Determining conservation potential of an opportunistically defined MPA boundary using fish telemetry

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ABSTRACT

Marine protected areas (MPA) that are created opportunistically must be evaluated in an ecological context to ensure that conservation goals and societal expectations are achievable. This study used acoustic telemetry to investigate movements of reef fish relative to the boundary of the Virgin Islands Coral Reef National Monument (VICRNM) in Coral Bay, U.S. Virgin Islands. Although created to enhance ecosystem protection, VICRNM boundaries were established purely on the basis of adjacency to public versus privately owned lands. Transmitters were implanted into a diversity of reef fish species representative of the local community whose movements were logged for one year on an array of acoustic-receivers that were positioned within, outside, and along the MPA boundary. Results indicate that the boundary has coincidentally aligned with a deep sandy area that does not cross through continuous reef or mangrove habitat. This acted as a natural barrier to movements of species such as *Lutjanus griseus*, *Epinephelus guttatus*, *Cephalopholis cruentatus*, *Holocentrus rufus*, and *Sparisoma aurofrenatum*. Other species were more mobile and were routinely detected outside VICRNM, especially at night, such as *L. synagris*, *Haemulon plumierii*, and *H. sciurus*. In addition to fish movements in relation to the VICRNM boundary, network analysis revealed several hotspots of concentrated fish activity including a reef promontory and bay mouths. Investment in enforcement of existing regulations to protect fish is warranted to realize the full potential of this MPA. Using these types of data, management actions in this and other MPAs can be focused on those species and locations that would experience the greatest benefit.

1. Introduction

Despite the multitude of analytical tools and theoretical recommendations now available to guide the design of marine protected areas (MPA), many are still created opportunistically where ease of designation plays the lead role in their inception (Agardy et al., 2011; Devillers et al., 2015). Such MPAs can perform as intended, but must be carefully evaluated to ensure that conservation goals and societal expectations are achievable (Knight and Cowling, 2007; Monaco et al., 2007; Day, 2008).

The Virgin Islands Coral Reef National Monument is one such area (hereafter VICRNM, or the Monument). Located in the northern Caribbean Sea in the US Virgin Islands, it was created in 2001 by Presidential Proclamation 7399 (2001) to expand the protected area of marine ecosystems around the island of St. John under the management of the National Park Service (NPS). The Proclamation defines ecosystem broadly and includes all of the interdependent organisms as well as the interconnected habitats necessary to sustain them. The boundary of the Monument however, is based entirely on land ownership records and the political opportunity offered by the Territorial Submerged Lands Act (1974). The Act transferred submerged areas within 3 n mi of shore from federal to territorial control, excluding "all submerged lands adjacent to property owned by the United States". This federal ownership of land and the adjacent submerged parts of Coral Bay area of St. John made it possible to convert them to National Monument status. Public and private land ownership records around Turner Point placed the boundary separating federal versus territorial control along the midlines of two smaller bays within Coral Bay, Hurricane Hole and Round Bay (Johnson and Thormahlen, 2002) (Fig. 1). The boundary ranges from ~0.25 to 1.25 km from shore. Therefore, although created to protect a marine ecosystem, ecology was never actually considered when the geographic boundaries of the Monument were established (Monaco et al., 2007). The Presidential Proclamation 7399 (2001) further states that the boundaries are "the smallest area compatible with the proper care and management of the objects to be protected", including the reef fish that reside within it. This study investigates the
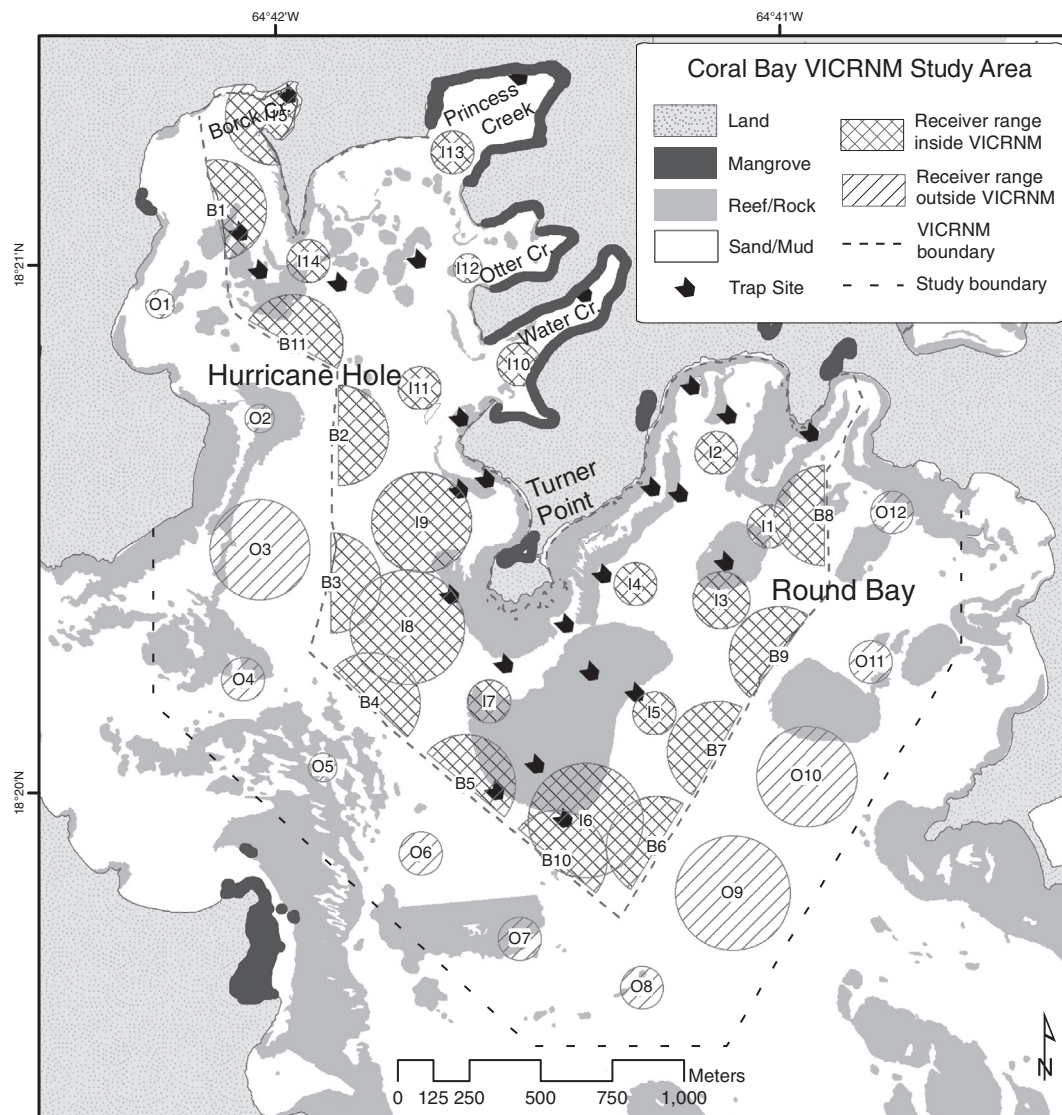
Fig. 1. Coral Bay portion of the VICRNM. Caribbean Sea, St. John US Virgin Islands.

movements of reef fish relative to the boundary of the Coral Bay portion of the Monument and evaluates its potential for reef fish protection.

