

be compared across individuals (Wang & Grimm 2007). Site fidelity can be used as a proxy to determine whether an individual has established a home range because such fidelity is a necessary condition to maintain a home range (Powell 2000). However, fish execute occasional exploratory movements outside their home range, and these movements should not be considered part of the home range (Burt 1943, Powell 2000). Some fish families, such as wrasses, surgeonfishes, and parrotfishes, require several days to 1 mo to cover short distances (Robertson & Hoffman 1977, Chapman & Kramer 2000, Garcia et al. 2010). By contrast, other species, such as groupers, snappers, and jacks, are able to swim long distances ranging from 10 to 100 km (Colin 1992, Holland et al. 1996, Farmer & Ault 2011).

The movement patterns of fish may determine the effectiveness of a marine reserve, defined in this study as a marine area protected from fishing activity (Afonso et al. 2008). Fish movements across reserve borders can affect the reef fish assemblage (abundance and/or distribution) within and outside the protected area (Chapman & Kramer 2000). Halpern & Warner (2003) presented a review of 89 studies of marine reserves showing a 63% increase in fish density, a 90% increase in fish biomass, and an 80% increase in fish size within the reserve. Spillover is a term used to describe the exportation of larvae and adults from a reserve to adjacent zones (Afonso et al. 2008, Meyer et al. 2010, Green et al. 2014). Spillover of mature and large individuals from a marine protected area (MPA) should support local fisheries (Ashworth & Ormond 2005). However, spillover is a complex mechanism that is difficult to demonstrate because it largely depends on species-specific life history (Russ et al. 2003), fish densities inside the reserve, and species movements.

MPAs, including marine reserves, are very popular and effective tools in biodiversity conservation. Nevertheless, the determination of the optimal size, design, and location of MPAs is a complex problem (Halpern 2003, Claudet et al. 2008). For species with small home ranges and strong site fidelity (Afonso et al. 2008, 2011), individuals' movements are often limited to the MPA, making the protection of those species effective. Individual export of these species from MPAs is often limited to the larval phase and is highly dependent on environmental conditions (Cudney-Bueno et al. 2009, Christie et al. 2010). However, species with large home ranges have a greater ability to leave MPAs to reach essential habitats (e.g. for refuge, nutrition, or reproduction). Although MPAs offer an effective conservation tool for some species,

benefits decrease considerably for species that have a home range larger than the MPA boundaries. Large reserves could be a solution for these species, but generate more social and economic problems with local fishermen and incur larger management and monitoring costs (Halpern & Warner 2003). Moreover, large reserves do not necessarily contain the essential habitats for the species (Chapman & Kramer 2000, Carlson et al. 2010). One solution proposed by scientists is to create networks of medium-sized MPAs (100–500 ha) with a mean distance of 4–6 km between them (Shanks et al. 2003, Claudet et al. 2008). Therefore, movement pattern studies (home range, maximum distance covered and site fidelity) of key ecological and economically important species such as grouper, snapper, and parrotfish (Vallès & Oxenford 2014) are necessary to improve MPA design.

Studies of fish movements have often used conventional external tagging with a mark-recapture technique that relies on experimental recapture or visual sightings (Chapman & Kramer 2000, Zeller et al. 2003, Amargós et al. 2010). This type of tag is utilised when the animal and species can be identified visually (Kohler & Turner 2001). This method allows the tagging of a large number of individuals of many different species, yet it remains difficult to determine fish activity between the capture and recapture events. Recently, ultrasonic telemetry has proven effective for studying the ecology and physiology of marine animals in their natural environments (Winter 1996). Based on the number and spacing of receivers and the frequency of fixed positions, acoustic tagging can produce spatio-temporal data of finer resolution than external tagging.

In the present study, the movement patterns of 3 coral reef fish, *Acanthurus chirurgus* (Acanthuridae), *Sparisoma viride* (Scaridae), and *Lutjanus apodus* (Lutjanidae), within and outside a Caribbean MPA were assessed using complementary methods. The main objectives were to (1) characterise the fish movements, (2) identify what type of habitat these species used, and (3) determine the MPA effectiveness for these 3 species. These species represent a large portion of the fish biomass (37.2%, J. Garcia et al. unpubl. data) in Martinique and are intensively targeted by artisanal fishing (Antillean trap) (Bruggemann et al. 1996, Nagelkerken et al. 2002, Choat et al. 2003). Therefore, effective protection is essential to ensure stock replenishment of these species. Conventional external tags and passive acoustic telemetry were utilised to monitor long-term fish movement, whereas active acoustic tracking was

used to determine short-term home range and site fidelity.

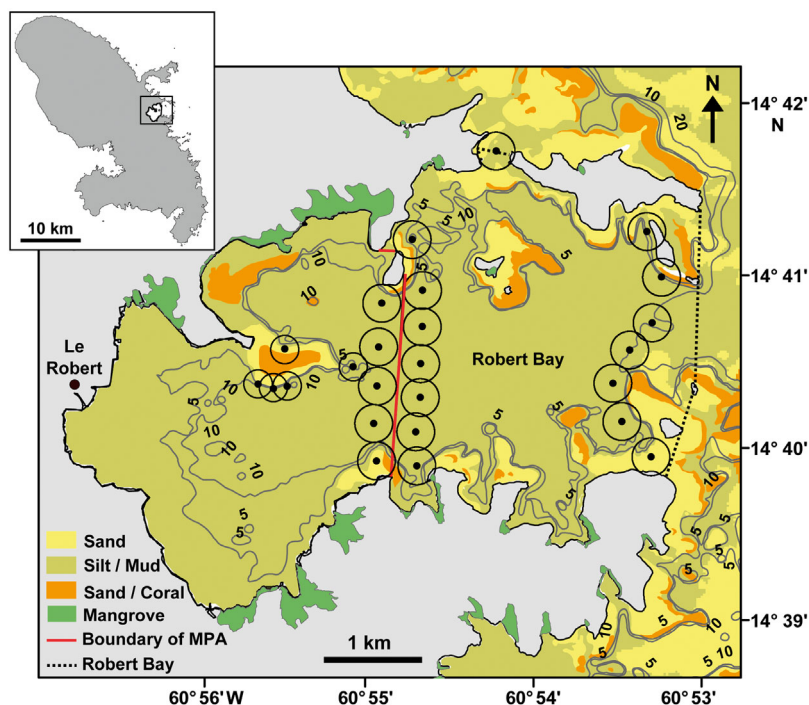
MATERIALS AND METHODS

Study area

Work was conducted in a coastal MPA located close to the village of Le Robert in Martinique (Lesser Antilles) (Fig. 1). The Robert MPA was created in 2000 and encompasses an area of 9.56 km². This MPA is closed to fishing, but diving and other activities are permitted. The Robert MPA (Fig. 1) is a large bay located on the Atlantic coast into which many rivers discharge. Consequently, coral reefs inside the MPA are greatly impacted by siltation and pollutants from the river discharge. The Atlantic side is a large insular shelf that stretches less than 10 nautical miles. Benthic community mapping around Martinique Island conducted by Legrand et al. (2012) indicates that Robert Bay (Fig. 1) consists of soft-bottom (sand or silt) (63.8%), algae (50.3%), and coral (10.5%). Furthermore, artificial reefs have been created on the borders of the natural reef inside the MPA.

