
Spatial behavior of two coral reef fishes within a Caribbean Marine Protected Area

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Abstract :

A better understanding of the key ecological processes of marine organisms is fundamental to improving design and effective implementation of marine protected areas (MPAs) and marine biodiversity. The movement behavior of coral reef fish is a complex mechanism that is highly linked to species life-history traits, predation risk and food resources. We used passive acoustic telemetry to study monthly, daily and hourly movement patterns and space use in two species, Schoolmaster snapper (*Lutjanus apodus*) and Stoplight parrotfish (*Sparisoma viride*). We investigated the spatial overlap between the two species and compared intra-specific spatial overlap between day and night. Presence-absence models showed different diel presence and habitat use patterns between the two species. We constructed a spatial network of the movement patterns, which showed that for both species when fish were detected by the array of receivers most movements were made around the coral reef habitat while occasionally moving to silt habitats. Our results show that most individuals made predictable daily crepuscular migrations between different locations and habitat types, although individual behavioral changes were observed for some individuals across time. Our study also highlights the necessity to consider multiple species during MPA implementation and to take into account the specific biological and ecological traits of each species. The low number of fish detected within the receiver array, as well as the intraspecific variability observed in this study, highlight the need to compare results across species and individuals to be used for MPA management.

Highlights

- ▶ Two species of tropical reef fish showed contrasting spatial behaviour. ▶ Models revealed interspecific diel differences in presence and habitat use. ▶
- ▶ Fish shifted their activity and use of habitats between day and night. ▶ Multi-specific approaches increase our understanding of fish spatial use in MPAs.

Keywords : Spatial behavior, Acoustic monitoring, Individual variability, *Lutjanus apodus*, *Sparisoma viride*, Martinique

1. Introduction

Animal movement plays a fundamental role in the structure and dynamics of populations, communities and ecosystems (Nathan et al., 2008) and is driven by key ecological processes that influence how animals occupy their environment at multiple spatial and temporal scales (Hitt et al., 2011a). The main difficulty in the study of marine animal movement resides in the complexity of choosing appropriate spatio-temporal scales and matching technology to that appropriate scale. In many studies, fish movement patterns have been investigated at various scales ranging from meters to kilometers and from a few minutes to several years (Quinn and Brodeur, 1991; Pittman and McAlpine, 2003). For example, fish often display diel migrations at sunrise and sunset between spatially distinct diurnal and nocturnal habitats inside their home range (McFarland et al., 1979; Krumme, 2009; Hitt et al., 2011b). Studies have revealed this phenomenon for different fish families, such as Haemulids (Ogden and Ehrlich, 1977; Rooker and Dennis, 1991; Nagelkerken et al., 2000), Lutjanids (Nagelkerken et al., 2000; Verweij et al., 2007; Hitt et al., 2011a, 2011b), Lethrinids (Chateau and Wantiez, 2008a) and Labrids (Ogden and Buckman, 1973; Dubin and Baker, 1982). However, a better understanding of spatio-temporal movement patterns at small and medium-scales can provide fundamental information to improve marine protected area (MPA) management. The parameters characterizing the design of MPAs such as size, shape and number of MPAs as well as optimal spacing between them should be determined by accounting for fish mobility and behavior (Claudet et al., 2008). The conservation of a species that spends a large amount of time outside a MPA will be less efficient than species whose ranges are within MPA boundaries (Chateau and Wantiez, 2008b; Meyer et al., 2010). Small marine reserves may not contain all essential habitats (refuge, nutrition and reproduction) and the complete home ranges of target fish species, leading to partial protection (Abecasis et al., 2015). Most studies on movement patterns have focused on residence time, home range size and site fidelity but few studies have investigated the movement patterns and habitat use at finer-scales (Toole and Szedlmayer 2011). Acoustic monitoring has been extensively used to determine movement patterns, habitat utilization and home range size (Meyer et al., 2000; Lowe et al., 2003; Topping et al. 2005; Marshall et al., 2011; Garcia et al., 2014). However, the performance of receivers, as a result diel detection patterns, could be affected by the number of tagged individuals within the array (Simpfendorfer et al., 2008) and the increased environmental noise at night (Payne et al., 2010; Koeck et al., 2013), which could impact our interpretations of fish behaviour.

59 A recent study (Garcia et al., 2014) used two complementary methods (acoustic telemetry and external
60 tagging) to investigate movement patterns, home range and site fidelity of three fish species (*Acanthurus*
61 *chirurgus*, *Lutjanus apodus* and *Sparisoma viride*) in a Martinique MPA. These authors found that most fish
62 used a small preferential site ($\approx 650 \text{ m}^2$) located on a rocky reef composed of sand, corals and seagrass for a long
63 period time (2 months to 1 year) and used silty substrate and artificial reef like corridors during short periods of
64 time (1-4 days). Using active tracking, the authors determined the home range location and size for these species.
65 However, the study did not include the diel dimension of these patterns of movement. In the present study, using
66 the same dataset as Garcia et al., (2014), we aimed to determine habitat use and movements for *L. apodus* and *S.*
67 *viride* at a finer spatial scale. The aims were to: 1) quantify spatial overlap between *L. apodus* and *S. viride*, 2)
68 determine the presence probability for each species on each habitat (coral, seagrass, soft bottom or artificial reef)
69 and movements within the study area, 3) investigate potential shifts in habitat use between day and night and
70 finally 4) determine if fish show cyclical patterns (hourly, daily and seasonal) of space use. Unfortunately,
71 acoustic data obtained for *A. chirurgus* by Garcia et al., (2014) were insufficient to be used for spatio-temporal
72 analysis at this fine scale.

73 *L. apodus* and *S. viride* are commercial abundant species in the Caribbean and are highly targeted by
74 artisanal fishers (Rooker, 1995; Nagelkerken et al., 2002; Choat et al., 2003). These two species have different
75 trophic levels (carnivorous and herbivorous, respectively) and mobility. On the basis of previous studies on
76 movements of these species and their ecological and biological differences, we hypothesized that these two
77 species would have different temporal and spatial habitat utilization in the study area. Indeed, Hitt et al. (2011b)
78 demonstrated using active tracking that *L. apodus* makes twilight migrations from its daytime seagrass feeding
79 zones toward its nighttime refuge areas in the coral reef. However, acoustic telemetry has never been used to
80 study *Sparisoma viride*. The only information available regarding the movement of this species is provided by an
81 experimental mark-release-recapture study conducted in a Jamaican marine reserve which demonstrated highly
82 variable movement patterns for *S. viride* with individuals recaptured multiple times at the same site (within 100
83 m), whereas others were caught more than 10 km away outside the reserve (Munro 2000). Better knowledge of
84 the spatial behavior of these two species at finer spatio-temporal scale is necessary to implement efficient
85 protection for these exploited fish species in Martinique.

86 **Materials and methods**

87 **Study site**

88 The work was conducted in a coastal MPA located near the village of Robert in Martinique (Lesser
89 Antilles; 14°36' N, 61°32' W, Fig. 1). Eight no-take zones (NTZ) were created and managed by local fishermen
90 who decide on the opening and closing of fishing within these MPAs. Some MPAs are opened once a year but
91 others have never been opened since their creation. Our study was carried out in Robert MPA (Fig. 1), which has
92 never been opened to fishing since its establishment in 2000. The whole protected area covers 956 ha. The
93 habitat is not continuous within the MPA and is dominated by silty substrate. Nevertheless, three patches of
94 rocky substrates (~650 m²) are present inside the MPA and are composed of coral, gorgonians, sponges, seagrass
95 and algae (Fig. 1). The fish community is strongly concentrated within these zones (Garcia et al. 2014).