The study area consists of mangrove-lined bays with scattered seagrass, sand and mud bottoms, fringing and patch reefs, rocky promontories, pavements, and spur and groove reefs (Costa et al., 2013) (Fig. 1). Biodiversity in this area has among the highest values throughout St. John and especially large numbers of several snapper (Lutjanidae) and grunt (Haemulidae) species reside there (Boulon, 1992; Friedlander et al., 2013b). Apart from permitted gathering of bait fish, all forms of extractive use as well as anchoring and tying to mangroves are prohibited (Presidential Proclamation 7399, 2001). Despite added protections, reef fish populations in the Virgin Islands have continued an overall decline (Rogers and Beets, 2001; Pittman et al., 2014b).

Many species of reef fish present in Coral Bay move among habitats during various phases of their life history. Many snappers and other species are known to utilize seagrass and mangroves as juveniles but then shift to coral reefs once they grow larger (Gratwicke et al., 2006; Huijbers et al., 2015). Several snapper and grunt species are known to undergo nightly migrations of several hundred meters from reefs to forage in adjacent sand habitats (Beets et al., 2003; Kendall et al., 2003; Luo et al., 2009; Hitt et al., 2011). Reef residents have diverse home range sizes that may take them across 10–100's of m of continuous reef

(Kramer and Chapman, 1999; Pittman et al., 2014a). Transient species including many jacks and sharks range even more widely among habitats on a daily basis (Wetherbee et al., 2004; Brown et al., 2010; Friedlander et al., 2013a). Less frequently, lunar- or seasonal-migrations take place for reproduction or foraging (Nemeth et al., 2007; Afonso et al., 2009; Luo et al., 2009; Pittman et al., 2014a). Each of these movement behaviors has the potential to temporarily or permanently relocate fish outside of the protected confines of the VICRNM boundaries. The timing and frequency of these movement behaviors relative to the local landscape, dimensions, and configuration of the VICRNM boundary in Coral Bay are unknown.

Acoustic telemetry is an effective tool for quantifying habitat utilization patterns, home range size, site fidelity, migration pathways, MPA boundary crossing, and the timing of such movements for marine fish (e.g., Wetherbee et al., 2004; Heupel et al., 2006; Garcia et al., 2014; Pittman et al., 2014a). In this approach, an acoustic transmitter that emits a unique identification code is implanted into a fish of interest. The fish's movements are logged on an array of acoustic receivers that are strategically positioned throughout the fish's ecosystem to track the location and timing of the fish's activity.

The objective of this study was to monitor movements of reef fish relative to the opportunistically drawn boundary of the Monument. Specifically, we sought to quantify residence patterns of reef fish

communities within the Monument, frequency of fish movements across its boundary, locations of concentrated fish activity, and differences in day/night activity space. This will provide managers with an ecological perspective on the relevance of the boundary in Coral Bay and demonstrate a general approach that can be used to quantify MPA efficacy in other locations.

2. Methods

2.1. Acoustic monitoring array

Acoustic receivers were placed strategically throughout the study area to monitor fish movements inside VICRNM (receiver numbers I1-15), along the VICRNM border (B1-11), and in adjacent areas outside the VICRNM border (O1-12) (Fig. 1). Positions and spacing were based on prior studies in the area (Friedlander et al., 2013a; Pittman et al., 2014a; Legare et al., 2015) and the theoretical detection range of the telemetry equipment (VEMCO model VR2W receivers and V7-4L transmitters). Receivers along the boundary were installed with a hemi-directional acoustic baffle and only able to detect fish presence within VICRNM (Kendall et al., 2016a). All receivers were anchored using sand screws and held vertical ~2 m off the bottom using cables and floats. Receivers were deployed in August and September 2013.

2.2. Fish capture and tagging

The entire reef-fish community within Monument boundaries is under NPS jurisdiction. Therefore, a broad approach encompassing a representative spectrum of fish species was taken. Fish traps were set in representative habitats and depths throughout the study area with approximately equal effort in Hurricane Hole and Round Bay. Catch composition was similar to other studies using fish traps in the area (Beets et al., 2003; Friedlander et al., 2013a) and was dominated by snappers and grunts but included a diversity of other reef fishes including groupers (Serranidae), parrotfish (Scaridae), squirrelfish (Holocentridae), porgies (Sparidae), jacks (Carangidae), and several other taxa that were too small to accommodate transmitters. Minimum fish size was 19 cm for tagging.

Uniquely coded transmitters (VEMCO model V7-4L, 7 by 18 mm, ~376 day battery life) were implanted into the body cavity of fish using best-practices for surgical procedures (Friedlander et al., 2013a; Reese Robillard et al., 2015). After surgery, fish were held over-night for recovery at a wet lab, and then released at their capture locations. Sixty-eight transmitters were deployed in August and September of 2013 and seven were deployed in December.

2.3. Detection range and area

Effective range for detecting transmitter signals was determined by deploying range-test transmitters at a variety of distances around the receivers (Kendall et al., 2016a, 2016b). Detection range for each receiver was defined as the distance where detection rate fell below ~50% in a plot of the decline in detection rate with increasing distance from the transmitter (Hobday and Pincock, 2012; How and de Lestang, 2012; Selby et al., 2016). Based on the observed detection patterns, if tagged fish were detected on an I or B receiver, they were assumed to be inside the Monument boundary. If they were on an O receiver, they were assumed to be outside the Monument boundary (Fig. 1).

A map of VICRNM's boundary overlaid with estimated ranges for each receiver was used to calculate the proportion of the study area monitored by receivers. This is needed to correct for bias in detection area during data interpretation and statistical tests. The offshore edge of the study area was defined using a line drawn beyond the detection range of outside receivers (O) such that receivers were equidistant from the drawn line and the VICRNM boundary (Fig. 1). Total area inside (308 ha) and outside (293 ha) of the Monument was subdivided into areas within detection range of inside (102 ha or 33%) and outside receivers (45 ha or 15%). If fish movements (i.e. detection locations) are random, the proportion of fish detections inside versus outside VICRNM should be similar to the proportion of area monitored inside versus outside of VICRNM. The ratio of these two values was used as a null hypothesis wherein, if fish were randomly distributed in the study area, 69% of detections should occur inside VICRNM and 31% should occur outside.