Monitoring system and fish tagging

Three species were chosen for this study: *Acanthurus chirurgus* (Acanthuridae), *Sparisoma viride* (Scaridae), and *Lutjanus apodus* (Lutjanidae). These common species belong to different trophic groups (herbivores and carnivores) and were expected to exhibit different degrees of mobility. Fish were caught with Antillean traps, which are the most common coastal fishing gear in Martinique. In the Robert MPA, traps were placed in areas of rocky substrate at a depth of ~5 m to reduce fish decompression. The aim was to tag sexually mature individuals in each of the 3 species. Sexual maturity is reached at ~17 cm for *A. chirurgus*, between 17 and 27 cm for *S. viride*, and at 25 cm for *L. apodus* (Munro 1983). However, only 2 mature *L. apodus* measuring more than 25 cm were captured; the rest of the individuals studied within this group were sub-adults. For *A. chirurgus* and *S. viride*, all studied individuals were mature individuals.



cavity. These transmitters pulse randomly every 120–360 s at a frequency of 69 kHz and have a nominal maximum battery life of 412 d. We used a specific implantation technique for Acanthuridae because the distance between the anal fin and the anus was too small to implant a transmitter. Instead, the transmitter was inserted in the peritoneal cavity, 0.5 cm above the fish's anus. For each species, fish were maintained in captivity for 1 wk following surgery. Fish were fed the day after surgery and released at their point of capture. All individuals above 16 cm (total length) were tagged. This fish size was considered sufficient to minimise the impact of the internal tag (mass = 1.8 g and length = 22.5 mm) on fish health. Unfortunately, 3 *L. apodus*, 2 *S. viride* (1 female and 1 male), and 9 *A. chirurgus* died during the tagging procedure.

Monitoring system. In this study, the movement patterns of fish were studied inside the Robert MPA and along the MPA borders (monitoring fish entries and exits). A total of 25 Vemco VR2W receivers were deployed within the MPA. A double receiver barrier was deployed around the MPA boundary (Heupel et al. 2006) and another barrier was deployed at the edge of the bay (Fig. 1). This fixed network of 20 receivers was deployed in Robert Bay (Robert MPA + outside MPA) from November 2009 to November 2011. In addition, 5 supplementary receivers were installed in the centre of Robert Bay from December 2010 to November 2011 (Fig. 1). The VR2W acoustic data were downloaded every 6 mo.

Range testing

VR2W test. Range tests were conducted at 3 different receivers placed in different key habitats (rocky reef, soft bottom and a combination of both) within the study area. For each habitat (i.e. receiver), 3 range tests were conducted, totalling 9 range tests. With a boat, we moved away from the receiver, stopped every 50 m, and recorded the position using a GPS. Range tests were restricted to a maximum distance of 250 m from the receiver. We chose to test several transmitters to investigate whether there were possible differences in the transmission of acoustic signals between transmitters. The detection range was estimated to be restricted to a maximum radius of 150 m over a soft bottom composed mainly of a silt substrate and a flat surface. The detection range for the rocky reef and combination of rocky reef and soft bottom receivers was limited to a radius of 100 m due to

the relief complexity of the bottom, which decreases the strength of the acoustic signal.

VR100 test. Two transmitters were fixed to a buoy attached to the bottom. We then moved the VR100 50 m farther away every 12 min. Range detection was tested up to 250 m. The transmitter signals were detected up to 100 m.

Relocation

To quantify fine-scale movement patterns, fish (*A. chirurgus*, *L. apodus*, and *S. viride*) were tracked using a Vemco VR100 mobile receiver once a week from December 2009 to August 2010. Using an omnidirectional hydrophone, we regularly relocated and monitored fish presence and their location within the study area. Overall, 30 tracking sessions were conducted on rocky and silty substrates: 15 inside the MPA and 15 outside the MPA. Every 15 min during tracking, the boat was positioned at a location inside the Robert MPA. This position was recorded using a GPS. Tracking was conducted once a week for 13 h during 3 sessions: 05:30 to 08:30 h, 11:00 to 14:00 h, and 18:00 to 01:00 h.

Data analysis

Movement data were obtained using the Animal Movement Extension (Hooge & Eichenlaub 1997) for ArcView 3.2 (ESRI). Home range sizes were calculated from active tracking positions using kernel utilisation distributions (KUDs) and minimum convex polygon (MCP) areas (Kernohan et al. 2001). The KUD is a probabilistic method that calculates the probability of finding a fish in an area based on position data; we used 50 % KUD (KUD^{50}) to represent the fishes' core activity areas and 95 % KUD (KUD^{95}) to calculate the fishes' home ranges. The MCP estimates the maximum area covered by each fish (Worton 1989, Seaman & Powell 1996). The null hypothesis, that the movements of each detected fish were random, was tested using a site fidelity test (Wetherbee et al. 2004). The observed data were compared against 100 simulated data sets within the site fidelity test that were created using a Monte Carlo simulation (Okubo 1980, Spencer et al. 1990, Hooge & Eichenlaub 1997, Wetherbee et al. 2004). The mean squared distances (MSDs) from the centre of activity and the linearity index (the linear distance between the first and last detection points divided by the cover distance) were also generated from the simulations (Schoener 1981,

Table 1. Summary results of mark-recapture with external tags. The numbers of tagged and recaptured fish, the percentages of recapture, and the mean \pm SD and minimum distance between sites of release and recapture of each species are presented

Species	Fork length (cm)		Mass (g)		Number tagged/ recaptured	Percentage recaptured (%)	Distance covered (m)	
	Mean	Range	Mean	Range			Mean	Range
<i>Acanthurus chirurgus</i>	15.8	10.0–23.5	90	40–260	673/38	5.6	778 \pm 1446	5–4992
<i>Lutjanus apodus</i>	22.1	15.0–34.0	188	80–640	131/35	26.7	671 \pm 1594	22–9701
<i>Sparisoma viride</i>	20.9	13.5–28.5	166	60–360	217/36	16.6	129 \pm 139	5–455

Spencer et al. 1990). We divided Robert Bay into 2 zones: inside and outside the MPA. A residency index (I_R) was calculated for each tagged fish and each zone (O'Toole et al. 2011) using passive monitoring data. The I_R values were obtained by dividing the number of days that fish were detected in each zone by the number of days in the array (i.e. the number of days between the release date and the last detection).