96 **Acoustic array**

97 From December 2009 to November 2011, we deployed 20 VR2W acoustic receivers (® Vemco) in
98 Robert Bay forming 3 lines of receivers. We used mobile tracking surveys using VR100 to determine fishes
99 preferred sites and the results were presented in Garcia et al. (2014). Five supplementary receivers were added to
100 the network from December 2010 to November 2011 at the preferred sites previously determined by the tracking
101 mobile system to determine *S. viride* and *L. apodus* diel patterns of movements within this habitat (Fig. 1). We
102 conducted range tests at different locations of the study area (See Garcia et al. (2014) for more details) showing a
103 maximum radius of 100 m for the receivers located on rocky substrates (R310, R307, R309, R308, R306) and
104 150 m for all the other receivers located on silty substrates.

105 **Fish capture and transmitter deployment**

106 Fish were caught using Antillean traps and immediately transported back to the laboratory where they
107 were placed in a holding tank. They were then equipped with VEMCO V7-4L[®] ultrasonic coded transmitters.
108 These tags pulse randomly every 120-360 seconds. Nominal battery life was expected to last over 412 days
109 according to the manufacturer. To reduce the impact of transmitters on fish mobility, the selected ratio of fish
110 weight to transmitter weight was kept below 1%. All fish were captured inside the MPA because of overfishing
111 outside the MPA, leading to difficulty in catching sufficiently large adult fish.

112 Each fish (N = 68) was anesthetized with clove oil at a concentration of 0.02 ml l⁻¹ and the transmitter
113 was inserted into the peritoneal cavity through a small incision (1 cm). To provide visual identification of these
114 fish after their capture, we also implanted an external T-tag (Floy Tags Inc.). Each individual was maintained in
115 captivity for 7 days, including one acclimation day, one operation day, 2 days for safe recovery, followed by 3
116 days of feeding. All individuals were released at the capture site along the coral reef patches (Fig. 1).

117 **Data analysis**

118 Receiver performance

119 We first filtered our raw detection data and deleted false detections. Data files downloaded from VR2W
120 receivers contained a number of parameters that can be used to investigate the receiver performance during the
121 deployment (Simpfendorfer et al., 2008). Three metrics were therefore calculated: code detection efficiency (cde
122 = D/S), rejection efficiency ($rc=C/S$) and noise quotient ($nq= P-(S.cl)$) - where D is the number of valid
123 detections, S is the number of synchs, C is the number of codes rejected because of invalid checksums, P is the
124 number of pulses detected and cl is the number of pulses used to make a valid code (detailed analysis are
125 presented in Simpfendorfer et al., 2008).

126 *Temporal analysis*

127 We calculated the number of days each fish was detected in the array as well as the proportion of days it
128 was detected during the experiment (i.e. the number of days from the time of release after tagging to the day the
129 receivers were removed from the water; Meyer et al., (2010).

130 We used time series analysis and fast Fourier transformations (FFTs) with Hamming window
131 smoothing (Statistica version 6.0) to describe the cyclicity in site utilization for each individual. For each fish,
132 we selected the receiver that most frequently detected that individual and pooled detections from that receiver
133 into hourly bins (Meyer et al., 2010).

134 *Spatial analysis*

135 Our first approach was to compare space use between species (Meyer et al. 2010). Based on the number
136 of days each individual was detected at each receiver, we generated a Bray Curtis similarity matrix and used a
137 one-way ANOSIM (Primer-E Version 6, Plymouth, UK) to assess the degree of spatial overlap between both
138 species. This statistical test quantifies spatial overlap between fish species and compares them against 999
139 random permutations. In addition, ANOSIM generates a Global R statistic (Clarke and Warwick, 2001) and a p-
140 value. If $p<0.05$, then the species do not show overlap and R indicates the degree of similarity between species
141 groups. We used R as an indicator of the degree of overlap between the groups (R<0.25: high overlap, R= 0.25-
142 0.75: medium overlap, R>0.75: low overlap). We used non-metric multidimensional scaling ordinations (nMDS)
143 to obtain a visual interpretation of space utilization and spatial overlap between species.

144 We then aimed to compare individual diurnal and nocturnal space use for each species (Meyer et al.
145 2010). We calculated the number of nocturnal (from 1659 to 0500 hrs) and diurnal (from 0501 to 1700 hrs)
146 detections per hour for each individual of each species. These periods corresponded to the annual average times
147 between sunrise and sunset in the study area. Using these individual measures, we generated a Bray-Curtis

148 similarity matrix and used a one-way ANOSIM (Primer-E Version 6, Plymouth, UK) as described above. We
149 used non-metric multidimensional scaling ordinations (nMDS) to obtain a visual interpretation of diurnal and
150 nocturnal space use for each species. We also determined the number of receivers visited by the fish. Individuals
151 were not tagged at the same time.

152 We used a generalized linear mixed-effects modeling framework (GLMM) that incorporates both
153 random and fixed variables, to examine the effects of time of year (calendar month), location (receiver) and time
154 of day (hour) on the presence of fish in the studied area. For each species, acoustic Tag ID was incorporated as a
155 random variable, rather than fixed factor, to account for pseudoreplication and enable model prediction to extend
156 to the rest of the population. Analysis was implemented using the `lmer()` function in the `lme4` package (Bates et
157 al. 2011) within R version 2.5.1 (R Core Development Team 2012). The analysis used a binomial error structure
158 with a logit link function. The binomial dependent variable was coded with a value of one if a fish was detected
159 ('present') and zero when no fish were detected ('absent'). 'Presence' was evaluated per hour for each level of
160 the qualitative variables 'Hour' and 'Receiver', and was modeled for the duration of the monitoring period. The
161 other qualitative variable was 'Month'. We used model selection and model-averaging procedures from the
162 MuMIn R package based on Akaike's Information Criterion corrected for small sample sizes (AICc) (Bardo
163 2013).

164 *Spatial network analysis*

165 In order to identify the patterns of movements and preferred area used by the two fish species, we used a
166 spatial network analysis. Instead of using a spatial network based on counts of directed movements between
167 receivers as proposed by Jacoby et al., (2012), which ignores temporal characteristics of movements such as
168 residency periods, we followed the Empirical derived Markov chain (EDMC) analysis proposed by Stehfest et al.
169 (2015) which takes into account this temporal dimension. A Markov chain is a random process that undergoes
170 transitions from one state to another (in our case from receiver to receiver) on a state space. For each species, the
171 raw series of acoustic detections was organized into an hourly detection time series for each fish. For every
172 hourly time step, if the fish was detected by a receiver then the receiver ID was assigned to the state and if the
173 fish was not detected it was assigned an absent state. Movement count matrices were then computed for each
174 individual fish containing movements between each receiver as well as the movements from each state to itself
175 (residency periods; the fish stay at the same receiver) and movements into absent state (transition periods outside
176 of the detection range of receivers). The Markov chain approach requires a number of assumptions including that
177 (1) the probability of moving from any given state to the next depends on the current state but not on the

178 preceding ones, (2) individuals move independently from each other, (3) transition probabilities between states
179 do not change over time and finally (4) tagged individuals represent a random sample of the population in the
180 study area. Transition probability matrices were constructed by dividing each number of transitions made from
181 one state to another or itself by the number of transitions made from the state. To identify preferred use of
182 locations (i.e. receivers) from the movement network, we calculated the eigenvector centrality of each node
183 which is a measure not only of the centrality of a state, but also of the centrality of the states it is connected too
184 (see Stehfest et al. 2015). It is calculated as the dominant eigenvector of the movement network or adjacency
185 matrix and is equivalent to the weighted proportion of the total number of paths in a network going to or coming
186 from a given node (Newman 2004). To test the difference between movements of the two species, we used a
187 Mantel test between the two transition probability matrices.

