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RESEARCH

DIEL ACTIVITY PATTERNS AND MOVEMENT OF INVASIVE LIONFISH (*PTEROIS VOLITANS/P. MILES*) IN THE FLORIDA KEYS IDENTIFIED USING ACOUSTIC TELEMETRY§

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ABSTRACT: The invasion of Indo—Pacific lionfish (*Pterois volitans/P. miles*) throughout the Caribbean and southeastern U.S. Atlantic represents a significant ecological threat, yet few studies have examined the daily activity and movement patterns of this invasive species. In this study, passive acoustic telemetry was used to track lionfish at 4 coral reef sites in the Florida Keys. Fourteen lionfish were tagged among the 4 sites, and the total number of days tagged fish were detected ranged from 5 to 141 days. Hourly detection data revealed diel activity patterns with peaks at dawn and dusk. Mixed model analysis of detection data indicated a significant effect of time of day, with lionfish activity greater at twilight than during day or night. These results support observations from previous studies that lionfish are most active at dawn and dusk when they are foraging. The 95% kernel utilization distribution home range size ranged from 360–18,812 m². Lionfish movements were generally localized, with mean daily distance moved ranging from 24–116 m, although one lionfish had a maximum daily distance moved of 427 m. Short—term activity centers revealed possible diel shifts in micro—habitat use for 2 lionfish, as well as an emigration of one lionfish to an adjacent patch reef ~200 m away. These findings increase our understanding of lionfish behavior on coral reefs and highlight the need for more detailed studies examining fine—scale habitat use and movements across more habitat types. The results from this study will further contribute to the spatial information required to improve the effectiveness of monitoring and controlling lionfish populations in the Florida Keys.

KEY WORDS: Invasive species, home range, crepuscular, tagging, coral reefs

INTRODUCTION

Invasive lionfish (*Pterois volitans/P. miles*) were first detected in Florida in 1985 (Morris and Akins 2009). This species' high potential for dispersal (Morris and Whitfield 2009) has resulted in its rapid spread throughout the Caribbean, southeastern U.S. Atlantic coast (Schofield 2010), and Gulf of Mexico (Fogg et al. 2013), resulting in the establishment of large populations in a wide variety of habitats in these regions (Kimball et al. 2004, Jud et al. 2011, Claydon et al. 2012). Since then, numerous studies have documented the ecological effects lionfish are having within their invaded range, such as reduced recruitment and population declines of native fishes (Albins and Hixon 2008, Green et al. 2012) and ecosystem phase shifts (Lesser and Slattery 2011). The lionfish invasion is now considered a global conservation issue (Sutherland et al. 2011).

Describing spatio—temporal movement patterns is a critical component to understanding and managing the spread of invasive marine species (Pittman and McAlpine 2003, Molnar et al. 2008). Yet, despite the extensive breadth of literature on lionfish ecology, only a few studies have ex-amined lionfish movements and habitat use within their invaded range. Jud and Layman (2012) showed that lionfish in a Florida estuary exhibited high levels of site fidelity, with nearly 74% of tagged lionfish re—sighted within 10 m of their initial tagging location. Lionfish tagged on patch reefs in the Bahamas showed similar levels of high site fidelity, while lionfish on continuous reefs moved between 200–1000 m (Akins et al. 2014, Tamburello and Côté 2015). These studies, however, used conventional tagging and mark—recapture techniques to track lionfish movements, which have limitations that could lead to underestimating movements. These limitations include limited temporal and spatial scale of recapture efforts (Appeldoorn 1997), failure to relocate or recapture tagged fish (Akins et al. 2014), and the inability to continuously track movements over a 24 h period. However, with more advanced tagging and tracking techniques it is possible to minimize or overcome these obstacles.

