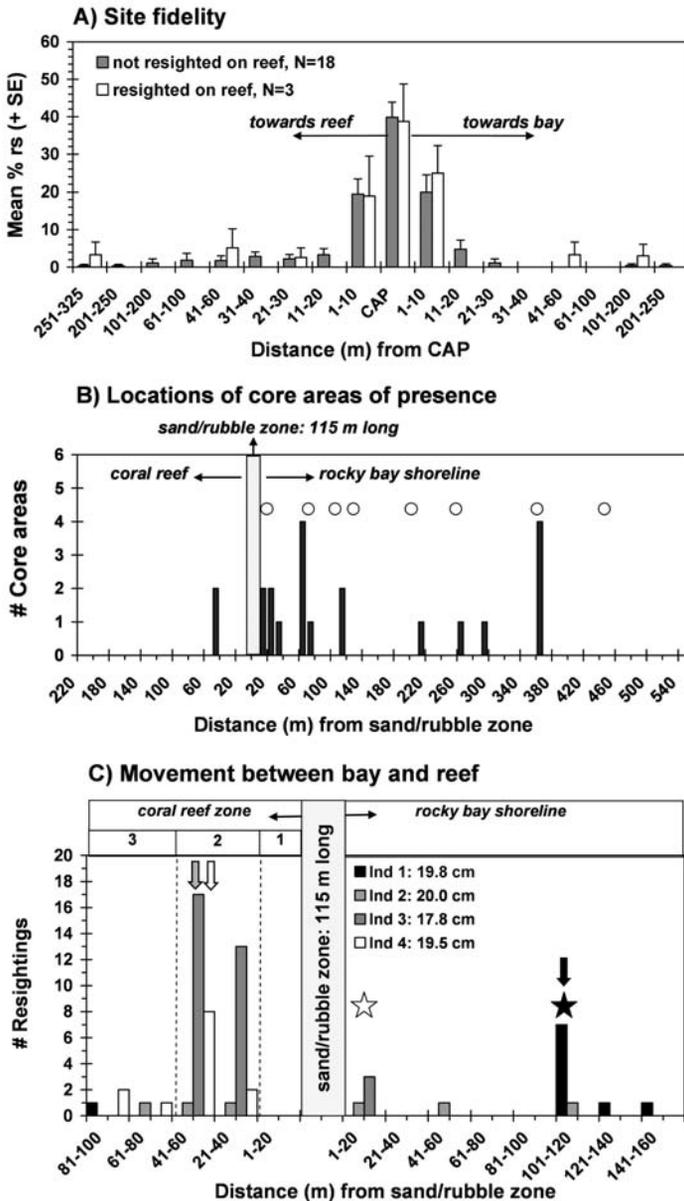


Figure 3. (A) Site fidelity expressed as the mean percentage of resightings (“rs”) at various linear distances away from the core area of presence (“CAP”), both in the direction towards the reef and deeper into the bay, calculated separately for fishes not resighted on the reef (grey bars) and those resighted on the reef at least once (white bars). The fourth fish resighted on the coral reef was not included in this figure, because it was resighted only six times. Note the increasing scale for the distance classes on the x-axis. (B) Locations of the core areas of presence along rocky shoreline and coral reef transect lines of *Lutjanus apodus* resighted at least 10 times (n = 21). Open circles indicate the eight capture and tagging locations. (C) Locations of all resightings of four *L. apodus* individuals that moved between the embayment and the coral reef. The three reef zones correspond to those given in Figure 1. The black star is the capture and tagging location of individual (“Ind”) 1, the white star indicates that of individuals 2–4. Arrows above bars indicate the core area of presence of individuals 1, 3, and 4 (individual 2 only had six resightings, so no core area of presence was calculated).

while the last three were on the reef. Individual 3 was resighted a total of 33 times: the only resightings at the bay rocky shoreline were the 1st, 2nd, and 20th resighting, meaning the last 13 resightings were on the reef. Individual 4 was resighted a total of 13 times: all of its resightings were on the reef.

DISCUSSION

DAYTIME ACTIVITY RADIUS AND SITE FIDELITY.—During daytime Lutjanidae are known to shelter in or near structurally complex habitat types (Valdés-Muñoz and Mochek, 2001; Verweij et al., 2006). In the present study, their inactivity was obvious from the small linear distances traversed within days (median distance 5 m), irrespective of whether they showed movement across days to the reef or not. The small within-day activity radii were not necessarily individual territories, as many fishes showed overlapping space use and core areas of presence, and often schooled with other, untagged *L. apodus*.