188 **Results**

189 Receiver performance

190 Overall the average receiver code detection efficiency (mean number of detections per synch) was 0.128
191 indicating that on average only 12.8% of the codes transmitted were detected. The mean rejection coefficient
192 was consistently low ($0.0022 \text{ rejections} \cdot \text{synch}^{-1}$) and the mean noise quotient was 7112 suggesting that the
193 environmental noise may have affected the receiver efficiency in the study area. While detection efficiency was
194 low, the rejection coefficient was also very low indicating that only small proportions of codes received were
195 rejected because of invalid checksums. It is therefore likely that most of the code detection inefficiency of the
196 receivers was the result of incomplete code sequences rather than rejected full sequences. The partial reception
197 of code sequences may be due to environmental characteristics such as the low depth of receivers around the reef
198 or due to individual movements during transmission. In this study, as we used 1 hour time intervals in most
199 analyses, the impact of missed code detections on our data analysis is likely to be low.

200 **Acoustic tagging**

201 We tagged and released 27 *S. viride* and 41 *L. apodus*. However, we detected only 12 *L. apodus* and 11
202 *S. viride* (Table 1), and only 7 *L. apodus* and 7 *S. viride* presented a percentage of time spent within the array
203 above 9%. *L. apodus* were monitored for periods of 2 to 208 days (mean = 87.3 days, SD = 92.9) and *S. viride*
204 for 5 to 215 days (mean = 67.7 days, SD = 71.9) (Table 1). *L. apodus* were detected from 1.5 to 100% of days
205 within the array (mean = 46.3%, SD = 0.5) and *S. viride* from 2.3 to 99.5% of days (mean = 29.6%, SD = 0.3)
206 (Table 1). Most fish remained in one patch of rocky substrate (650 m²). Despite overlap between detection
207 ranges of some receivers, no individuals were detected by two receivers simultaneously.

208 Spatio-temporal analysis

209 All 33 fish detected during this study, were recorded between December 2010 and November 2011 (Fig.
210 2, Fig. 3). The results of the ANOSIM analysis showed that there were statistical differences in space utilization
211 ($p < 0.05$) between *S. viride* and *L. apodus*, although overlap was still high ($R = 0.103$) (Fig. 4a). Three receivers
212 detected most of the fish along a rocky substrate: R307, R308 and R309 (Fig. 2) and separated by less 500 m
213 (Fig. 1). We observed that some individuals (ID#162, ID#169, ID#176, ID#265 and ID#167) made sunset and
214 sunrise movements between different sites but unfortunately some day or night locations remain unidentified

215 *Lutjanus apodus*

216 Global movement analysis

217 The best fitting GLMM models incorporated the covariates Hour, Month and Receiver (Table 2).
218 Although globally low, hourly probability of presence was lower during the day than at night within the receiver
219 array and higher at coral patches (receivers R307, R308 and R309) than other habitats (Fig. 5, Supplementary
220 Table 1). *L. apodus* showed a peak in its probability of presence in February compared to the other months
221 (Supplementary Table 1).

222 In general, our data show high intra-species variability in movement patterns between day and night.
223 The majority of movements between receivers occurred at sunset and sunrise. The results from the ANOSIM
224 showed a significant difference ($R = 0.608$, $p = 0.001$) between diurnal and nocturnal patterns of space use for all
225 *L. apodus* (Fig. 4b). The results of the Fast Fourier analysis revealed that individuals ID#169, ID#176, ID#308,
226 ID#265 and ID#167 had a 24-h cyclical pattern of movement (Table 1). Individual ID#265 had a supplementary
227 dominant peak at 12 h and individual ID#167 had a peak at 8 h. Fish ID#162 and ID#270 did not reveal any
228 cyclical patterns.

229 Movements within coral patches

230 Some fish displayed a shift in their diurnal and nocturnal site utilization during the study period (Figs 2
231 and 5). For example, Individual ID#176 appeared to reside near receiver R307 during the day and move to
232 receiver R309 at night but it stopped moving to R307 during the day between August and November. Moreover,
233 individual ID#167 stayed at the same receiver during the day and it moved to an unidentified site during the
234 night. However, it changed its behavior between September and October 2011 and stayed at receiver R309
235 between September and October 2011, and was also frequently detected by receiver R307 during the day in
236 August 2011. As another example, ID#169 resided at R309 during the night but was almost never detected
237 during the day.

238 Movements to the artificial reef

239 The artificial reef (R306) seems to play an important role in the spatial behavior for some fish because it
240 recorded the last detections of most fish that left the MPA. Indeed, individuals ID#308 and ID#265 were evenly
241 detected on the artificial reef at the end of the rocky substrate between January and May 2011. This site was
242 sporadically (19 pings) used by one *L. apodus* (ID#265), and frequently used by individual ID#308 (88.5% of
243 total detections). The receiver at this site recorded the last detections of both fish (Fig. 2). In addition, four
244 individuals (ID#154, ID#160, ID#164 and ID#170) have been detected 2-3 times by the second barrier of
245 receivers located outside the MPA. These fish were not detected again within the MPA.

246 *Sparisoma viride*

247 *Global movement*

248 The best fitting GLMM model incorporated Hour, Month and Receiver as covariates (Table 2). Hourly
249 probability of presence was higher within twilight periods with a peak of presence at 5-6 am and 5-6 pm (Fig. 6).
250 *S. viride* was also more present at coral patches but non-negligibly used seagrass beds (R310) and more
251 surprisingly silty substrates (R298 and R299) (Fig. 5). *S. viride* showed a peak of presence in March
252 (Supplementary Table 1).

253 Temporal patterns of stoplight parrotfish were highly variable among individuals (Table 1). Three fish
254 (ID#151, ID#173, and ID#178) were detected frequently (>63% of the time) within the array (Table 1). In
255 contrast, individuals ID#142, ID#144 and ID#180 were less frequently detected (< 4.6% of the total time; Table
256 1). Three fish (ID#151, ID#173, and ID#178) showed cyclical periods of 24, 12, 8, 6 and 4 h (Table 1) as
257 revealed by FFT analysis. In addition, there was no overlap between diurnal and nocturnal spatial patterns of *S.*
258 *viride* (ANOSIM, $R=0.712$, $p=0.001$) (Fig. 4c). Only one fish (ID#150) was detected by one receiver located
259 outside the MPA and was not detected again within the MPA.

260 *Movements within coral patches*

261 For *S. viride*, diel detection patterns varied consistently between individuals (Fig. 3 and 5). Three individuals
262 (ID#146, ID#173 and ID#178) were frequently detected during the day but never at night. Receivers R309 and
263 R307 predominantly detected these fish. In addition, they occasionally moved to receiver R310 (1-19 pings).
264 Nevertheless, individual ID#151 was detected almost only at night (1659 to 0500 hrs) as well as at sunset and
265 sunrise at R307, but only a few detections (6 pings) were recorded during the daytime. One individual (ID#165)
266 did not display a diel pattern. This fish was mainly detected on silty substrate by R299 ($F_d = 90.7\%$ of total
267 detection) and also occasionally moved to R298 (2 detections) and R297 (12 detections). This fish was the only

268 one to use these three receivers, which were located on silty substrates at a depth of 20 meters. Individuals
269 ID#146, ID#178 and ID#173 moved to receiver R309 during May. Three individuals (ID#151, ID#178 and
270 ID#173) were detected from 15th to 19th of April 2011 by receiver R310.

271 Movements on silty substrates

272 Some individual *S. viride* moved on silty substrates (R298; R297; R298 and R269) located on the boundaries of
273 the MPA and kept the same location for consecutive days (Fig. 3). This behavior was observed for four
274 individuals and exclusively in males. The fish were detected 1 to 8 times a day over 1-8 consecutive days.

275

276 Network analysis

277 For *L. apodus*, most hourly direct movements occurred between receiver R307, R308, and R309 located
278 all on coral patches (Fig. 6) with receiver R309 being the most central node of the network as shown by the
279 highest eigenvector centrality value (0.15). However, *L. apodus* were most likely to be in the spatially absent
280 states (summed probabilities = 0.89). Out of the detectable states, R309 had the highest rank, followed by state
281 R308, then R307 (Fig. 6). States R306 (artificial reef) and R310 (coral patch) were rarely reached.