2.4. Analysis

All receivers were recovered and downloaded 18 months after initial deployment to ensure that all transmitter batteries had expired and no additional movement data could be obtained. The acoustic data for each fish that was detected on a minimum of 3 different days was subjected to several analyses. This 3-day cut-off prevented analyses from being influenced by those fish that may have quickly died due to capture and handling or emigrated from the study area. Data were processed into individual detection profiles that conveyed basic information about their movements including: the time-span of detections, number of detections, percent of days detected, number of receivers visited, number and frequency of VICRNM boundary crossing events, proportion of detections inside versus outside VICRNM, and location of day versus night activities (Table 1). Rather than using the raw number of detections, which can be biased by the unequal acoustic-dampening properties of various fish habitats (e.g. mangrove, bare sand, coral reef), an index of detections was employed to more simply indicate fish presence on an hourly interval. The index is a simple tally of the number of hours a fish was detected on a receiver (e.g. a value of 1 is tallied whether a fish is detected on a receiver 1 or 100 times between 8 and 9 AM). This index value is referred to as 'detection-hours'. The crepuscular period around sunrise and sunset was excluded (5 to 7 AM and PM) to better represent the core times in day vs. night comparisons.

Table 1
Description of variables used to summarize detection data for each fish.

Variable	Description
Detection timespan	Number of days between fish release and last detection
No. detections	Total number of detections across all receivers
% of days detected	(No. days with ≥ 1 detection)/(Detection timespan)
No. of receivers	Number of receivers at which a fish was detected
No. boundary crossings	Number of times a fish crossed the VICRNM boundary (in or out)
Boundary crossings per week	(No. boundary crossings)/(No. detection days/7)
% of detection hours inside vs. outside VICRNM	Percentage of all detection-hours inside (B or I receivers) versus outside (O receivers) of VICRNM boundary. A detection-hour is defined as any 1 h interval (e.g. 1 AM to 2 AM) in the detection timespan with ≥ 1 detection.
% of inside detection hours during day vs. night	Percentage of all detection-hours inside VICRNM that occurred during day vs. night (excluding crepuscular periods).
% of outside detection hours during day vs. night	Percentage of all detection-hours outside VICRNM that occurred during day vs. night (excluding crepuscular periods).

Values for individual fish were then summarized for those species with ≥ 5 fish included in the analysis (i.e., *H. plumierii, H. sciurus, L. griseus, L. synagris,* and *O. chrysurus*). ANOVA (parametric) or Wilcoxon tests (non-parametric) were used to detect species effects. When significant effects were found, post-hoc tests were used to examine differences among species. A Tukey type multiple-means comparison test was used when parametric assumptions of normality and homogeneity of variance were met. Dunn's test for multiple group comparisons based on ranked values was used when parametric assumptions could not be met through transformation.

Individual detections for each fish cannot be considered independent observations for statistical analysis. It is reasonable to assume, however, that summary values for each fish are independent given the diversity of fish and widespread locations from which they were sampled. Consequently, most statistical tests are based on summary values for each fish as replicates. This meets the statistical assumption of independent observations and has the added benefit of weighting each fish equally in identifying movement patterns rather than having those fish with many detections dominate the results.

Detections inside versus outside of VICRNM for each fish were evaluated against the null hypothesis that fish are randomly moving throughout the study area. If each fish is randomly using the area, their observed proportion of detection-hours inside versus outside VICRNM should be approximately the same as the proportion of the study area within detection range of receivers that is inside (69% of the detection area) versus outside of VICRNM (31%). Although ~69% of observed detection-hours should be inside VICRNM, ~50% of the fish should have observed values above and below this value due to random variability. This was evaluated by scoring each fish as having greater than, or less than, the expected proportion of detection-hours. A G-test with Williams' correction for low sample size (Sokal and Rohlf, 1981) was then used to determine if the observed results differed from the expected 50:50 ratio.

A similar approach was used to test if the observed detections during the day versus night were different than expected at random. This was done to determine if fish were more likely to be detected inside VICRNM during the day and outside VICRNM at night, as may be expected for fish that undergo nocturnal foraging migrations. In these G-tests, random movements and therefore number of detection-hours, could be expected to split roughly evenly between day and night since the length of day and night are approximately equal at this latitude. In this case, each fish was scored as having greater than, or less than, the expected proportion of detection-hours inside the Monument during the day. A separate test scored each fish as having greater than or less than the expected proportion of detection-hours outside VICRNM at night.

Network analyses including node (receiver) statistics, bipartite analyses, and unipartite plots were used to analyze and depict spatial aspects of fish activity (Finn et al., 2014). First, data from all species were combined into plots depicting the total number of fish, as well as total detections recorded at each receiver. Because receivers with larger detection range will be more likely to record greater numbers of fish and detections, these values were standardized by dividing them by the detection area (m²) of each receiver. Last, to investigate whether the spatial patterns of fish movement varied by time of day, detections were divided into diurnal (sunrise to sunset) and nocturnal (sunset to sunrise) time periods. The number of detections per hectare within each of these time categories was depicted at each receiver in bar graph format.

Bipartite graphs were used to identify patterns of association between receivers (first node set) and fish (second node set) where the detection of an individual fish at an individual receiver represented a connecting edge. Unweighted and weighted bipartite graphs were considered wherein presence/absence of an edge was the data input for the unweighted analysis and number of detections of each fish at each receiver was used for the weighted analysis. Eight different clustering algorithms were applied to the bipartite graphs to identify communities

of associated receivers and fish detected on them. The algorithms were 'edge betweenness', 'fast greedy', 'infomap', 'Louvain', 'leading eigenvector', 'label propagation', 'spin-glass', and 'Walktrap'. Modularity was calculated for each scenario, and the significance of communities was determined using a Wilcoxon rank sum test (Finn et al., 2014). These analyses were implemented using the 'igraph' package (Csardi and Nepusz, 2006) for R (R Core Team, 2015). Membership of significant clusters was compared across the various weighting and algorithm scenarios and general patterns consistent among the results were identified.

Unipartite graphs were used to visualize differences in day versus night movement pathways for those species that showed strong diel patterns in preliminary analyses. This focused on *Lutjanus synagris* and Haemulids with similar life history (*Haemulon plumierii* plus *H. sciurus*) due to their nocturnal foraging habits. These analyses were further limited to those fish with detection timespans > 100 days and detected on > 10% of days between release and last detection to ensure sufficient sample size. Input data for the analysis consisted of successive detections that were < 2 h apart for each fish. Successive detections were scored as either occurring during the day (sunrise to sunset) or the night (sunset to sunrise). Successive detections were also scored as those suggesting little or no fish movement (occurring on the same receiver) or those suggesting larger movements (on different receivers). The percentage of successive detections indicating larger movement was calculated for both daytime and nighttime for each fish, and day versus night differences were tested for significance using a Paired Wilcoxon Signed Rank Test.

3. Results

3.1. Species composition

The 75 fish tagged in this study included 7 families and 17 species (Table S1). Comparison of the relative abundance of fish tagged in this study to those seen on visual surveys in the same area (Friedlander et al., 2013b) was broadly similar (Kendall et al., 2016b). Fish from the snapper (n = 38 fish) and grunt (n = 24) families were the most common. Lane snapper (*Lutjanus synagris*, n = 16) and bluestriped grunt (*Haemulon sciurus*, n = 11) were the most commonly tagged species. Roughly equal numbers of fish were tagged from the Hurricane Hole (n = 38) and Round Bay (n = 37) sides of the Monument.