RESULTS

Spatial movements

Mark-recapture experiment. A total of 1021 fish were tagged (673 *Acanthurus chirurgus*, 131 *Lutjanus apodus*, and 217 *Sparisoma viride*) with external tags, of which 109 individuals were recaptured (10.7% recapture; Table 1). The percentage of recaptures differed among species, with 5.6% of tagged fish recaptured for *A. chirurgus*, 26.7% of tagged fish recaptured for *L. apodus*, and 16.6% of tagged fish recaptured for *S. viride*. Several individuals were recaptured multiple times (6 *L. apodus*, 4 *S. viride*, 1 *A. chirurgus*; Fig. 2). *L. apodus* covered a mean (\pm SD) distance of 671 \pm 1594 m; however, one male covered a distance of ~9701 m (Fig. 3) and was caught outside the MPA behind the coral reef barrier only 23 d after its release. *Acanthurus chirurgus* was the most frequently tagged species and travelled a mean distance of ~778 \pm 1442 m; however, 7 individuals were caught on the coral reef outside the MPA and had travelled a mean distance of 3529 \pm 1026 m, with one individual covering a distance of at least 4992 m (Fig. 3, Table 1). *Sparisoma viride* covered the smallest mean distance (129 \pm 139 m) in comparison with the 2 other tagged species, and the longest observed movement for *S. viride* was 455 m (Table 1). There was high intra-specific variability in the distance covered by individuals.

Acoustic telemetry. Thirty *A. chirurgus* were tagged with acoustic transmitters between December 2009 and April 2010. A total of 47 *L. apodus* were

tagged between November 2009 and May 2011. Twenty-seven *S. viride* were tagged between March 2010 and April 2011, comprising 18 terminal phases and 9 initial phases.

Relocation survey. A total of 49 fish were detected at least once, but only 12 individuals (7 *L. apodus*, 2 *A. chirurgus*, and 3 *S. viride*) were detected frequently enough to be included in the home range analysis (Fig. 4, Table 2). The hypothesis that the observed movements were random was rejected for all tracked fish except individual ID158 ($p < 0.05$; Table 2). These data confirmed that the individuals that were included in the home range analysis occupied home ranges that were restricted to a consistent area inside the MPA. The mean (\pm SD) MCP home ranges observed for *L. apodus* ($n = 7$) were 15 827 \pm 16 912 m², 11 685 \pm 19 889 m² for the KUD⁵⁰, and 66 871 \pm 114 398 m² for the KUD⁹⁵. All *L. apodus* had home ranges (KUD⁵⁰) varying from 1300 to 12 300 m² except one fish (ID5257) that occupied a larger home range (56 000 m²; Table 2). This fish made several movements between 2 different sites on rocky substrate. Only individual ID5257 showed spatial overlap with all other *L. apodus*. However, other individuals also presented some overlap in their distributions (Fig. 4). The home range of ID258 only overlapped with that of individual ID5257 and the border of the KUD⁹⁵ of individual ID276. We observed spatial overlap for all individuals. For *A. chirurgus*, only 2 individuals were detected frequently enough to enable kernel analyses. Each fish demonstrated differences in their home range area. The MCPs varied between 5238 and 9444 m² (Table 2). The same observation was visible for KUD⁹⁵, which varied from 24 108 to 31 863 m², and KUD⁵⁰, which ranged from 3406 to 5913 m². No spatial overlap was observed between the 2 individuals. Three male *S. viride* were detected a sufficient number of times to permit kernel analysis. These 3 individuals exhibited very different MCP (ID153 = 924 m²; ID158 = 7548 m²; ID297 = 1189 m²) and KUD⁹⁵ areas (ID153 = 19 826 m²; ID158 = 44 015 m²; ID297 = 3845 m²). The MCP of individual ID158 was 18 times larger than

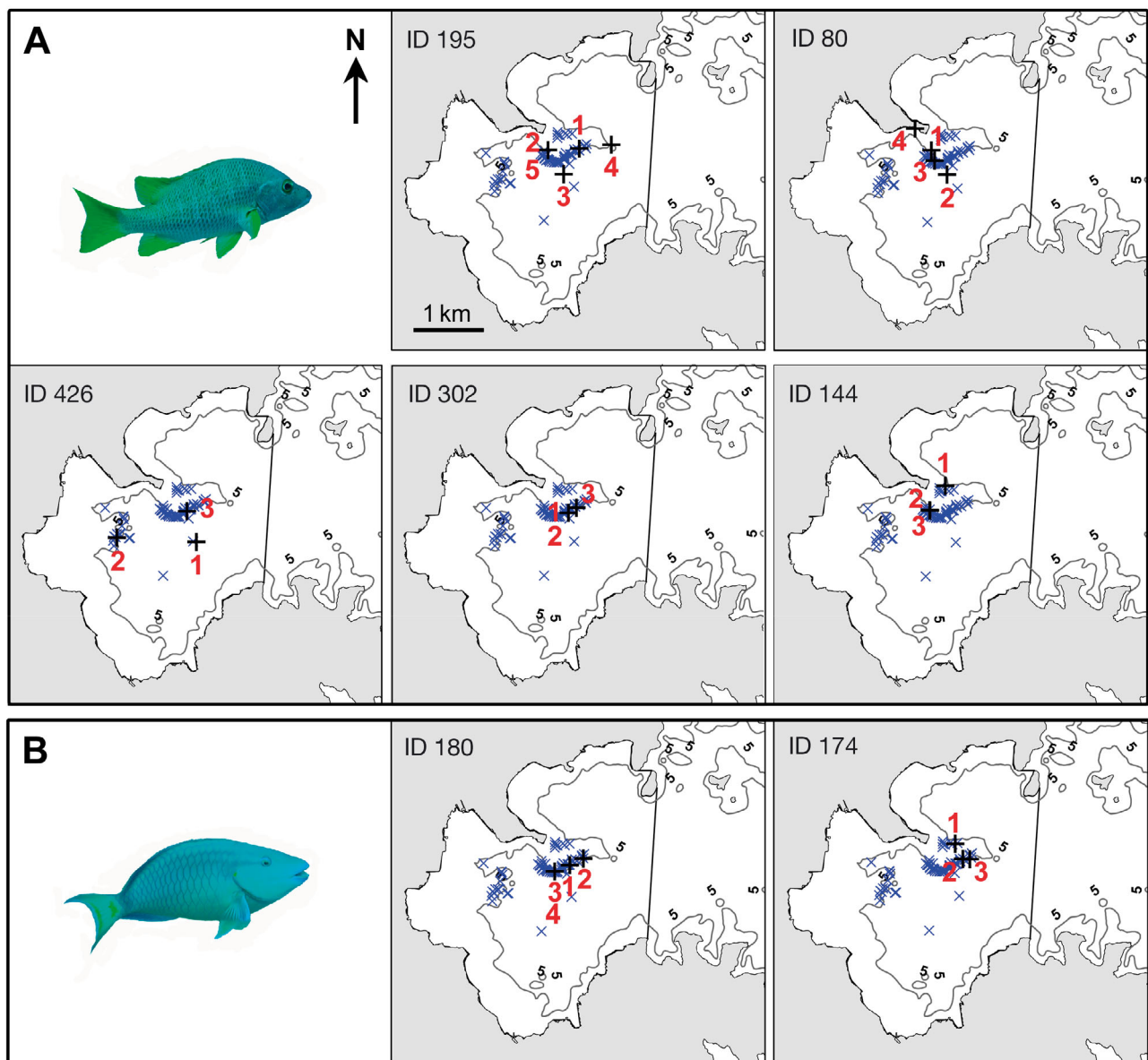


Fig. 2. Locations of multiple captures and recaptures for (A) *Lutjanus apodus* and (B) *Sparisoma viride* tagged with T-bar tags. Only individuals with multiple recapture spacing of a minimum of 50 m are presented. \times : locations of all captures, $+$: sites of recapture for each individual. Numbers correspond to recapture chronology

that of individual ID153. We observed that the smallest individual had the largest home range (Table 2). Spatial overlap was present between the 3 individuals (Fig. 4).