282 For *S. viride*, most movements occurred between R306 (artificial reef) and R299 (silty substrate) although the
283 most central node was R307 (coral patch) given the movements between the trio of receivers R307, R309 and
284 R310 located all on coral patches (Fig. 6). Like *L. apodus*, *S. viride* were most likely to be in the spatially absent
285 states (summed probabilities = 0.94). *S. viride* similarly used receivers R307 and R309 but also R310 located on
286 the other side of the reef. However, they also used a larger number of receivers than *L. apodus*, often being
287 present in receivers R297, R299 (silty substrate) and R306 (artificial reef) (Fig. 6). These movements were
288 driven by the short-term activities of 4 individual fish in this area. There was also no clear significant similarity
289 between patterns of movements of both species (Mantel test: $r = 0.04$, $P = 0.058$).

290 Discussion

291 In this study, we provide evidence for inter- and intra-specific differences in spatio-temporal patterns of
292 reef fish movements. Individual variability can be influenced by species life-history traits, risk of predation,
293 competition and food resources (Hitt et al., 2011a, 2011b). In addition, our analysis was applied to a small
294 number of individuals, which may increase variability in the results, which is a recurrent problem with acoustic
295 telemetry studies (Luo et al., 2009). Nevertheless, our results highlight several patterns of space use at different
296 temporal scales among tagged fish.

297 We observed that *S. viride* individuals often visit habitats composed of silt and mud where feeding or shelter
298 habitats are absent. These results are surprising for *S. viride* because this species usually lives in coral reef and
299 mangrove habitats (Bruggemann et al. 1994). Female parrotfish can share the same territory, while males also
300 share territory but show intraspecific competition against other males to defend their harem. Therefore, male *S.*
301 *viride* (specifically young males) tend to cover a larger home range than females (van Rooij et al., 1996; Mumby
302 et al., 2002) and have more exploratory movements than females. Another explanation could be that fish were
303 predated. However, this possibility seems to be unlikely as tagged fish had been detected over long periods (2-6
304 months) and ingested acoustic tags by predators are generally expelled within a few days (Armstrong et al.,
305 1992). Additional studies are required to confirm our finding that *S. viride* visits silt habitats for a period of
306 consecutive days (1-8 days). These two species did not have the same spatial utilization of the habitat
307 (ANOSIM: $p < 0.05$) but they have a high overlap ($R = 0.13$; Fig 4). This result can be explained if there are many
308 replicates at each site (Clark and Warwick 2001). In our analysis, we have 33 fish detected by 18 different
309 receivers. The number of replicates is high which may explain the R value. Consequently, it is likely that there
310 habitat use by the two species is only weakly overlapped and a low signal.

311 For both species, we observed that many fish repeatedly shift locations between day and night for
312 several months (4-7 months). Most individuals had a preferred diurnal and nocturnal site, making daily
313 crepuscular migrations between sites when they were within the range of the receivers. This behavior, also called
314 “commuting”, has been described in other coral reef fish species (Meyer and Holland, 2005; Marshall et al.,
315 2011; Taylor and Mills, 2013). Some of these individuals interrupted their daily crepuscular movements at some
316 periods of the year. These behavioral modifications appeared to take place over a period of 1 to 3 months and
317 then the fish returned to twilight movement patterns. The unexpected modifications of diel movements could be
318 due to potential spawning migrations (Taylor and Mills, 2013), although this hypothesis remains difficult to
319 confirm with our present data. Most studies on *L. apodus* were conducted over 3 months using external tags or
320 mobile acoustic tracking (Verweij et al., 2007; Hitt et al., 2011a) and showed evidence of variability in patterns
321 of space use between different individuals.

322 On a daily scale, crepuscular movements as shown by shift in space use seemed to be a frequent
323 behavior in reef fish demonstrating cyclical diel movement patterns. Unfortunately, we did not use a control tag
324 to test the influence of diel variations on detection efficiency. Previous studies showed that the variations of diel
325 detection patterns observed could be the result the increased of environmental noise at night that may decrease
326 detection probabilities (Payne et al., 2010; Koeck et al., 2013). Environmental noise could be created by an

327 increase in biological activity (Radford et al. 2008). In our study, only individuals ID#162 and ID#165 were
328 detected by the same receiver during all hours of the day (Fig. 2; Fig 3). For these two individuals no cyclical
329 diel patterns were revealed by the FFT analysis. Other individuals (ID#176 and ID#167) were detected by the
330 same receiver during all hours of the day but simply over short periods (<5 days) and showed cyclical diel
331 movement patterns (Fig. 2). Consequently, it remains difficult to confirm the diel patterns hypothesis for these
332 individuals. However, the results from the GLMM of presence-absence data show distinct daily presence
333 patterns between species (Fig. 5) that is unlikely a result of environmental noise on detection probabilities.
334 Globally, *L. apodus* tended to increase their presence at receivers during the night while *S. viride* showed an
335 increased probability of presence during sunrise and sunset periods (Fig. 5).

336 For other individuals that moved between different receivers, there was no ambiguity in the presence of
337 diel movement patterns. These movement patterns have previously been observed for *L. apodus* (Rooker and
338 Denis, 1991; Nagelkerken et al., 2000; Verweij et al., 2007; Hitt et al., 2011a) and for the Scarine labrids (Meyer
339 et al. 2010; Welsh and Bellwood, 2012; Howard et al., 2013) and were attributed to homing or sheltering. In
340 other species, these diel patterns have been widely documented (Lowe et al. 2003; Meyer 2007), with fish
341 moving between feeding and refuge areas at sunset and sunrise (Dahlgren and Eggleston 2000; Meyer et al.
342 2010; Welsh and Bellwood 2012). The variability of the movements observed in other studies was frequently
343 attributed to the availability and proximity of foraging areas. In the present study, the narrow band of rocky
344 substrate is composed of patchy corals, sponges, seagrass and algae at the depth of 3 to 8 m, but is also damaged
345 by a high level of sedimentation. In addition, this area is surrounded by anoxic mud at 9 to 20 m depth, which
346 may isolate this habitat patch. However, although this rocky substrate concentrates common marine organisms, it
347 appears unlikely that it can supply sufficient foraging or refuge areas for all fish present in this zone. We
348 therefore hypothesize that some fish move to other sites, such as nearby mangroves or other coral patches (Fig.
349 1).

350 Of the 68 fish tagged, only one third were detected and half of the monitored individuals were detected
351 less than 3% of the time within the array of receivers (Table 1) with 85% of tagged fish being transitory in the
352 study area. In a previous study, Garcia et al., (2014) used a mobile tracking system (VR100) to follow the
353 individuals outside of the study area. No tracked individuals were found outside of the study area (in /out MPA).
354 These fish may have moved outside the receiver array after release and found another preferred site;
355 alternatively, they may be less site-attached than the others and have no specific shelter site. It is very likely that
356 these individuals showed preferences to other sites that were not covered by the range of our receivers. Meyer et

357 al. (2010) tagged 70 individuals but only 53 fish were detected in a period varying from 1 to 612 days (median=
358 52 days). Our results can be explained by the degraded and restricted rocky habitat present on the study area.
359 This zone seems unfavorable or of an insufficient size to establish a residency site for all *L. apodus* and *S. viride*
360 individuals. However, it seems that only some individuals could shelter during long periods in the study area.

361 Moreover, the last detections recorded for 12 tagged fish were before the end of transmitter battery life
362 and 6 of these were detected for the last time outside of the MPA. Previous studies have shown that the number
363 of fish detected declined soon after release and during all the monitoring period (Chateau and Wantiez 2008b;
364 Meyer et al., 2010). Many reasons could explain this fact: 1) premature failure of battery life, 2) effect of tagging
365 procedures (increased mortality or tag expulsion), 3) fishing or natural mortality 4) relocation to another site
366 (Meyer et al., 2010). Our previous study showed that fish can leave the bay and be recaptured several kilometers
367 away (Garcia et al., 2014), a finding which could support the last hypothesis.