3.2. Detection patterns

Of the 75 fish tagged, 18 were detected on < 3 distinct days after release or never detected at all, and were excluded from further analysis. These were assumed to have either quickly emigrated undetected from the study area or possibly died in an undetectable location in the array. Detection results for each remaining fish show large differences among and within species (Supplementary Fig. S1a–i). For example, some fish had only a few dozen detections spanning just a few days, others were consistently detected for over a year and had > 15,000 detections.

Over half of the fish were detected on just four or fewer of the 38 receivers in the study area. Those detected on only 1 receiver were assumed to be alive due to variable detection patterns through time. One fish, a *L. synagris*, was detected on 14 different receivers. A majority of the fish (34 or 60%) were never detected outside of the VICRNM boundary, and only one, a *L. synagris*, was detected crossing the VICRNM boundary on a regular basis over consecutive days.

Of the 57 fish with sufficient data, 54 (96%) had a greater proportion of their detection-hours inside VICRNM than expected if they were moving randomly. Only three fish, an *H. plumierii* and two *L. synagris*, had more detection-hours outside VICRNM than expected. This was a significant departure from the expected ratio if fish were utilizing the study area at random [null hypothesis of 50:50,

$G_{adj} = 55.03 > \chi^2_{(0.001, \, 1)}$]. Also of note, the detection-hours index showed the same statistical outcome compared to preliminary analysis using raw number of detections but is less influenced by potential bias in unequal detectability among habitats.

Of the 57 fish with sufficient data that were detected inside VICRNM, 30 had a majority of detection-hours during the night, whereas 27 had more detection-hours during the day. This was not significantly different from the expected ratio based on random fish activity and the length of day at this latitude [null hypothesis 50:50, $G_{adj} = 0.16$, NS]. Outside VICRNM, only 21 fish were detected. Of those, twice as many (14) had more nighttime detections than daytime detections (7). However, this was not significantly different from the expected ratio based on random fish activity [null hypothesis 50:50, $G_{adj} = 2.3$, NS]. Similar to the previous analysis using detection-hours, the index showed the same statistical outcome compared to preliminary analysis using raw number of detections.

3.3. Species differences

The five species with sufficient sample size (n ≥ 5 fish) showed relatively consistent values for % of days detected and % of detections inside VICRNM. Significant differences were found between *L. synagris* and *L. griseus* wherein *L. synagris* were detected crossing the VICRNM boundary more often and regularly than *L. griseus* (Fig. 2a–i). In the case of *L. griseus*, tagged fish were never detected outside VICRNM. Both species of Haemulidae showed similar patterns for these variables. All other species and variables showed no significant differences in statistical tests, however, sample size was low which limited the statistical power. For example, average number of days detected for

O. chrysurus was less than half of the days detected for all other species but no significant differences was found at p < 0.05. Similarly, *O. chrysurus* was detected at the highest median number of receivers among all species but, due to the conservative multiple comparison test, low sample size, high variability, and rank-based test, was not significantly different than other species.

3.4. Activity hotspots

Receivers inside VICRNM typically detected more fish than those outside or on the border (Fig. 3a). Receivers detecting the most fish were at the mouths of Otter and Water Creeks, in the northern extremity of Round Bay, and off the high-relief reef area southeast of Turner Point. One location outside VICRNM along the southern edge of the study area (O7), also detected many fish despite having a relatively short detection range. A similar spatial pattern was observed based on the standardized number of detections at each receiver, only more concentrated in just three areas (Fig. 3b). These were the mouths of Otter and Water Creeks as well as the boundary receivers off the southern edge of the reef at Turner Point.

Examining the number of fish detected during the day versus night at each receiver revealed a generally even split at most locations although often slightly skewed toward more fish being detected during the night (Fig. 4a). In a few locations, nearly two-thirds or more of the fish detected occurred during the night. These included sites near the mouth of Borck Creek, receivers at the southern end of the reef off Turner Point, and the receiver in the patch reef area farther south (O7).

The number of detections at each receiver during the day versus night showed a similar pattern (Fig. 4b). Only 7 out of the 38 receivers
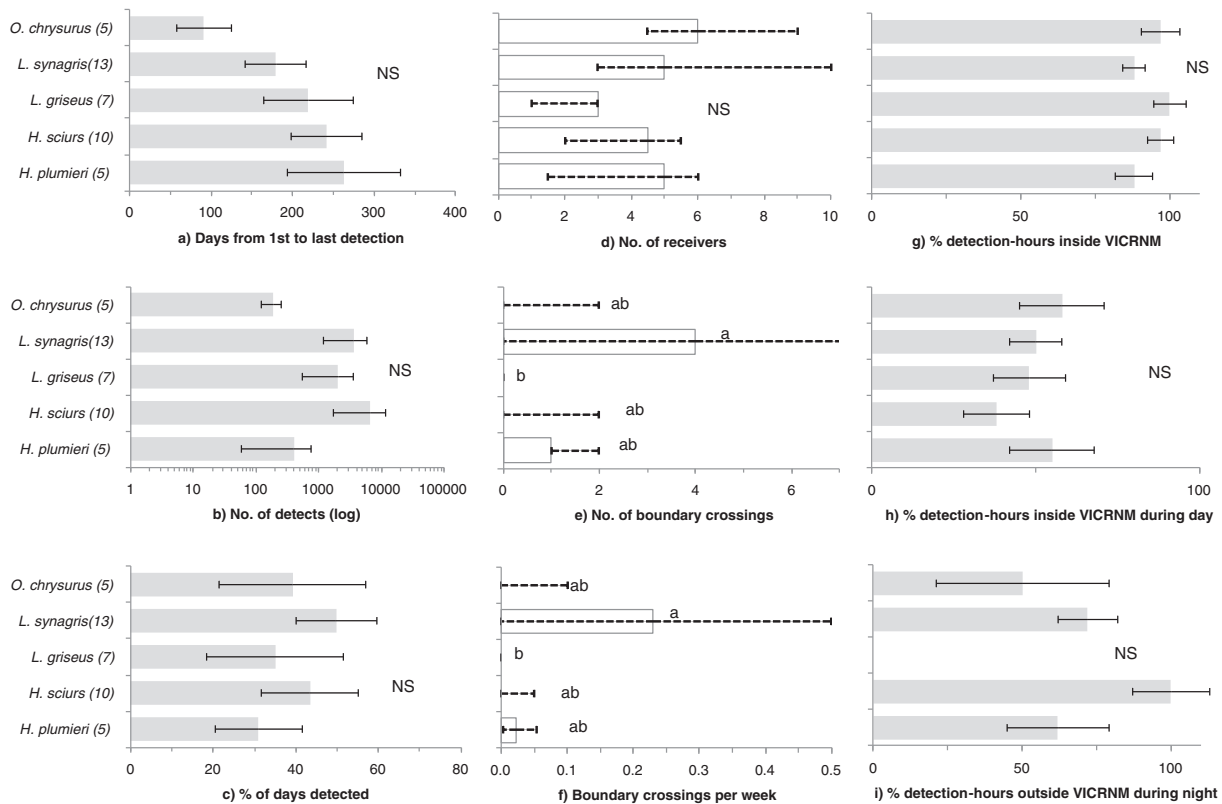