Passive survey. A total of 49 fish were detected at least once on the receivers. Our analysis was restricted to 38 individuals that had a sufficient number of detections (19 *L. apodus*, 16 *S. viride*, and 3 *A. chirurgus*). We considered a minimum of 3 consecutive detections to be representative of a true presence of the fish. The results from the acoustic monitoring confirm those from the external tagging, which

showed evidence that *L. apodus* and *S. viride* were able to travel outside the Robert MPA (Fig. 5). The map of monthly numbers of detections (Fig. 5) illustrates that the maximum number of detections was restricted to the rocky substrate in the centre of the bay inside the MPA. *Lutjanus apodus* individuals were predominantly detected by the receiver located farthest inside the bay, whereas males of *S. viride* were frequently detected close to the MPA boundaries (Fig. 5). *Lutjanus apodus* individuals ($n = 19$) were detected primarily by the 5 receivers located along the rocky substrate (number of detections per

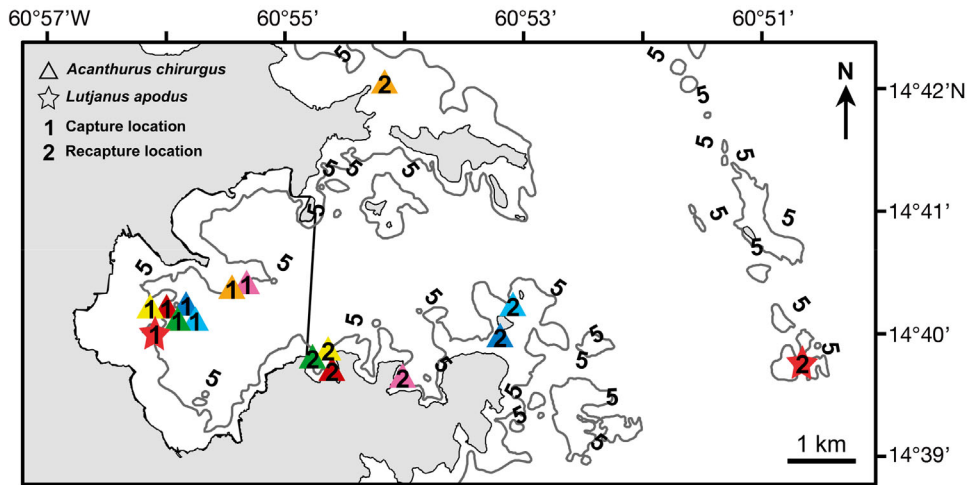


Fig. 3. Locations of the longest observed movements covered by 7 *Acanthurus chirurgus* (▲) and 1 *Lutjanus apodus* (★) obtained using T-bar tags. Different colours represent individual fish

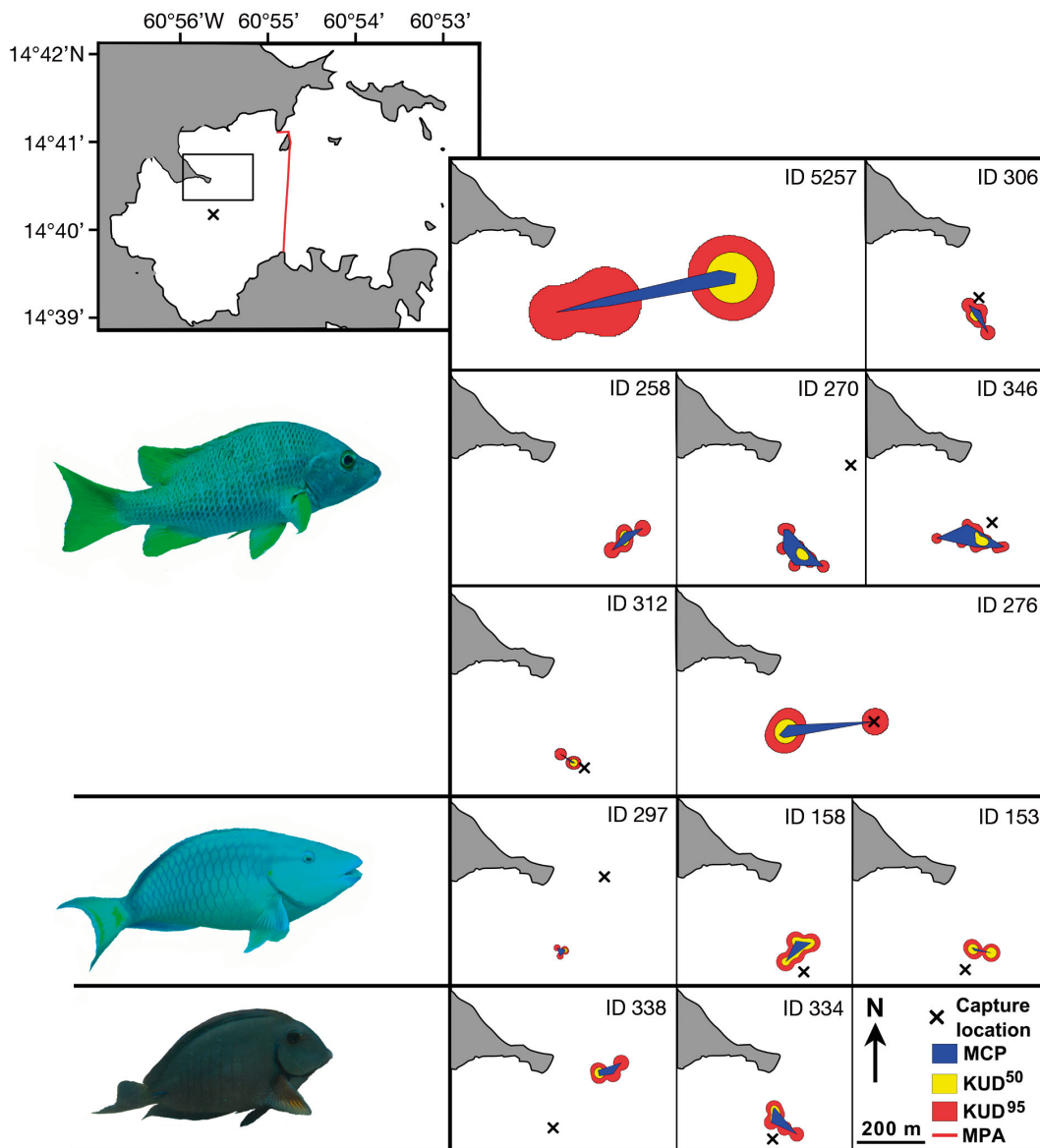


Fig. 4. Location and size of the home range relocation (minimum convex polygon [MCP] and kernel utilisation distribution [KUD⁹⁵]) and core area (KUD⁵⁰) of 7 *Lutjanus apodus*, 3 *Sparisoma viride* and 2 *Acanthurus chirurgus*. The capture and release location of each individual is represented by x on each individual home range map. Individuals 5257 and 258 were captured in the same location outside the map, indicated by the x on the Robert Bay map, inset