368 Despite the small number of detected fish, we observed similar patterns of movements and simultaneous
369 movements for 2-3 individuals for each species. There are a number of potential explanations for these
370 simultaneous spatial temporal movements: 1) spawning seasons, 2) changes of environmental conditions
371 (precipitations, high wind, and variability of physico-chemical water conditions), 3) anthropogenic activities
372 (boat noise, nautical activities), 4) predation pressure, 5) competitors or 6) temporal dietary requirements (Hitt et
373 al., 2011b).

374 The probability of an individual fish being outside receiver range in the experimental study were high
375 for both species suggesting that fish spent a large proportion of their time outside of the array. It also suggests
376 that, when travelling, fish might use different routes and use random walk strategies rather than directed walks.
377 Random walks are used when the locations of resources are unknown, whereas directed walks should be optimal
378 when the location of favorable habitats is known (Papastamatiou et al., 2011). In new and unfamiliar locations or
379 areas where patches are outside the sensory range of the animal, some form of random-walk must be performed.
380 This might be the case in our study as the environment is composed of two distinct habitats including a restricted
381 reef surrounded by unfamiliar silt habitats. Our results also show that fish may have centers of activity along
382 specific parts of the reef and occasionally visit other habitats such as silt areas (Fig. 6). In accordance with our
383 results, previous research found that individual reef fishes can cluster their activities within small sections of the
384 available linear reef habitat, and those movements within and outside of these home ranges are made along
385 predictable routes (Fox and Bellwood, 2014). Short excursions outside an established center of activity are
386 commonly observed (Kramer and Chapman, 1999, Chateau and Wantiez, 2008b) and generally attributed to

387 exploratory movements outside their areas of normal activity or spawning activity. Both species are coral reef
 388 attached and it remains unclear why some explore silt habitats where corals are absent.

389 In conclusion, our study showed that within a MPA, two fish species of separate trophic guilds show
 390 different spatial behavior. At the species level, individuals showed behavioral differences and clear diel and
 391 seasonal shifts in area used. Although both species showed preferences to reef habitats, they also explored silt
 392 habitats in the border of the MPA. The use of silt habitats however, remains unexplained by our data and
 393 deserves further investigations. In this study, while our data do not allow us to conclude if this MPA helps
 394 protecting our studied species, intra and interspecies variability in spatial behavior indicates that it is important to
 395 consider multiple species and a large number of individuals in telemetry studies to improve MPA monitoring and
 396 effectiveness.

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404 405 References

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526 Figure Legends

527 Fig. 1: Map of the study area in Martinique (▲: Artificial reef, ✕: Location of *Lutjanus apodus* capture and ✕,
 528 Location of *Sparisoma viride* capture). Locations of the VR2W acoustic receivers are displayed (Point: receiver
 529 location; Circle: detection range). The artificial reef is indicated and the town of Le Robert is represented by a
 530 dark circle.

531 Fig. 2: Diel detection patterns of 6 *Lutjanus apodus* captured inside Robert MPA on rocky substrate from
 532 December 2011 to November 2012. Horizontal curves show daily sunrise and sunset. Colors of the symbols on
 533 the scatterplots correspond to the receiver locations indicated in the map on the top of the figure.

534 Fig. 3: Diel detection patterns of 5 *Sparisoma viride* captured inside Robert MPA on rocky substrate from
 535 December 2011 to November 2012. Horizontal curves show daily sunrise and sunset. Colors of the symbols on
 536 the scatterplots correspond to the receiver locations indicated in the map on the top of the figure.

537 Fig. 4: a: non-metric multidimensional scaling ordination of space utilization by *Lutjanus apodus* and *Sparisoma*
538 *viride* in the study area. b: Non-metric multidimensional scaling ordination of diurnal and nocturnal space
539 utilization by *Lutjanus apodus*. c: Non-metric multidimensional scaling ordination of diurnal and nocturnal space
540 utilization by *Sparisoma viride*.

541 Fig. 5: Boxplot showing the predicted probabilities of presence from the GLMM most parsimonious model for
542 both species as a function of time of day and habitat.

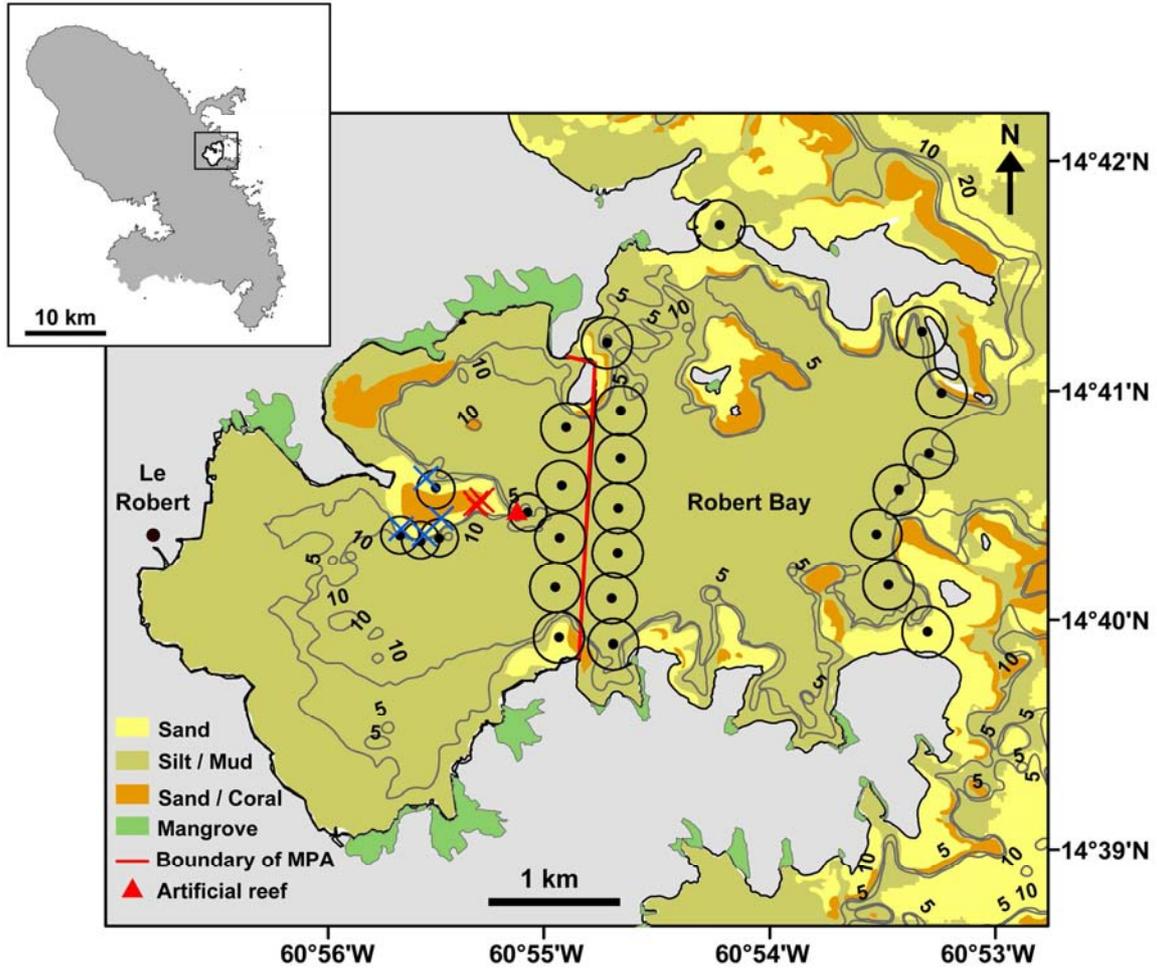
543 Fig. 6: Spatial networks of movements for each fish species with node representing receiver locations and node
544 size and color proportional to the eigenvector centrality computed for the adjacency matrix of between-state
545 transition frequencies. Edges represent frequencies of movement between receivers. For each network, the
546 transition probability matrix is given with colour of the cells related to probabilities.