Fig. 2. a–i. Summarized detection patterns for species (n) with at least 5 individuals tracked. When parametric tests were used to evaluate differences among species, the mean (gray bars) and SE (solid lines) are shown. When non-parametric tests were used to evaluate differences among species, the median (open bars) and interquartile range (dashed lines) are shown. NS denotes a non-significant result within each variable. NA denotes too few values for any statistical comparison. Lower case letters denote significant differences in group membership at α = 0.05. Where: a) mean detection time-span expressed as the number of days from release to last detection, b) mean number of detections, c) mean percentage of days with detections during the detection timespan, d) median number of receivers visited for each fish, e) median number of times the VICRNM was crossed, f) median frequency of boundary crossings expressed as number of times per week, g) mean percentage of detection-hours inside VICRNM, h) while inside VICRNM, mean percentage of detection-hours during daytime, and i) while outside VICRNM, mean percentage of nighttime detection-hours.
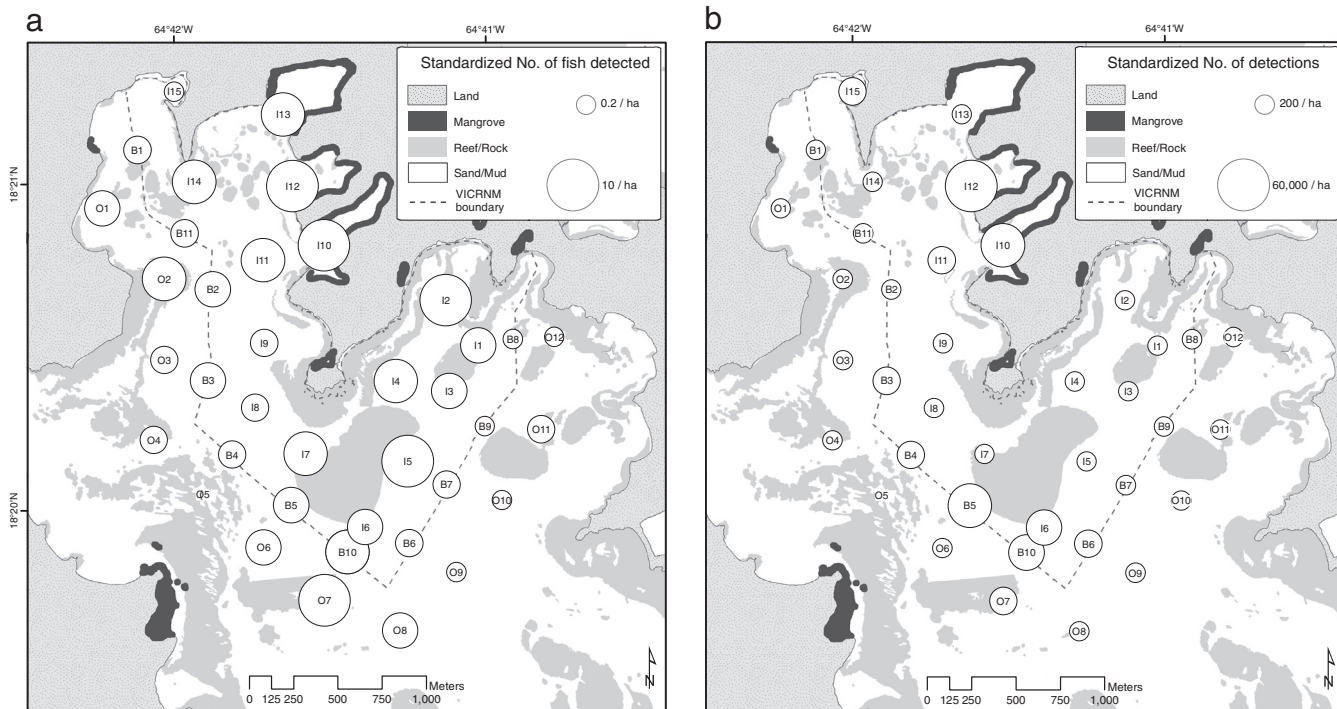
a

b

Fig. 3. a. Standardized number of fish detected at each receiver. Symbol size is scaled to the number of unique transmitters (fish) detected at each receiver divided by the detection area for each receiver in hectares. b. Standardized number of detections at each receiver. Symbol size is scaled to the number of detections at each receiver divided by the detection area for each receiver.

had a greater proportion of detection during the day. Most receivers had the bulk of their detections at night. In addition, receivers outside the Monument had a much greater proportion of their detections during the night.

Comparison of results among bipartite analyses using different weighting schemes and clustering algorithms revealed several consis-

tent patterns. In general, significant communities were composed of receivers that were near each other, included fish whose trap/release locations were nearby, and tended to show similar fish and receiver membership among algorithms. However, the specific number of communities, number of significant communities, details of community membership, and modularity varied. The results of the Louvain
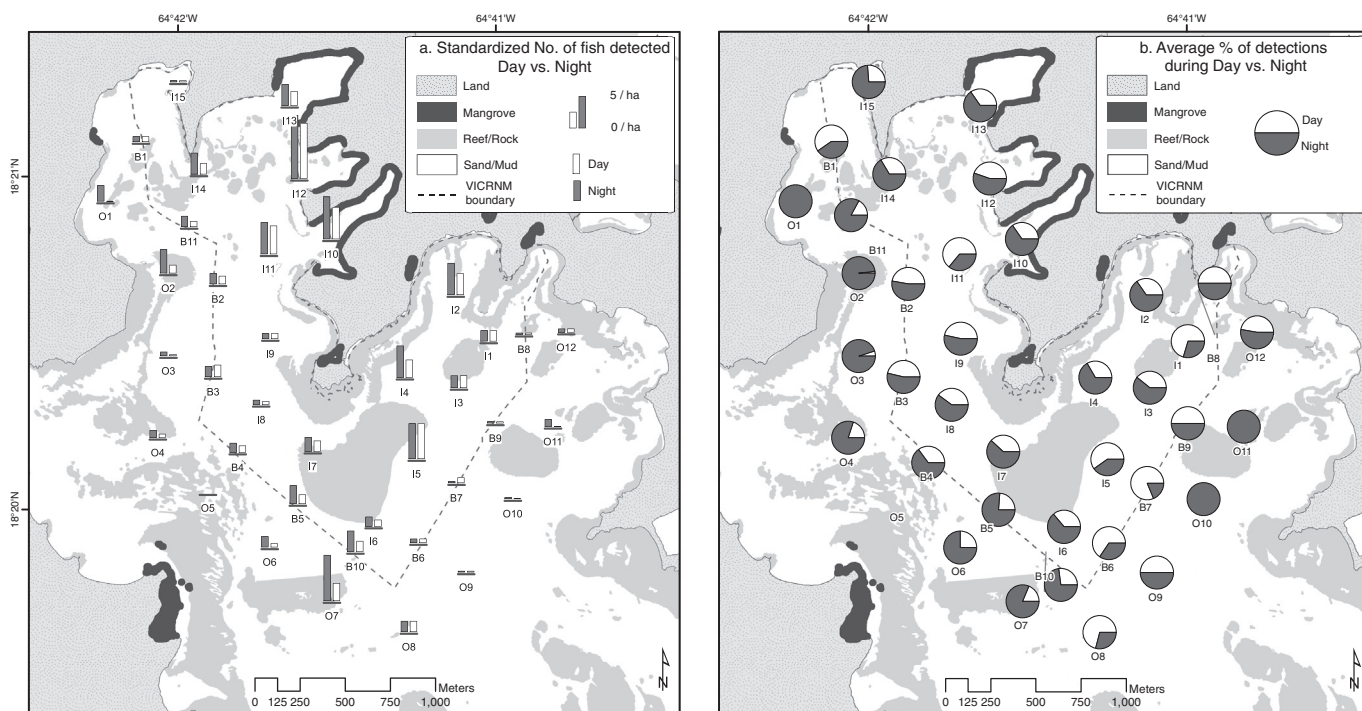