Table 2. Summary of the home range relocations (MCP: minimum convex polygon; KUD: kernel utilisation distribution) for the 7 *Lutjanus apodus*, 2 *Acanthurus chirurgus*, and 3 *Sparisoma viride* individuals. The percentage of days detected is (no. days detected/no. monitoring days) \times 100. p is the proportion of Monte Carlo simulated movement paths with higher mean squared distance (MSD; from the centre of activity) values than the observed data. ND: not determined

ID tag	Sex	Fork length (cm)	Release date (d/mo/yr)	Period of monitoring (d)	Percentage of days detected	Home range relocation			MSD (\pm SD) (m ²)	Site fidelity (p)
						MCP (10 ³ m ²)	KUD ⁵⁰ (10 ³ m ²)	KUD ⁹⁵ (10 ³ m ²)		
<i>L. apodus</i>										
306	ND	25	27/04/2010	11	72.7	3.1	2.8	17.2	6.6 \pm 3.03	0.049
312	ND	20.5	22/03/2010	13	23	0.28	1.3	6.3	58.2 \pm 0.01	0.001
270	ND	22.5	16/03/2010	13	69.2	14.6	2.3	19.4	15.7 \pm 8.1	0.01
258	ND	22	10/11/2009	15	60	4.9	3.5	21.7	9.3 \pm 3.03	0.01
276	ND	23.5	25/02/2010	15	40	15.6	12.3	54.5	0.78 \pm 0.23	0.001
5257	ND	24	10/11/2009	15	40	49.7	56	324.1	217.3 \pm 63.37	0.001
346	ND	22	27/04/2010	11	90.9	22.5	3.6	24.9	23 \pm 9.99	0.01
<i>A. chirurgus</i>										
338	ND	16	22/03/2010	13	30.7	5.2	3.4	24.1	14.4 \pm 0.71	0.01
334	ND	16	29/03/2010	11	45.5	9.4	5.9	31.9	25.5 \pm 1.2	0.01
<i>S. viride</i>										
153	Male	24	30/06/2010	5	60	0.9	6.6	19.8	5.3 \pm 0.009	0.01
158	Male	17.5	30/06/2010	5	80	7.5	17.7	44	4.7 \pm 0.01	0.89
297	Male	22.5	16/03/2010	13	30.8	1.2	0.5	3.8	2.1 \pm 0.088	0.01

month = 4702); detections decreased outside the MPA (number of detections per month = 0.51 recorded by the remaining 15 receivers). The receivers located in the centre of the bay (silt substrate and deeper sites) recorded more detections (range of detections: 111–2600) than the receivers on the borders (rocky side) of the bay (range of detections: 8–110) for *L. apodus*. The specific site located on the artificial reef also achieved a higher detection rate. A total of 17 *L. apodus* were regularly detected at the same site, and 8 of those travelled outside the MPA (47% of individuals). Females of *S. viride* remained around the rocky substrate inside the MPA, whereas males tended to extend their movements to the artificial reef and borders of the MPA, including one male that left the MPA (Fig. 5). Several detections of *A. chirurgus* individuals were recorded outside the MPA. The detections were always made in the central bay VR2W location (silt substrate). Two individuals were detected by the last barrier of receivers and travelled more than 4 km. These individuals were never detected by a receiver within the study area of the MPA.

The residency patterns of each species indicated that, apart from 2 *L. apodus* (ID265 and ID160) and one individual *S. viride* (ID142), all fish were present for a long continuous period (range 29–279 d) within the MPA (Fig. 6, Table 3). *Lutjanus apodus* individuals exhibited more frequent movements between the MPA and the adjacent zones than *S. viride*. When individuals left the MPA, they were detected only sev-

eral times (3 detections) during a short period by the receivers of the MPA boundaries and were not detected again. One *L. apodus* individual (ID336) left the MPA and crossed Robert Bay in several hours. One *S. viride* individual (ID150) stayed outside the MPA for 38 continuous days before its signal was lost. *Acanthurus chirurgus* was not detected by the receiver placed on the rocky substrate, which explains why we could not calculate a residency index for this species.

Temporal movement

Acoustic monitoring allowed us to determine when individuals left the Robert MPA. Only one male *S. viride* (ID150) left the MPA; that fish was detected outside the MPA for 38 d (Fig. 6, Table 3). Several *L. apodus* left the MPA (47%), and none returned. These individuals travelled these long distances outside the MPA during June (n = 2), September (n = 3), and October (n = 2). All individuals measured at least 23 cm in length. One individual (ID265) left the MPA in December. Four individuals (1 *L. apodus* and 3 *A. chirurgus*) left the MPA on the same day (30 October 2010).

DISCUSSION

This study investigated home range size, site fidelity, and movement patterns of *Lutjanus apodus*, *Acanthurus chirurgus*, and *Sparisoma viride* inside