Acoustic telemetry is a widely accepted method for quantifying aspects of a species' movement behavior. It has been

widely used to study short– and long–term movement patterns in a variety of marine fish species (Topping and Szedlmeyer 2011, Heupel and Webber 2012, Huveneers et al. 2016). Data generated from telemetry studies can be used to quantify a wide range of movement behaviors, including residency and site fidelity (Abecasis and Erzini 2008), diel activity patterns (La Mesa et al. 2013), short–term centers of activity (Heupel et al. 2012), home ranges (March et al. 2010), and migration patterns (Reyier et al. 2014). Despite these advantages, only one study to date has applied the use of acoustic telemetry to describe lionfish movement and habitat use. In that study, Bacheler et al. (2015) described the site fidelity and daily movement patterns of lionfish on a temperate hard bottom reef off North Carolina during winter and found that lionfish showed strong site fidelity to areas no larger than 400 m in diameter.

Quantifying the spatial extent of lionfish movement behavior among habitats is needed as they can significantly reduce the local biomass of reef fish prey species (Green et al. 2012) and therefore likely have a greater ecological impact on native coral reef fish communities relative to similar–sized native predators (Albins 2013). In this study, passive acoustic telemetry was used to examine the movement patterns and habitat use of invasive lionfish in a subtropical coral reef ecosystem in the Florida Keys. Specifically, the objectives of this study were 1) to quantify daily activity pat-

terns of lionfish over a 24 h cycle, 2) quantify lionfish home range size, and 3) describe lionfish movement patterns. Results from this study provided further insight into lionfish behavior in a coral reef ecosystem. Such information is essential for further understanding the ecological effects of lionfish within its invaded range and improving existing management plans used to help control the lionfish population.

MATERIALS AND METHODS

Study Site

This study was conducted on a subtropical coral reef system in the coastal waters of the Florida Keys, USA (Middle Keys, Florida), from April through October 2014. Data from both directed lionfish surveys (Fish and Wildlife Research Institute, unpublished data) and reef fish visual censuses (Ruttenberg et al. 2012) were used to compile a list of potential tagging sites with high lionfish abundance (at least 5 lionfish per site). Four study sites were selected (Figure 1A). These 4 sites ranged in depth from 3–20 m, with 1–3 m of vertical relief, and were dominated by micro– and macro algae with low live coral cover (B. Binder, personal observations). Three of these sites were patch reefs surrounded by sand and seagrass, and the fourth was a continuous reef.

Acoustic Array Design

A series of Vemco VR2W 69 kHz acoustic receivers
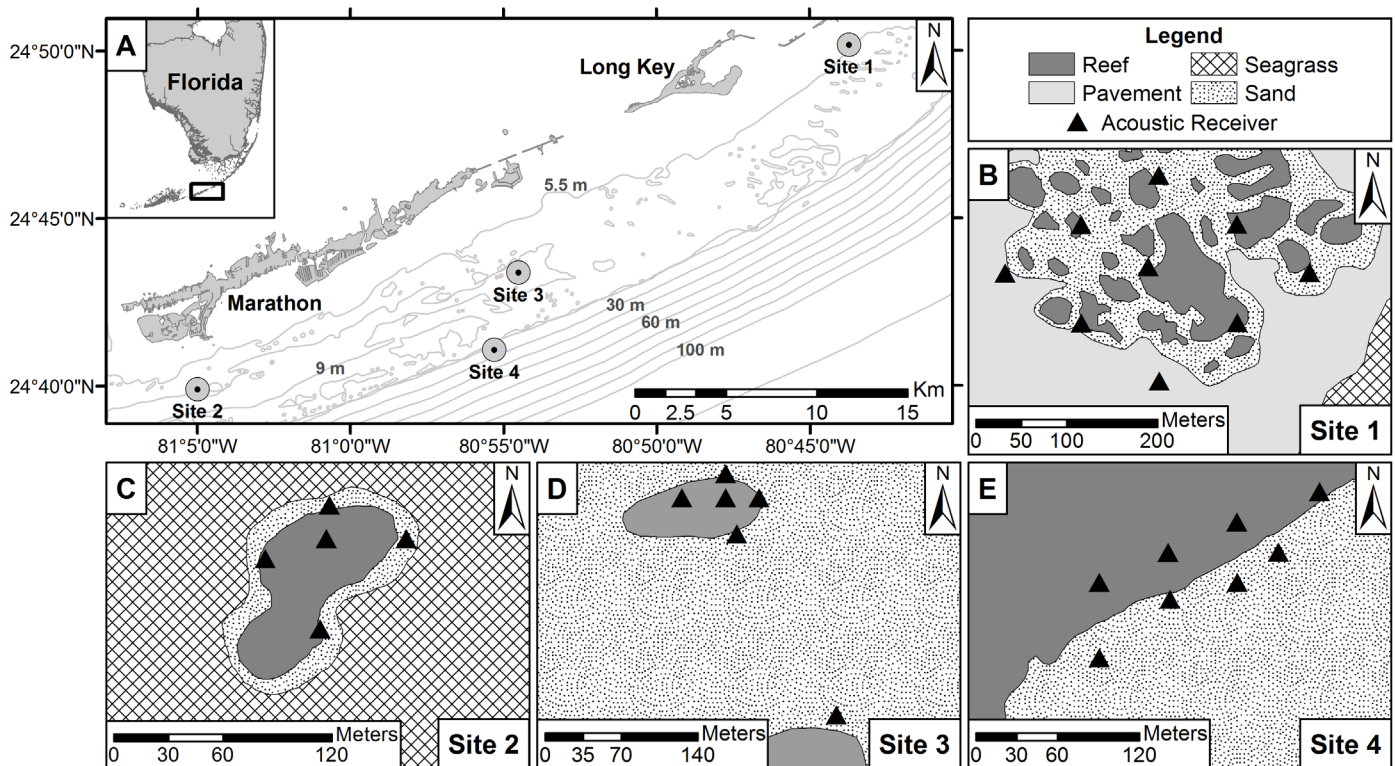
FIGURE 1. Overview of study area with locations of study sites throughout the Middle Keys, Florida. A. Entire study site. B. Array design and receiver locations for site 1. C. Array design and receiver locations for site 2. D. Array design and receiver locations for site 3. E. Array design and receiver locations for site 4. Triangles show the locations of acoustic receivers at all sites. Shaded areas (B – E) represent hard-bottom habitat, with darker gray representing high-complexity reef habitat and lighter gray representing pavement (low-relief carbonate rock with variable sand and soft-coral coverage).