Fig. 4. a. Standardized number of transmitters (fish) detected at each receiver during the day versus night. Number of fish detected during the day versus night divided by the detection area of each receiver. b. Average proportion of detections during the day versus night for fish detected at each receiver. Detections for each fish were converted to proportions from day versus night. These values were averaged for all the fish detected at a given receiver.
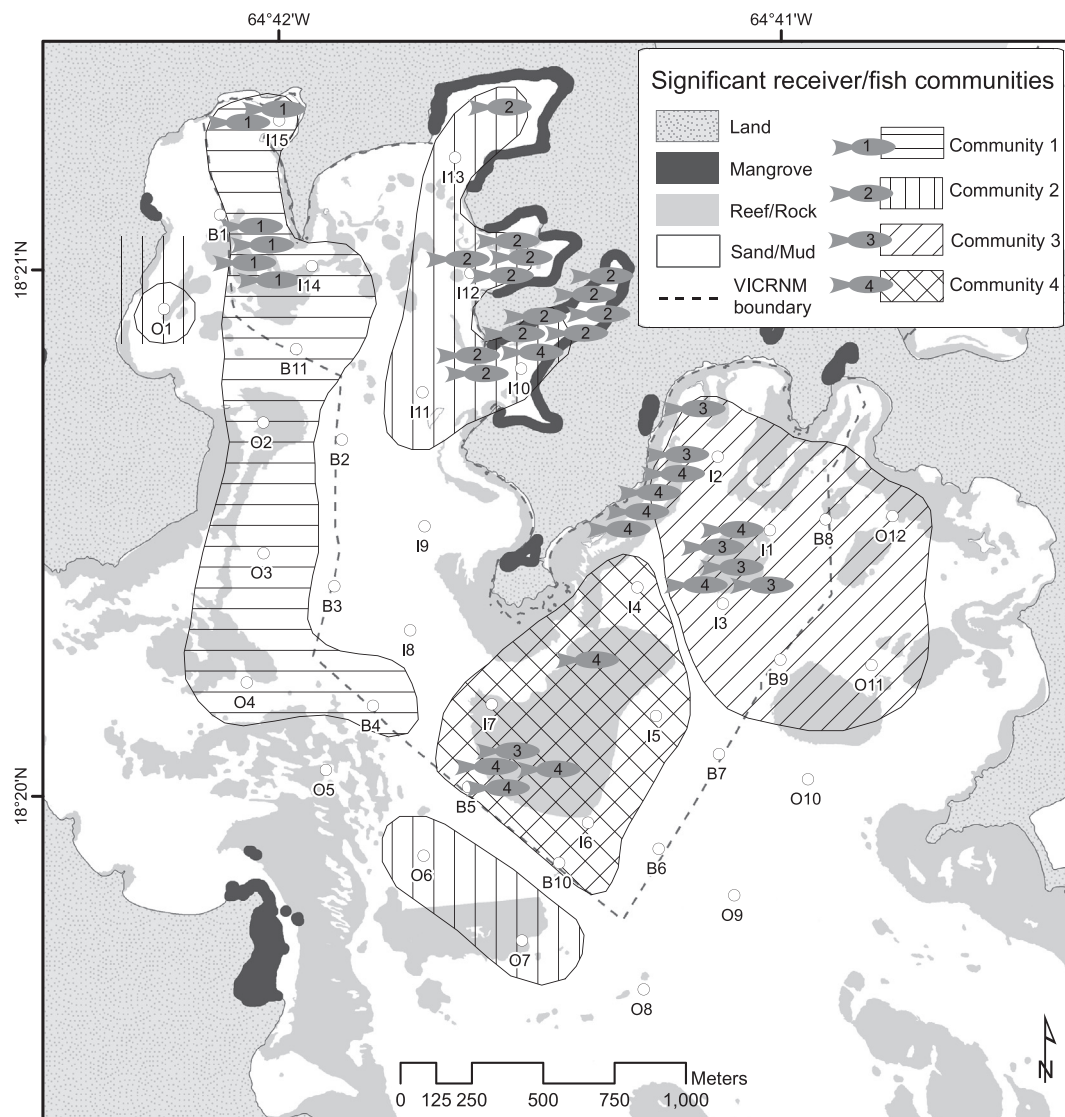
Fig. 5. Receiver/fish modules identified from the bi-partite analysis. Results are from the Louvain algorithm on un-weighted detection data (Modularity = 0.479). The four significant modules are shown (receivers and fish catch/release sites) of the six modules identified.

clustering algorithm applied to the unweighted bipartite graph provide a representative example of the overall spatial pattern in community structure shared among several scenarios (Fig. 5). Modularity was among the highest values observed at 0.479, six communities were identified, and four of those were significant ($p < 0.05$). Significant communities 1 and 3 straddled the Monument boundary in Hurricane Hole and Round Bay. Significant community 2 had a core of receivers within Princess, Otter, and Water creeks but also included some outside the Monument southwest of Turner Point. Significant community 4 was entirely within the Monument boundary off Turner Point.