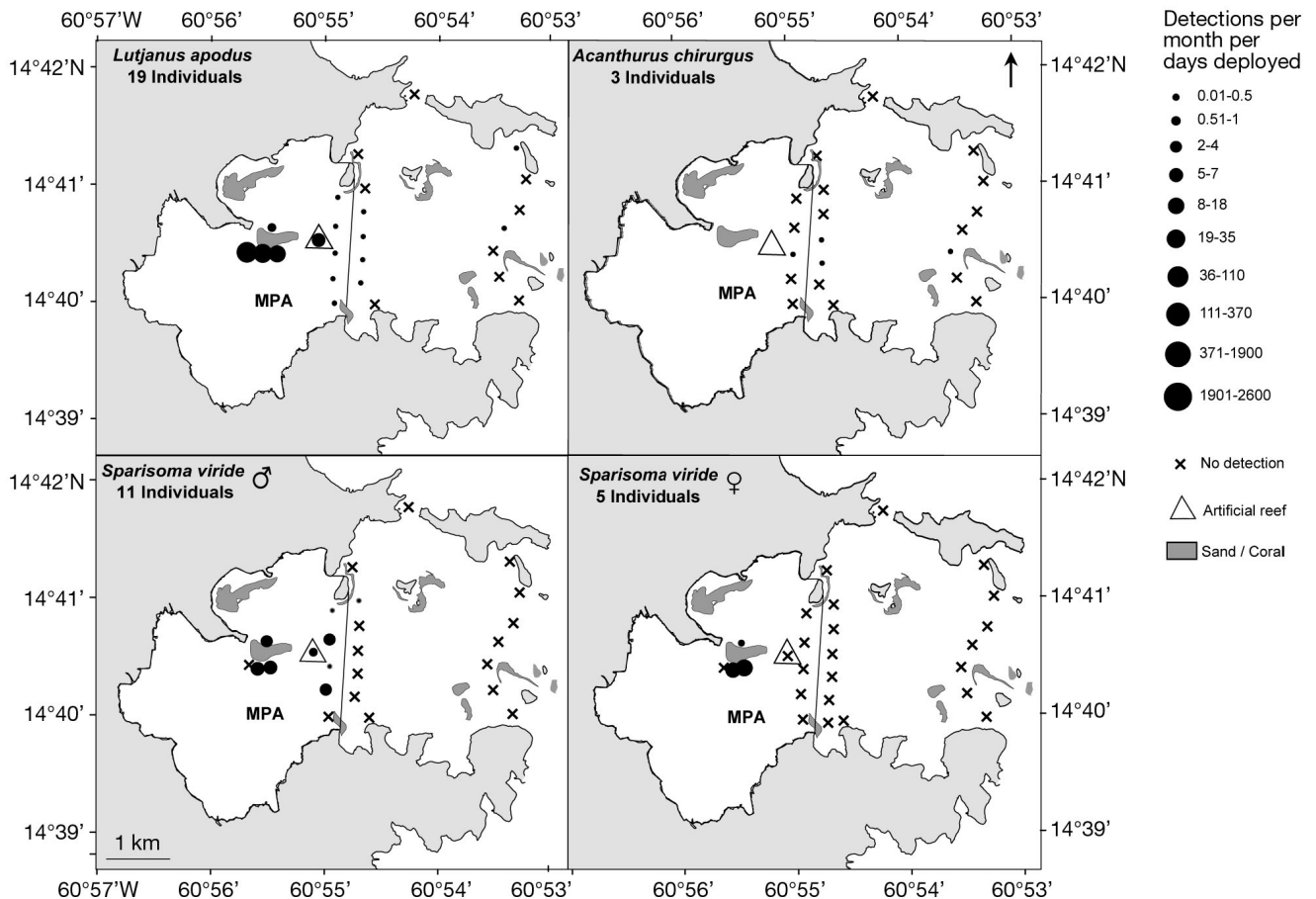


Fig. 5. Numbers of detections per month over the number of days of deployment for each receiver (each receiver was deployed during different periods) for *Lutjanus apodus*, *Acanthurus chirurgus*, and *Sparisoma viride* (males and females) in Robert Bay. Circle size is proportional to the number of detections per month per number of days of deployment that were recorded on each receiver. The black line represents the border of the marine protected area (MPA)

the Robert MPA in Martinique. This is the first time that (1) fish movement patterns have been studied in Martinique and that (2) these movements (home range and site fidelity) have been described for *S. viride* and *A. chirurgus* using acoustic telemetry. These species are among the most abundant species in the coral reef fish population in Martinique (Bruggemann et al. 1996, Nagelkerken et al. 2002, Choat et al. 2003) and play an important role in coral reef ecosystems (Bruggemann et al. 1996). In another study (J. Garcia et al. unpubl. data), visual censuses were conducted in the Robert MPA and revealed that these 3 species represented 37.2% of the total biomass of reef fish. These species represent a large proportion of fishing captures in Martinique and in other locations in the Caribbean (Polunin & Roberts 1993). In Martinique, reef fish stocks have been intensively exploited by artisanal fishing (Munro 1983). Several larger parrotfish species such as *S.*

viride are listed on the IUCN Red List with the status of Least Concern (Rocha et al. 2012); however, these species are highly fished in Martinique and other Caribbean islands (Hawkins & Roberts 2004).

For individuals identified by the relocation survey (*S. viride*, *L. apodus*, and *A. chirurgus*), we observed that movement patterns were restricted to the same small area located within the MPA. This coastal MPA is highly silty, but the area of site fidelity is located on the largest band of rocky substrate, which is less than 650 m². This rocky substrate consists of a 1-m-deep plateau surrounded by a drop-off ranging from 1 m to 6 m. The plateau is covered with algae, seagrass, coral and gorgonian patches (Legrand et al. 2012). The acoustic monitoring results demonstrate that the individuals in this study remained within a small area for long periods of time (from 2 mo to 1 yr) within the MPA and that many individuals were also able to travel very long distances (2–4 km) in a short period

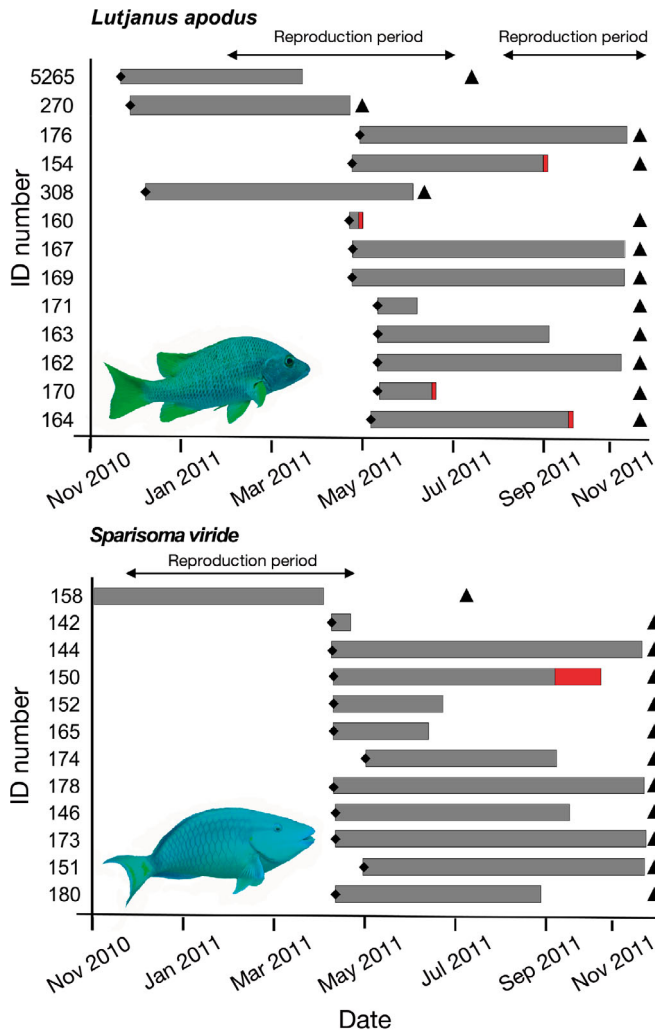


Fig. 6. Residency patterns of *Lutjanus apodus* and *Sparisoma viride* inside the marine protected area (MPA) (grey bar) and outside the MPA (red bar). Each bar begins on the day of release (diamond) and ends on the day of the last detection recorded on VR2Ws. Full bars represent continuous detections recorded by the VR2Ws. Triangles represent the predicted date of transmitter battery depletion. The double-headed arrows represent the reproduction period (= spawning season) for each species

of time (1–4 d) and were not detected again within the MPA. The external tagging results showed that several individuals covered large distances ranging from 2 to 9 km.