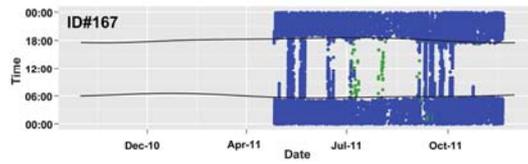
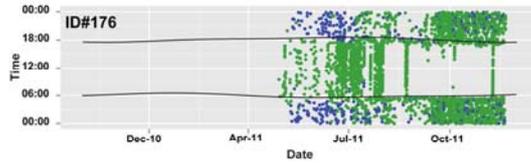
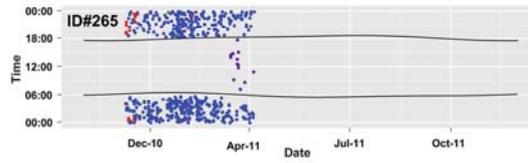
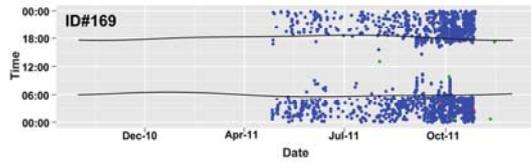
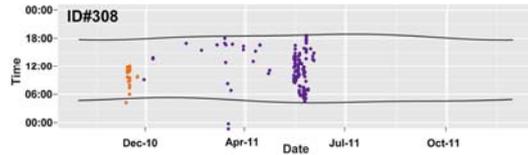
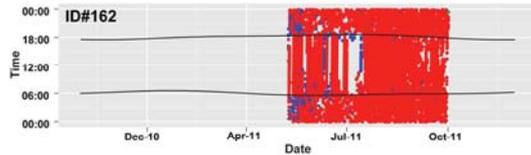
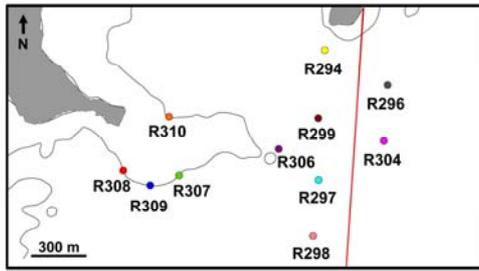
Table 1: Descriptive information about tagged individuals and dominant peaks calculated with time series analysis (FFT) for *Lutjanus apodus* and *Sparisoma viride*.

Species	Sex	Individuals	Total length (cm)	Weight (g)	Number of days detected	% of time within array	Number of VR2Ws visited	Dominant peaks (h)
<i>L. apodus</i>		ID#162	23.5	200	195	100%	3	0
<i>L. apodus</i>		ID#169	18.5	100	208	98%	3	24
<i>L. apodus</i>		ID#176	20	120	208	98.1%	2	24
<i>L. apodus</i>		ID#308	19.5	120	36	10.7%	2	24
<i>L. apodus</i>		ID#265	22.5	150	118	99.2%	4	24, 12
<i>L. apodus</i>		ID#167	19.5	120	208	100%	3	24, 8
<i>L. apodus</i>		ID#270	22.5	180	57	40.4%	1	0
<i>L. apodus</i>		ID#154	23.5	240	3	1.5%	5	/
<i>L. apodus</i>		ID#160	19	120	2	0.9%	2	/
<i>L. apodus</i>		ID#164	26.5	300	6	3.1%	5	/
<i>L. apodus</i>		ID#170	22.5	200	3	1.6%	3	/
<i>L. apodus</i>		ID#171	24.5	260	4	2.1%	2	/
<i>S. viride</i>	Female	ID#146	19	140	68	31.5%	3	0
<i>S. viride</i>	Female	ID#151	21.5	190	215	99.5%	2	24, 12, 6, 4
<i>S. viride</i>	Male	ID#165	22.5	190	21	9.7%	3	0
<i>S. viride</i>	Female	ID#173	18	100	128	63.7%	3	24, 8
<i>S. viride</i>	Male	ID#178	21	160	158	73.1%	3	24, 8, 4
<i>S. viride</i>	Male	ID#174	27	300	21	10.1%	2	/
<i>S. viride</i>	Male	ID#142	25	220	10	4.6%	1	/
<i>S. viride</i>	Male	ID#144	20.5	150	5	2.3%	1	/
<i>S. viride</i>	Male	ID#150	19	120	22	10.2%	4	/
<i>S. viride</i>	Male	ID#158	17.5	100	92	18.4%	2	/
<i>S. viride</i>	Female	ID#180	21	160	5	2.3%	2	/

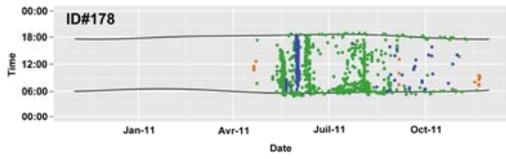
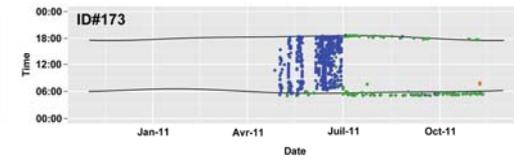
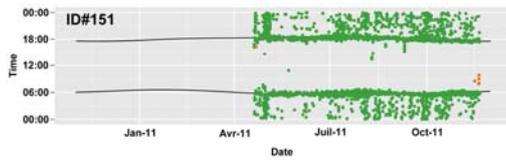
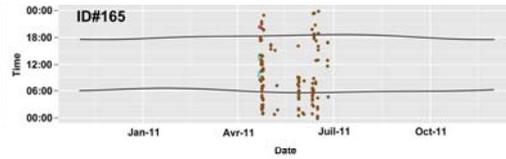
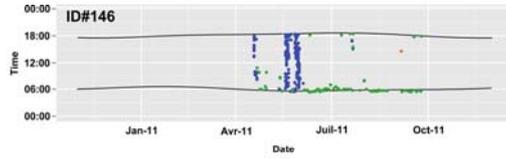
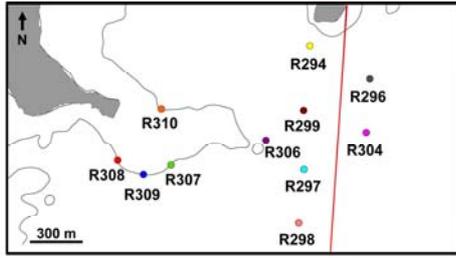
Table 2 : GLMM analyses model comparison results

<i>Lutjanus apodus</i>	Model covariates	df	logLik	AICc	Δ AICc	Weight
	Pres ~ Hour + Month + Receiver + (1 Fish)	46	-22910.30	45912.6	0.00	1
	Pres ~ Hour + Receiver + (1 Fish)	35	-23311.83	46693.7	781.07	0
	Pres ~ Month + Receiver + (1 Fish)	23	-24195.18	48436.4	2523.76	0
	Pres ~ Receiver + (1 Fish)	12	-24591.27	49206.5	3293.94	0
	Pres ~ Hour + Month + (1 Fish)	36	-35003.72	70079.4	24166.85	0
	Pres ~ Hour + (1 Fish)	25	-35382.49	70815.0	24902.37	0
	Pres ~ Month + (1 Fish)	13	-36103.25	72232.5	26319.91	0
	Pres ~ (1 Fish)	2	-36481.94	72967.9	27055.28	0
<i>Sparisoma viride</i>		df	logLik	AICc	Δ AICc	Weight
	Pres ~ Hour + Month + Receiver + (1 Fish)	46	-10487.65	21067.3	0.00	1
	Pres ~ Hour + Receiver + (1 Fish)	35	-10802.85	21675.7	608.40	0
	Pres ~ Month + Receiver + (1 Fish)	23	-10950.27	21946.5	879.23	0
	Pres ~ Receiver + (1 Fish)	12	-11261.40	22546.8	1479.49	0
	Pres ~ Hour + Month + (1 Fish)	36	-14078.00	28228.0	7160.68	0
	Pres ~ Hour + (1 Fish)	25	-14380.69	28811.4	7744.07	0
	Pres ~ Month + (1 Fish)	13	-14380.69	29040.6	7973.27	0
	Pres ~ (1 Fish)	2	-14809.27	29622.5	8555.22	0