Compared to within-day movements, the activity radius across days was relatively large (6–325 m), indicating that *L. apodus* does not always use the same shelter sites every day and that these sites are sometimes located at some distance from one another. However, the median activity radius across days was relatively small (34 m), when compared to the 540 m long area of structurally complex habitat available and surveyed along the bay shoreline. Moreover, only a small area within the activity radius across days was used most intensively: 80% of all *L. apodus* resightings were concentrated within a core area with a 10 m radius. The present study shows that in continuous rocky shoreline and mangrove patches, where fishes theoretically have a choice from a wide range of apparently suitable resting sites, *L. apodus* shows fidelity to specific locations over periods between 17 to 90 d. However, it should be noted that about half of the tagged fishes were never or rarely resighted. These fishes may have been much less site-attached than the others. Even though we performed surveys in an area that was as large as possible, the space use of the tagged fishes was limited to the confinements of the surveyed area (scale bias: see Pittman and McAlpine, 2003). In a different study (tag-recapture: Verweij et al., unpubl. data) carried out in the same embayment, but at a much wider spatial scale (up to 1500 m across the entire bay) and during much longer time periods (up to 422 d), all recaptured *L. apodus* ($n = 4$ of $n = 88$ tagged with coded wire tags, *Northwest Marine Technology*) were still present at their initial tagging sites even after 287–422 d at liberty (average FL at tagging = 15.2 cm; average FL at recapture = 19.9 cm). This indicates that some *L. apodus* may show site fidelity across much longer time spans than was found in the present study, even when larger spatial scales are examined. *Lutjanus apodus* is known to move away from daytime resting sites to nocturnal foraging grounds during twilight (Sbikin, 1977; Rooker and Dennis, 1991; Nagelkerken et al., 2000c), so a high site fidelity would imply that fishes often return to the same familiar sites in the morning (i.e., homing). However, occurrence of twilight migrations and homing may not be true for all fishes because in our study half of the tagged fishes recorded during nighttime observations were still present in their daytime habitat or near their daytime core area of presence.

Fishes are expected to increase their home range as they grow larger (Grant, 1997; Jones, 2005), or may even move to an alternative habitat type, e.g., due to an ontogenetic diet shift (Cocheret de la Morinière et al., 2003). In the present study, however,

fish size did not influence daytime activity radii or site fidelity. This may be due to the restricted size range of the tagged fishes which may have had similar diets: in Spanish Water Bay, all *L. apodus* sized 13.2–21.0 cm mainly fed on decapod crustaceans and fish (Cocheret de la Morinière et al., 2003). Furthermore, increased home ranges due to diet change may only be observable for nocturnal activity radii, and not for daytime activity radii, because this species forages predominantly at night (Starck and Davis, 1966; Collette and Talbot, 1972; Sbikin, 1977). Reproductive behavior can probably also be ruled out as cause of variation in movement patterns because all fishes in this study were sub-adults smaller than the maturation size of 25.0 cm (Starck, 1971; Claro, 1983; Munro, 1983). However, fishes that moved to the coral reef were among the largest (17.8–20.0 cm) of the tagged individuals and may have been driven to do so due to the onset of ontogenetic changes in diet and social or reproductive behavior.

BETWEEN-HABITAT MOVEMENT.—Resightings of tagged *L. apodus* in the small and scarce mangrove stands were rare and may be a function of habitat geometry rather than fish preference, in which case fishes simply follow the structurally complex shoreline at a similar depth profile and do not distinguish between habitat types. We argue that this is not the case for the four *L. apodus* that were resighted on the reef, because (1) reef resightings were at greater depths (0.5–5.0 m) than bay resightings (0.2–1.0 m), (2) their daytime activity radius across days was much larger than that of other *L. apodus* individuals, (3) the core area of presence of two of the four fishes was located on the coral reef, (4) three of the four reef visitors were repeatedly resighted on the coral reef and their last resightings were on the coral reef (i.e., they were not observed to move back to the embayment), and (5) all reef visitors had to cross a 115-m long, open-spaced sand/rubble zone to move between two shelter-rich habitats (i.e., the bay shoreline and the coral reef). This also means that these fishes were probably not present on the coral reef just because the reef habitat was inside their average activity radius. Their reef visits may have represented an explorative first step (McKeown, 1984; Kramer and Chapman, 1999) in their presumed ontogenetic migration, when they are assumed to move to the reef habitat as sub-adults or adults. An alternative explanation is that the reef-visitors were in fact “bay-visitors” that occasionally visited the bay area and were captured and tagged at the rocky bay shoreline because they were attracted by the bait in the cage. This might be true for the two individuals that were resighted mainly or exclusively on the coral reef, but is less likely for the other two individuals, because their first resightings were inside the bay before they were observed on the reef, and one of these fishes moved back into the bay after the first reef-resighting and was not observed on the reef thereafter. We argue that these four fishes may have been at different stages of moving their home range to the coral reef. They were in the size range of fishes expected to start moving from the bay to the coral reef, as suggested by size-frequency distributions on fringing reefs of Curaçao and Bonaire where the smallest size of *L. apodus* is 20 cm, besides a very small percentage of 15–20 cm sized *L. apodus* on the 0–3 m shallow coral reef (Nagelkerken et al., 2000a,b). The possible stepwise migration process that these fishes might undertake is comparable to the observation that spiny lobsters move gradually between juvenile and adult habitats (Kanciruk and Herrnkind, 1978).

In summary, *L. apodus* moved small distances (~ 5 m) within days, while distances between daytime resting sites across days ranged between 6–325 m, and were larger for the fishes resighted on the reef (median = 217 m) compared to fishes that were

only resighted inside the embayment (median = 28 m). Despite the fact that hundreds of meters of structurally complex habitat were available along the bay shoreline, fishes showed high fidelity to daytime shelter sites. Even though only 4 out of 59 fishes moved between the bay and the coral reef, the present study is the first showing a linkage between a putative nursery area in a tropical non-estuarine embayment and the adult coral reef habitat, based on observations of tagged fishes. Although the importance of this observation should still be established (e.g., by similar observations in other areas), this habitat connectivity has the management implication that a coral reef ecosystem should be protected in combination with back-reef habitats.

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