Limitations of this study

Despite 6 *L. apodus*, 4 *S. viride*, and 1 *A. chirurgus* being recaptured multiple times (range: 2–4 recaptures per individual), most of the external tagging data were calculated for only one recapture of each

individual. We tagged a high number of individuals, and the mean distance was calculated for more than 35 individuals per species. Under natural conditions, recapture events are variable, but mark-recapture techniques provide a reliable tool to gain information on the minimum distance that fish can cover between release and recapture sites. However, the precise routes followed by individuals remain unknown. Acoustic monitoring is also an effective approach that provides a higher sampling effort than fishing sessions. However, this method is relatively expensive, and thus, the data may be spatially restricted by the number and location of receivers utilised in the study. Although the largest recorded movements were only exhibited by several individuals, the results from passive acoustic monitoring tend to confirm the same trend as external tagging: some individuals were able to travel several kilometres. We did not observe any fish returning to the MPA, although the presence of only one receiver barrier close to the bay may have limited our ability to assess whether fish detected at this barrier truly left the MPA or simply returned between the 2 barriers of receivers. The detection range of receivers on the soft bottom was limited to 150 m, which corresponded to 600 m of detection distance for the double barrier composed of 2 juxtaposed lines of receivers. The transmission rate of acoustic tags varied randomly between 120 and 360 s. Therefore, to remain undetected by the receiver barriers, the swimming speed of fish must be faster than 1.67 m s^{-1} . Although information about swimming speed for the adult phase of our studied species was not available in the literature, we chose the swimming speeds of related species that are biologically and ecologically similar as a proxy for the swimming speeds of our studied species. We used the swimming speed of *Lutjanus griseus* ($<1 \text{ m s}^{-1}$; Luo et al. 2009), *Scarus niger* ($<0.53 \text{ m s}^{-1}$; Wainwright et al. 2002), and *Acanthurus coeruleus* ($<0.34 \text{ m s}^{-1}$; Morgan & Kramer 2004) for the maximum values of *L. apodus*, *S. viride*, and *A. chirurgus*, respectively. Therefore, given the related swimming speeds, we are confident that any fish crossing the double barrier would be detected even if the tag transmission rate was low, as it appears impossible for any of the species to cross the 600 m detection range in under 120 s.

Site fidelity and movement patterns

This study is the first to determine the home ranges of *S. viride* and *A. chirurgus* using acoustic telemetry. Their home ranges were identified inside the Robert

Table 3. Summary data and residency index (%) for *Lutjanus apodus* (n = 17) and *Sparisoma viride* (n = 12) obtained by passive acoustic telemetry for each zone (inside and outside the marine protected area (MPA). Results are restricted to the fish detected on at least 15 consecutive days. The number of days in the array is the number of days between the release and the last detection of the individual. ND: not determined

ID tag	Sex	Fork length (cm)	Tag date (d/mo/yr)	No. of days in array	Residency index (%)	
					Inside MPA	Outside MPA
<i>L. apodus</i>						
5265	ND	22.5	17/06/2010	295	100	0
265	Male	26	03/12/2009	23	95.7	4.3
260	ND	23	23/06/2010	130	99.2	0.8
270	ND	22.5	16/03/2010	405	100	0
257	ND	24	22/03/2010	202	99.5	0.5
336	ND	19	29/03/2010	89	93.1	6.9
176	ND	20	26/04/2010	208	100	0
154	ND	23.5	26/04/2010	131	99.2	0.8
308	ND	19.5	27/04/2010	402	100	0
160	ND	19	19/04/2011	19	94.7	5.3
167	ND	19.5	26/04/2011	208	100	0
169	ND	18.5	26/04/2011	208	100	0
171	ND	22.5	09/05/2011	29	100	0
163	ND	23.5	09/05/2011	122	100	0
162	ND	23.5	09/05/2011	195	100	0
170	ND	23	09/05/2011	40	97.5	2.5
164	ND	26.5	09/05/2011	142	99.3	0.7
<i>S. viride</i>						
158	Male	17.5	30/06/2010	279	100	0
142	Male	25	19/04/2011	15	100	0
144	Male	20.5	19/04/2011	208	100	0
150	Male	19	19/04/2011	174	78.2	21.8
152	Male	23.5	19/04/2011	75	100	0
165	Male	22.5	19/04/2011	65	100	0
174	Male	27	26/04/2011	128	100	0
178	Male	21	19/04/2011	211	100	0
146	Female	19	19/04/2011	155	100	0
151	Female	21.5	19/04/2011	211	100	0
173	Female	18	03/05/2011	194	100	0
180	Female	21	19/04/2011	137	100	0

MPA using acoustic relocation. The 3 tagged species showed important intraspecific variability in home range. Several factors, such as resource availability, competitor density, body size, fish behaviour, or environmental conditions, could explain home range variations (Eristhee & Oxenford 2001, Hitt et al. 2011a). For *A. chirurgus* (n = 2) and *S. viride* (n = 3), these variations could be caused by the low number of fish studied, which could be insufficient to obtain a reliable estimation of their home range. However, this study provides an important initial estimation of the home range for these species.

This study demonstrated that *S. viride* regularly maintain a restricted home range with a high degree of site fidelity (Table 2). The biology and ecology of the Caribbean fish fauna are relatively well docu-

mented, but there is little information on movement patterns (van Rooij et al. 1996, Chapman & Kramer 2000). Chapman & Kramer (2000) tagged 56 *S. viride*, and the longest movement they recorded was 110 m. These differences are most likely related to both the number and size of essential habitats used by this species, including seagrass and corals, inside the MPA. If their essential habitats are absent from the MPA, individuals may leave in search of feeding or reproduction areas. Moreover, not every *S. viride* was detected in every session of acoustic tracking. Several hypotheses may explain the absence of detection in active and passive monitoring: (1) fish may hide in crevices in the rocky substrate; (2) *S. viride* may have moved to the silt area at a 15 m depth, where the water turbidity is high (J. Garcia et al. unpubl. data), which could have reduced detection efficiency; (3) the boat travelling over the shallow reef plateau was very near the bottom (depth < 1 m), and thus, the depth may have been insufficient to detect the acoustic signal; or (4) fish were frightened by the boat and moved outside the detection range. In these last 2 scenarios, the transmitter signals would not have been detected by acoustic telemetry (VR2W and VR100) due to technical and environmental limits. *Sparisoma viride* is often reported to inhabit seagrass beds

(Nagelkerken et al. 2000); thus, the nearby seagrass habitat may have sheltered the *S. viride* that were no longer detected.

For *A. chirurgus*, our home ranges ($KUD^{50} = 4660 \text{ m}^2$, mean distance covered = $725 \pm 1442 \text{ m}$, maximum distance = 4992 m) were larger than the values previously reported in the literature (Chapman & Kramer 2000, dos Santos et al. 2010). Moreover, some individuals likely left the MPA. Using external tagging, Chapman & Kramer (2000) have shown that *Acanthurus bahianus* and *Acanthurus coeruleus* can cover a distance of ~100 m; however, Caribbean surgeonfish movement patterns have been poorly documented.

Some *L. apodus* were not detected by active and passive acoustic monitoring. The death of individuals

is one possibility to explain these results. However, this species is robust to tagging procedures (J. Garcia et al. unpubl. data), and the tagged individuals recovered well during the acclimation period in captivity, displaying normal swimming and feeding behaviour. It is possible that some individuals may have left the MPA due to the stress induced by the capture and tag implantation. It is also possible that some individuals may have explored the waters outside the MPA to find another preferential site. Although individuals that left the MPA should have been detected by the double barrier of receivers deployed at its boundaries, it is possible that some individuals may have passed through the receiver array without being detected. It is also possible that fouling developed on the receivers, which may have decreased the detection range despite regular cleaning.