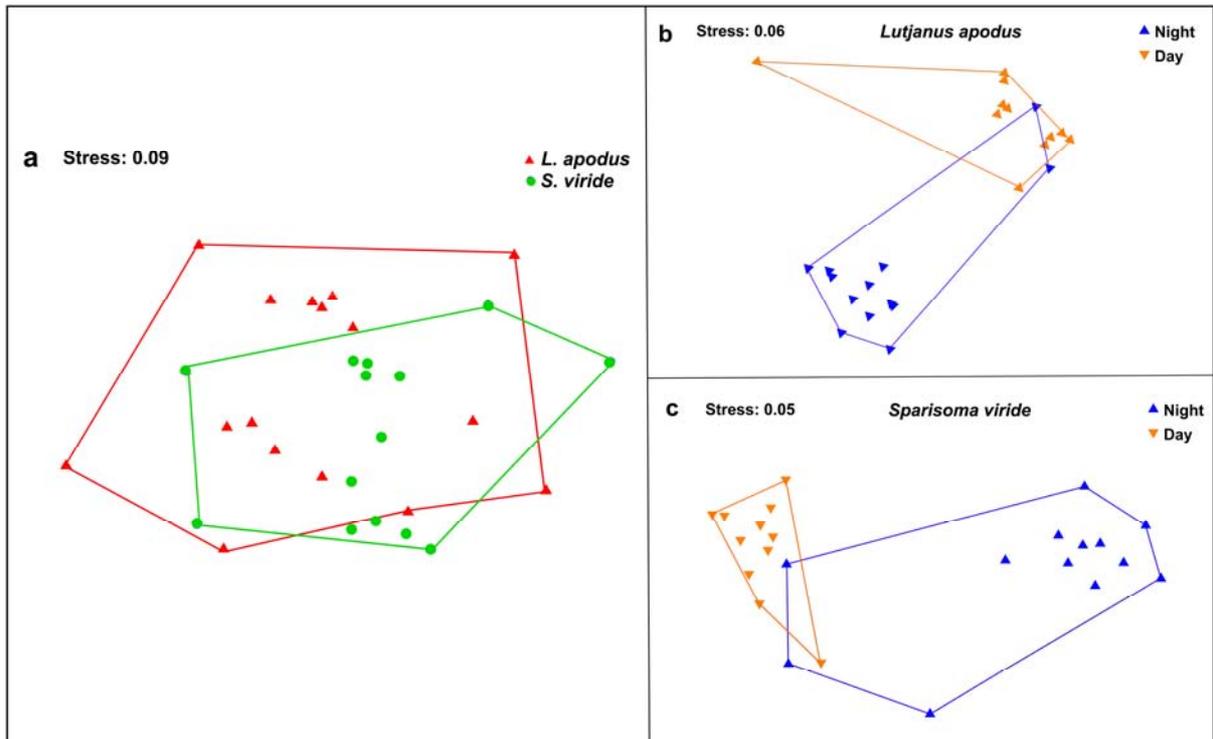


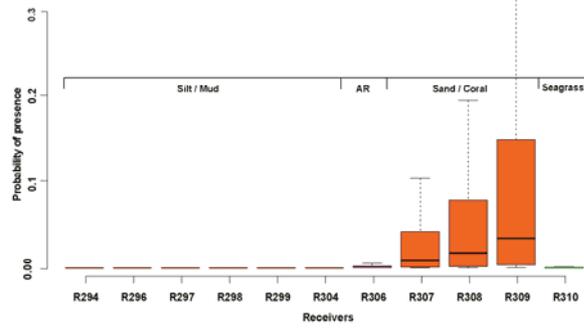
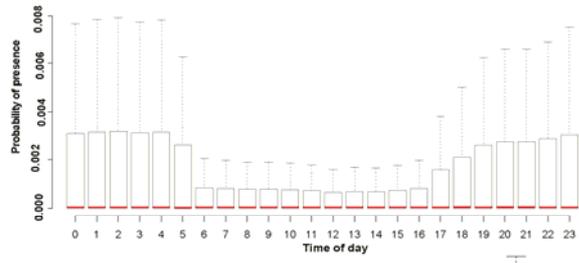
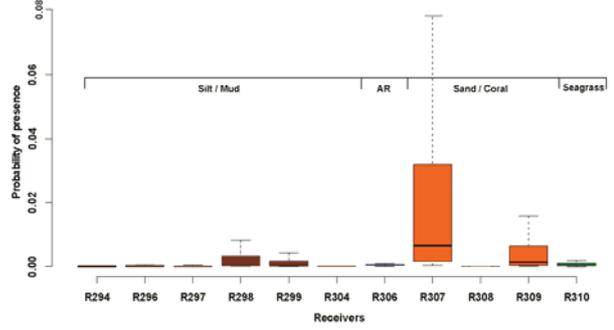
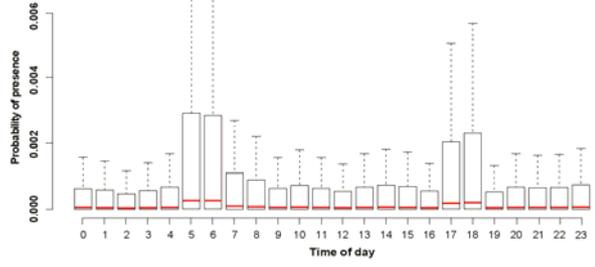


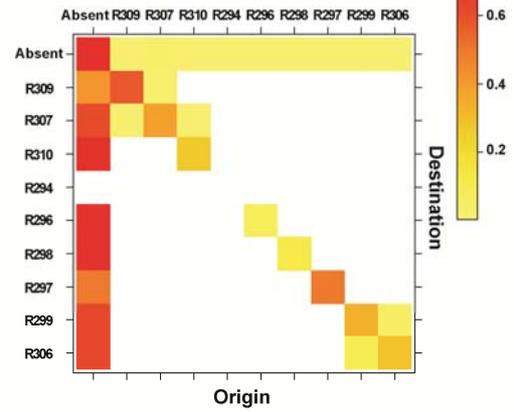
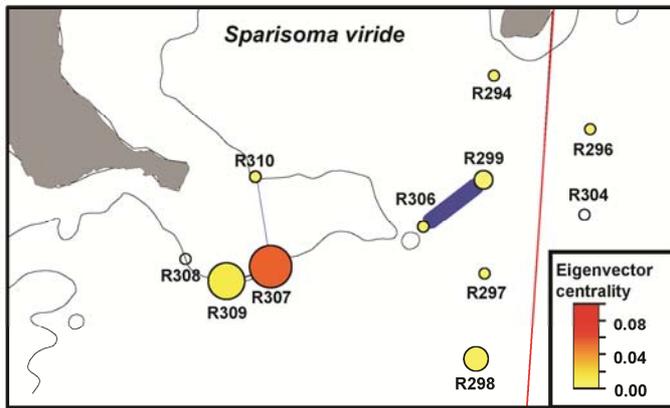
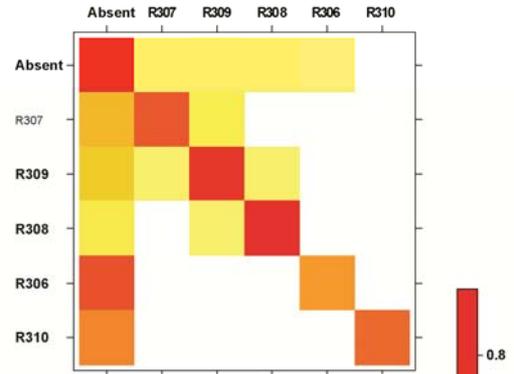
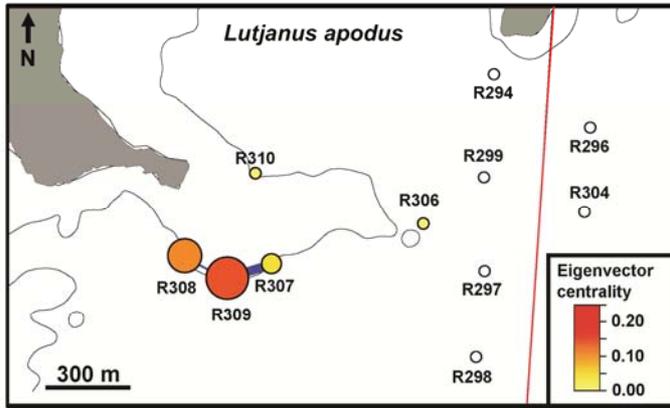
ACCEPTED MANUSCRIPT