Unipartite plots of the detections for *L. synagris* (n = 10) and *H. plumierii/H. sciurus* (n = 10) revealed distinct differences in their day versus night movement patterns (Fig. 6a–d). For *L. synagris*, successive detections were significantly more likely to be from movement between different receivers during the nighttime than the daytime in paired tests ($t_{0.5,9} = 2.73$, $p < 0.02$). Mean percentage of successive detections on different receivers during the day was 3% whereas nighttime was 16%. Two receivers outside VICRNM recorded detections during the day whereas seven outside receivers recorded *L. synagris* detections at night. Successive detections were also significantly more likely to be from movement between different receivers during the nighttime than the daytime for *H. plumierii/H. sciurus* in paired tests ($t_{0.5,9} = 2.57$,

$p < 0.03$). Mean percentage of successive detections on different receivers during the day was 1% whereas nighttime was 13%. One receiver outside VICRNM recorded *H. plumierii/H. sciurus* detections during the day whereas four outside receivers recorded detections at night.

4. Discussion

Founding documents that created VICRNM assert that its boundaries encompass the smallest area compatible with sustaining and protecting the marine resources within it (Presidential Proclamation 7399, 2001). This telemetry study provides evidence both for and against this claim. Overall, it appears that VICRNM offers potential protection to a majority of the small but representative fish community studied here. Receivers inside VICRNM typically detected more fish than those outside or on the border, over half of the fish were never detected outside of the VICRNM boundary, and a large majority of the fish had a significant majority of their raw detections as well as detection-hours inside the boundary.

In contrast to these apparently encouraging statistics however, are several other variables that must also be considered to get a more complete understanding of protection. First, while some fish were
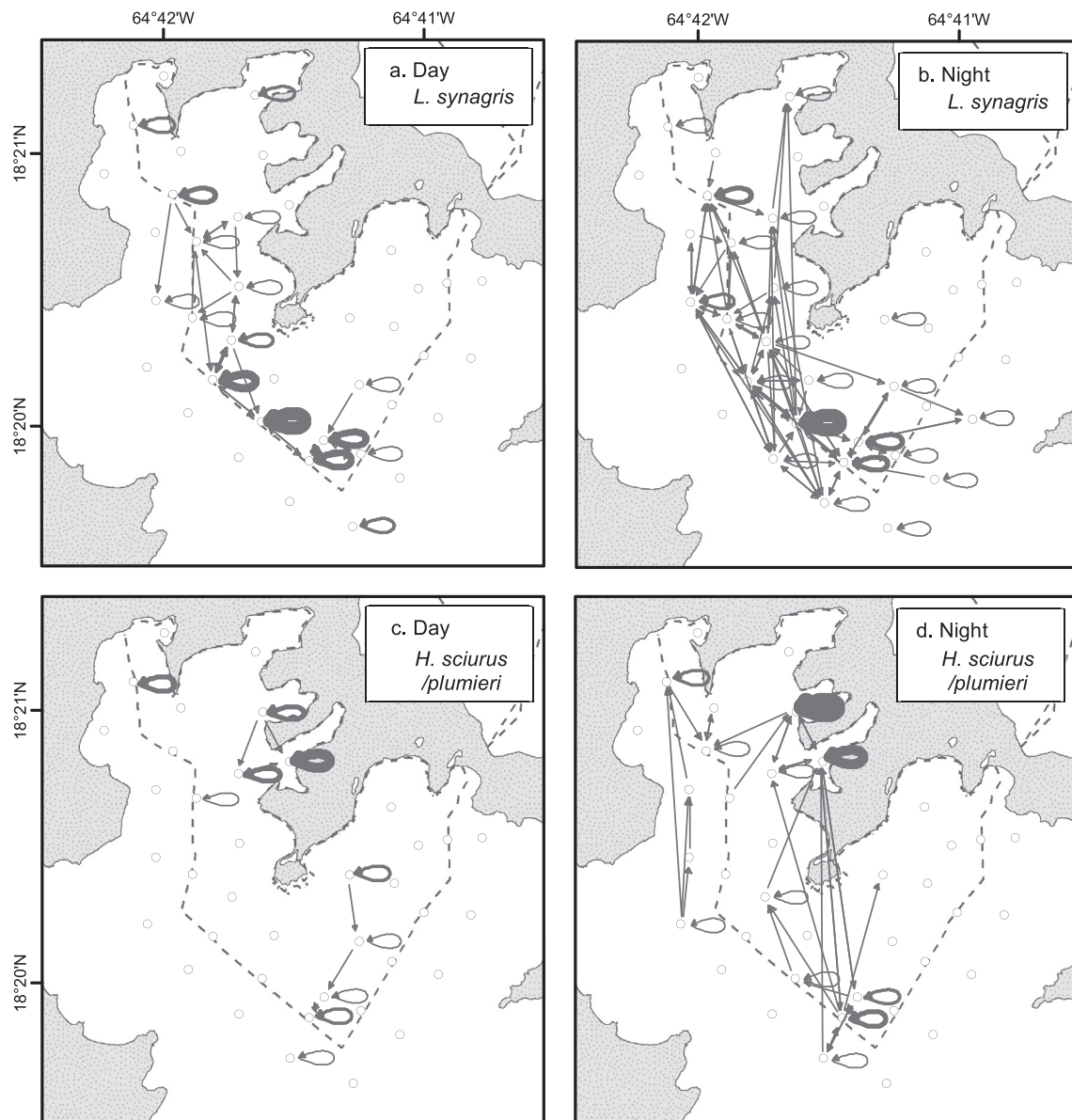
Fig. 6. a–d Day versus night detection pathways for *L. synagris* (n = 10) and *H. sciurus/H. plumieri* (n = 10). Line thickness denotes more frequent pathways. Loops represent successive detections on the same receiver (no movement). Gray polygon denotes land, dotted line is the VICRNM boundary, and receivers are marked by open circles. a. Successive detections (< 2 h.) for *L. synagris* during the day, b. successive detections (< 2 h.) for *L. synagris* during the night, c. successive detections (< 2 h.) for *H. sciurus/H. plumieri* during the day, and d. successive detections (< 2 h.) for *H. sciurus/H. plumieri* during the night.

potentially resident within the monitoring area for the whole duration of the study, most were not based on their detection timespan and presumably emigrated or were removed by poaching or natural mortality. Most of the significant communities identified using network analysis either straddled or had sites outside of VICRNMs boundary. Nighttime activity on receivers outside VICRNM is demonstrably more than that during the day. Fish that emigrated beyond the outer receivers in the study area leave no data record and therefore statistics such as "percent of detection-hours inside VICRNM" must be interpreted cautiously. The maximum duration of any inference must also be limited to ~1 year given the battery life of transmitters.

Although the VICRNM boundary in Coral Bay was not delineated using ecological criteria, it appears to have coincidentally aligned with an important ecological principle of MPA design for reef fish; the boundary does not cross through continuous reef habitat. Ownership of Federal land in Coral Bay was the sole basis for boundary delineation and resulted in the boundary being placed roughly along the centers and deepest parts of Hurricane Hole and Round Bay. This put the boundary in the sand or mud bottom that separates the reef and mangrove habitats which fringe both sides of the bays (see Costa et al., 2013). The boundary therefore rests on a physical feature that acts as a natural barrier to movements of many reef fish (Eristhee and Oxenford, 2001; Popple and Hunte, 2005; Farmer and Ault, 2011). Fishes that are generally full-time residents on those fringing habitats may be well protected by the boundary and include several species tracked in this (i.e., *L. griseus*, *E. guttatus*, *C. cruentatus*, *H. rufus*, and *S. aurofrenatum*) and other studies (Beets et al., 2003; Popple and Hunte, 2005; Luo et al., 2009; Pittman et al., 2014a). The VICRNM boundary also happens to completely encompass the spur and groove reef that extends southward from Turner Point. This reef promontory has among the highest values of diversity and abundance for reef fish around St. John (Costa et al., 2013; Friedlander et al., 2013b).