The present study reports the largest home range size (KUD⁹⁵) thus far described for *L. apodus* (previously reported by Hitt et al. 2011a,b). Our estimates were 6 times larger than the home ranges (KUD⁹⁵) reported by Hitt et al. (2011a). Environmental conditions, predation risk, competition, and body size could explain these differences in home range (Hitt et al. 2011a,b). The residency index we calculated suggests that 8 *L. apodus* (47 %) left the Robert MPA after a period (from 3 weeks to several months) spent at their preferential sites. Once a fish left the MPA, it was not detected again. Except for 2 individuals, all fish that left the MPA had a minimum size of 23 cm (sexual maturity ~25 cm; Munro 1983). These departures from the MPA occurred within the reproductive period indicated by Munro (1983). Departures were concentrated within the months of June (n = 2), September (n = 3), and October (n = 2), which coincide with the reproductive season estimated by Munro (1983), thus suggesting that these movements could be linked to reproduction. The capture of sexually mature *L. apodus* (>25 cm) in the Robert MPA was rare. The tagged individuals were mostly sub-adult and were nearing maturity. Therefore, it could be assumed that individuals that left the MPA were migrating for their first reproduction event. Hammerschlag et al. (2010) suggested that some *L. apodus* individuals may forage around their preferential sites, whereas others may extend their movements to investigate further foraging areas. In the present study, residency inside the MPA was very high, and foraging most likely occurred along the reef inside the MPA. We propose 2 complementary hypotheses: (1) immature individuals may remain within their home range and forage inside the MPA, and (2) mature individuals may

stay in the proximity of their home range but may migrate outside the MPA during the reproductive period. However, 2 individuals measuring 19 cm left the MPA, whereas 2 other fish measuring 23.5 cm remained within the MPA. This finding could reflect individual variability in maturation.

We also observed 4 individuals (1 *L. apodus* and 3 *A. chirurgus*) that left the MPA on 30 October 2010. This date also corresponds to the occurrence of Tropical Storm Tomas on Martinique Island. We propose that the storm or associated strong precipitation could have induced rapid, escape-like movements in some species. For the *L. apodus* individual, it is difficult to conclude whether this departure was caused by the storm or movements associated with reproductive behaviour. Some studies have observed that hurricanes cause modifications to fish assemblages (Craig 1996, Heupel et al. 2003, Greenwood et al. 2006, Rousseau et al. 2010) and are capable of inducing fish movement (Kawabata et al. 2010). In the present study, we suggest 2 possible explanations regarding why none of the tagged fish that left the MPA returned: (1) fish were most likely caught by fishing traps that are abundant at the edges of the MPA (J. Garcia et al. unpubl. data), or (2) fish may have settled in a new area (relocation). Another possible hypothesis is the 'member-vagrant hypothesis' that has been developed in a series of papers (Iles & Sinclair 1982, Sinclair & Iles 1988, 1989). The individuals that left the MPA can be considered migrant individuals of this population. These individuals were lost from the local population of the MPA, and if they survived outside the MPA, they spawned in other locations.

Mangroves, as well as small coral patches (not represented due to scale used in mapping benthic communities; Legrand et al. 2012), are present close to a location where individuals were found to show high site attachment (Fig. 1), thus suggesting mangroves are an essential habitat type for the species under investigation. We also observed that many fish used the centre of the bay (silty and deep) to leave the MPA. This observation is contrary to the common hypothesis that large bands of silty or sandy substrate represent a physical barrier for reef fish movement (Chapman & Kramer 2000). However, Chateau & Wantiez (2008) demonstrated that some reef-associated species used sand substrate during their inter-island movements. Our results demonstrated that presumably unfavourable habitats were occasionally used by reef fish as corridors. We suggest that sand or silt substrates could play a temporary ecological role in reef fish life.

Implications for the design of marine reserves

The Robert MPA is relatively small in comparison with other MPAs in the world. In addition, it is mainly composed of large expanses of silty bottoms with small patches of coral reef. The size and location of the Robert MPA were established by fishermen without complementary scientific information regarding benthic or fish communities to support the decision-making and design process. However, we observed a high site attachment as well as restricted movements, indicating that most fish were resident within the MPA, as only a few individuals migrated outside this zone. The Robert MPA appears to be effective for the 3 species in this study. The fish spent most of their time in areas of rocky substrate within the MPA where corals, seagrass, and algae occur, suggesting that these rocky areas are essential habitats for the 3 species. However, the surface covered by this type of substrate within this MPA is limited. It appears that this MPA was effective to protect juveniles and sub-adults of *L. apodus*, as they mostly remained within the MPA. However, adult *L. apodus* were able to travel long distances outside the MPA and were therefore more vulnerable to fishing pressure occurring outside the MPA. Such movements are usually made by the largest individuals, which are the most important for population or stock replenishment (Birkeland & Dayton 2005). Indeed, we observed intensive fishing concentrated on the MPA boundaries and around the numerous rocky substrates of the unprotected area of Robert Bay (Fig. 1). We suggest that the MPA should include additional rocky substrate to improve its effectiveness. Even if the Robert MPA seems to be of adequate size to protect these species, we encourage an expansion of the MPA to include the entire bay, which will increase the quantity of protected rocky substrate. By protecting more of the habitats that are essential to commercially valuable species during different life cycle stages, the Robert MPA can ensure better protection of these species, thus allowing them to reach maturity, which in turn will allow stock replenishment, increase fish abundance, and increase biomass. Moreover, the spillover of the largest individuals and mature individuals could further benefit fishermen and the local economy. The locations of spawning aggregation sites for *L. apodus* are currently unknown in Martinique. The identification of these sites should be a priority for future studies to determine whether any of these sites are protected under the current MPA design. In addition, the number of traps placed on the MPA boundaries should be

restricted and controlled to encourage successful stock replenishment.

This study showed that MPAs established on degraded coral reef habitat could be effective to protect some species. Currently, marine coastal habitats are increasingly degraded by anthropogenic activities (Ban et al. 2010). Although the protection of healthy coral reefs should be a priority, the present study demonstrates that the protection of degraded habitat can also be effective within the context of degraded ecosystems.

In conclusion, the utilisation of multiple tools such as conventional external tagging and active and passive acoustic tracking provided complementary information on spatial and temporal patterns of fish movements. Small MPAs can be very useful to protect fish if they include the essential habitat used by coral reef fish. However, we revealed that some individuals were able to occasionally travel several kilometres outside the MPA; the silty habitats were not impassable natural barriers for these species. An understanding of the biological and environmental factors inducing these large movements is essential and should be a priority for improving MPA design and effectiveness.

Acknowledgements. Financial support for this study was provided by Fondation d'entreprise TOTAL and the École Pratique des Hautes Études. We thank the Observatoire du Milieu Marin Martiniquais (OMMM) and the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) for technical support. We are grateful to fishermen Pierre Pancarte and Rémy Surena. We thank Johann Mourier for his helpful comments, which improved the manuscript and Romain Crec'hriou and Anne Tessier for assistance in the field. We are grateful to Gary Fowler and American Journal Experts for English language and manuscript revisions.

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