ACCEPTED MANUSCRIPT



Lutjanus apodus*Sparisoma viride*



ACCEPTED MANUSCRIPT

Supplementary Table 1: GLMM for model with best fit based on AIC rankings

ACCEPTED MANUSCRIPT									
<i>L. apodus</i>	$\beta \pm SE$	Z	P	<i>S. viride</i>	$\beta \pm SE$	Z	P		
(Intercept)	-2.153e+01	3.499e+02	-0.062	0.950947	(Intercept)	-9.360e+00	1.178e+00	-7.943	1.97e-15
October	-2.007e+00	1.440e-01	-13.937	< 2e-16	February	1.499e-01	2.152e-01	0.697	0.485914
November	-2.438e+00	1.492e-01	-16.338	< 2e-16	March	7.518e-01	1.921e-01	3.914	9.07e-05
December	-5.025e-01	1.341e-01	-3.748	0.000178	April	-2.850e+00	3.367e-01	-8.464	< 2e-16
February	3.545e-01	1.098e-01	3.229	0.001244	May	-3.057e+00	3.326e-01	-9.191	< 2e-16
March	-3.634e-01	1.283e-01	-2.833	0.004617	June	-3.189e+00	3.330e-01	-9.577	< 2e-16
April	-2.867e+00	1.735e-01	-16.524	< 2e-16	July	-3.419e+00	3.341e-01	-10.235	< 2e-16
May	-2.497e+00	1.441e-01	-17.335	< 2e-16	August	-3.557e+00	3.345e-01	-10.635	< 2e-16
June	-2.511e+00	1.441e-01	-17.425	< 2e-16	September	-3.684e+00	3.353e-01	-10.987	< 2e-16
July	-2.446e+00	1.440e-01	-16.986	< 2e-16	October	-3.881e+00	3.363e-01	-11.541	< 2e-16
August	-2.415e+00	1.438e-01	-16.793	< 2e-16	November	-3.982e+00	3.411e-01	-11.676	< 2e-16
September	-2.229e+00	1.435e-01	-15.529	< 2e-16	December	-6.606e-01	2.663e-01	-2.480	0.013132
hour1	2.234e-02	7.078e-02	0.316	0.752277	hour1	-7.730e-02	1.733e-01	-0.446	0.655535
hour10	-1.391e+00	9.445e-02	-14.730	< 2e-16	hour2	-3.000e-01	1.831e-01	-1.639	0.101195
hour11	-1.430e+00	9.552e-02	-14.976	< 2e-16	hour3	-1.088e-01	1.746e-01	-0.623	0.532983
hour12	-1.548e+00	9.893e-02	-15.644	< 2e-16	hour4	6.799e-02	1.677e-01	0.405	0.685224
hour13	-1.484e+00	9.705e-02	-15.295	< 2e-16	hour5	1.536e+00	1.367e-01	11.234	< 2e-16
hour14	-1.505e+00	9.766e-02	-15.410	< 2e-16	hour6	1.511e+00	1.370e-01	11.030	< 2e-16
hour15	-1.437e+00	9.570e-02	-15.019	< 2e-16	hour7	5.501e-01	1.532e-01	3.590	0.000331
hour16	-1.329e+00	9.280e-02	-14.321	< 2e-16	hour8	3.448e-01	1.587e-01	2.172	0.029871
hour17	-6.634e-01	7.914e-02	-8.382	< 2e-16	hour9	-2.330e-03	1.703e-01	-0.014	0.989088
hour18	-3.846e-01	7.519e-02	-5.116	3.12e-07	hour10	1.341e-01	1.654e-01	0.811	0.417453
hour19	-1.688e-01	7.268e-02	-2.322	0.020215	hour11	-2.314e-03	1.703e-01	-0.014	0.989163
hour2	3.235e-02	7.072e-02	0.457	0.647359	hour12	-1.413e-01	1.759e-01	-0.803	0.421869
hour20	-1.144e-01	7.211e-02	-1.587	0.112591	hour13	6.799e-02	1.677e-01	0.405	0.685227
hour21	-1.134e-01	7.208e-02	-1.573	0.115785	hour14	1.469e-01	1.650e-01	0.891	0.373095
hour22	-6.817e-02	7.167e-02	-0.951	0.341502	hour15	9.491e-02	1.668e-01	0.569	0.569292
hour23	-1.736e-02	7.118e-02	-0.244	0.807273	hour16	-1.249e-01	1.752e-01	-0.713	0.476035
hour3	8.624e-03	7.092e-02	0.122	0.903213	hour17	1.172e+00	1.412e-01	8.301	< 2e-16
hour4	2.122e-02	7.084e-02	0.299	0.764559	hour18	1.292e+00	1.396e-01	9.255	< 2e-16
hour5	-1.648e-01	7.265e-02	-2.268	0.023326	hour19	-1.745e-01	1.773e-01	-0.984	0.325090
hour6	-1.293e+00	9.188e-02	-14.076	< 2e-16	hour20	6.796e-02	1.677e-01	0.405	0.685325
hour7	-1.329e+00	9.280e-02	-14.321	< 2e-16	hour21	4.036e-02	1.687e-01	0.239	0.810968
hour8	-1.366e+00	9.377e-02	-14.570	< 2e-16	hour22	5.429e-02	1.682e-01	0.323	0.746914
hour9	-1.366e+00	9.377e-02	-14.567	< 2e-16	hour23	1.581e-01	1.645e-01	0.961	0.336764
R296	-4.191e+00	2.866e+03	-0.001	0.998833	R296	2.486e+00	1.041e+00	2.388	0.016935
R297	1.241e+01	3.499e+02	0.035	0.971711	R297	1.387e+00	1.118e+00	1.240	0.214987
R298	-4.481e+00	3.306e+03	-0.001	0.998919	R298	5.378e+00	1.003e+00	5.364	8.13e-08
R299	-4.359e+00	3.114e+03	-0.001	0.998883	R299	4.721e+00	1.005e+00	4.699	2.62e-06
R304	1.172e+01	3.499e+02	0.033	0.973291	R304	-1.438e+01	1.324e+03	-0.011	0.991338
R306	1.612e+01	3.499e+02	0.046	0.963262	R306	3.047e+00	1.024e+00	2.976	0.002921
R307	1.913e+01	3.499e+02	0.055	0.956404	R307	7.633e+00	1.000e+00	7.630	2.35e-14
R308	1.978e+01	3.499e+02	0.057	0.954919	R308	-1.337e+01	8.014e+02	-0.017	0.986686
R309	2.048e+01	3.499e+02	0.059	0.953316	R309	6.015e+00	1.001e+00	6.007	1.89e-09
R310	1.466e+01	3.499e+02	0.042	0.966578	R310	3.917e+00	1.010e+00	3.878	0.000105
Random effects					Random effects				
Acoustic Tag ID estimated variance \pm SE=6.172 \pm 2.484					Acoustic Tag ID estimated variance \pm SE=3.05 \pm 1.747				