Several previous studies have used telemetry to investigate the movements of marine fish relative to MPA boundaries and revealed some similar patterns to those seen in Coral Bay. In studies spanning various species, many fish exhibited strong site fidelity (Popple and

Hunte, 2005; Marshell et al., 2011; Bond et al., 2012) and spent most of the study periods within protected areas (Holland et al., 1993; Meyer et al., 2000; Lindholm et al., 2005; Garcia et al., 2014; Pittman et al., 2014a). Others show only temporary residence of weeks to a few months and a gradual disappearance of fish from the MPA over time, likely due to seasonal or permanent emigration, tag failure, or mortality (Meyer et al., 2007; Afonso et al., 2009; Chateau and Wantiez, 2009; Knip et al., 2012). This diversity of findings based primarily on single-species studies, highlights the need to understand patterns of fish movement for a diversity of taxa when designing MPAs to protect whole ecosystems. Also of note, when the same species is studied in multiple locations, results can be specific to the local configuration of habitats and coastal morphology. General movement principles are becoming established but they can be modulated by local setting (Eristhee and Oxenford, 2001; Meyer and Holland, 2005; Garcia et al., 2014).

It is clear that some fish species have the potential to be better protected than others by VICRNM boundaries. For example, detection data suggest that *L. griseus* was among the least mobile fish in the study. They were never detected outside VICRNM, and were rarely detected beyond the confines of the mangrove-lined bays from which they were tagged. Less protected will be those species that regularly migrate out large distances into sand areas or range even more widely (Meyer et al., 2007; Afonso et al., 2009; Pittman et al., 2014a; Legare et al., 2015). For example, all five *O. chrysurus* were detected on many receivers, frequently crossed the VICRNM boundary, and were detected for less than one-third of the study duration. This short time and likely emigration is similar to the tracking period observed for this species in the Dry Tortugas (Farmer and Ault, 2011) but is in contrast with evidence suggesting higher site fidelity in the northern Florida Keys (Lindholm et al., 2005). Similarly, of the nine *L. apodus* tagged, only two were detected for more than 3 days suggesting possible emigration (Garcia et al., 2014). Detection patterns for *L. synagris* also indicate that it is among the more mobile species. They were detected at more receivers and crossing the VICRNM boundary more often and regularly than most other species. In the middle of this spectrum were fishes such as those in the family Haemulidae which were detected at an intermediate number of receivers and crossed the VICRNM boundary a moderate number of times.

In addition to spatial patterns relative to the VICRNM boundary, this study identified specific locations where fish activity was concentrated. Telemetry has effectively identified sites in other systems where multiple individuals regularly converged at shared refuges, for social schooling behavior, or along a common movement pathway (Holland et al., 1996; Eristhee and Oxenford, 2001). In VICRNM, both the number of fish and number of detections were highest at receivers at the mouths of Otter and Water Creeks and off the high-relief reef area south of Turner Point including one location outside the Monument. These patterns do not simply reflect locations where fish were tagged. In the case of Otter and Water creeks, the high values were due to a combination of the resident fish in those bays such as *L. griseus* as well as fish passing in front of those bays along the reef-lined promontories that separate them (i.e., *H. sciurus*, *H. plumierii*, *L. synagris*, and *H. flavolineatum*).

In the case of the area south of Turner Point, several factors may be contributing. This submerged promontory is the most seaward extension of reefs connected to the inshore bays within VICRNM (Costa et al., 2013). It may be a staging or spawning locale for those species known to seek such features (Sadovy de Mitcheson et al., 2008; Karnauskas et al., 2011). It also may be a migration pathway/departure point toward deeper waters farther south. Rather than more directly leaving their inshore residence areas through open bottom areas during departure, fish could be protected for as long as possible by travelling close to the structural refuge of the reef (Pittman et al., 2014a) until leaving the area via this promontory. The patch reefs farther offshore of the area also recorded many fish but few detections, potentially indicating that fish were moving relatively quickly through this area.

Tracks of several fish suggested their departure via this route (i.e., *L. synagris*, *O. chrysurus*, *L. apodus*, *H. plumierii*, and *C. penna*). Although fish tended to stay within the side of VICRNM in which they were trapped, it could also be a simple pinch-point for fish transiting between Hurricane Hole and Round Bay as in the case of an *L. apodus* tracked moving around Turner Point.

Day versus night differences lacked significance in analyses that incorporated all species. This was potentially due to differences among species in day/night detectability even though the detection-hour index reduced this bias. For example, nighttime fish behavior such as parrotfish sleeping under corals reduces detectability whereas snappers and grunts foraging over open sand are more detectable. The opposite is likely the case during the day, as parrotfish emerge to forage on the reef but snappers and grunts retire to daytime resting sites within rugose reef or mangrove habitats which restrict acoustic transmissions (Lindholm et al., 2005; Hitt et al., 2011; Selby et al., 2016). Movements of fish beyond the outer edge of the study area during the day versus night may have also biased the proportions of day/night detections. Despite these issues, some important contrasts were evident. First, a much greater proportion of detections occurred during the night on most receivers outside VICRNM indicating more fish activity. Results for particular species suggested the cause of this pattern. The significant differences in the unipartite graphs show that increased nighttime detection outside VICRNM was from fish that underwent nocturnal migrations away from reefs into adjacent habitats (Beets et al., 2003; Kendall et al., 2003; Hitt et al., 2011). This movement pattern was evident in both *H. plumierii*/*H. sciurus* and *L. synagris* which were largely stationary during the day, but at night were tracked moving hundreds of meters among receivers. Community 2 in the bipartite analyses resulted from these movements as well. These migrations will clearly limit VICRNMs ability to protect such species. It should be noted however, those species which periodically move away from the reef do so over regular routes, across predictable distances, and have high site fidelity when returning to the reef (Holland et al., 1993; Meyer et al., 2000; Hitt et al., 2011). Other MPAs could easily incorporate this knowledge in design of their boundaries.

It is crucial to note that even for fish which have a robust record of residence inside VICRNM, their actual protection generously assumes compliance with no-take regulations. Hence, it must be acknowledged that discussion of protection of fish within VICRNM really refers to potential-protection, pending adequate enforcement. Results of telemetry studies such as this can be used to justify investment in enforcement of existing rules and even prioritize species or locations within VICRNM in Coral Bay that may be more important or responsive to management actions than others.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.05.010.

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