TABLE 1. *Acoustic array details for lionfish tagging sites in the Florida Keys. Dates are given in mm/dd/yyyy.*

Site	Mean depth (m)	# Receivers	Deployed	Retrieved	Total receiver coverage (m²)*
1	3.2	9	06/10/2014	10/04/2014	130,584
2	8.1	5	06/12/2014	10/30/2014	121,363
3	10.5	7	04/21/2014	09/10/2014	18,300
4	20	8	04/23/2014	09/03/2014	59,667

* Total area is a conservative measurement based on the minimum ranges found during the range tests at each site, and does not count overlapping areas twice.

(Vemco Ltd., Bedford, Nova Scotia, Canada) were deployed to create an array at each study site from April to October 2014. Locations for the acoustic receivers were mapped in ArcGIS 10.2.1 (Figure 1B–E), and each receiver was secured on the bottom using a concrete block and PVC stand. At sites 1–3, acoustic receivers were placed in a grid (Heupel et al. 2006) around the patch reefs (Figure 1B–D). At site 4, the acoustic receivers were placed in 2 parallel lines along the shallow and deep side of the reef slope (Figure 1E). Given the habitat complexity of the 4 sites, acoustic receivers were placed close to each other to ensure overlapping coverage (Welch et al. 2012). The average distance between any 2 adjacent receivers ranged from 38.4 m to 104.8 m (full details for each array are provided in Table 1). Receivers were downloaded every 2 months.

Fish Capture and Underwater Tagging

Lionfish were caught during roving diver surveys at each site using the method described by Akins (2012). Teams of divers collected lionfish for tagging using handheld dip nets, then moved to a nearby sandy area and surgically implanted the acoustic tags. *Ex–situ* tagging of lionfish results in more barotrauma and higher mortality rates associated with anesthesia than *in–situ* tagging (Akins et al. 2014). The use of *in–situ* tagging greatly reduces the negative effects of barotrauma that result from rapid ascent (Starr et al. 2000, Lindholm et al. 2005). Additionally, previous work by the Florida Fish and Wildlife Conservation Commission (FWC) has shown that *in–situ* tagging minimizes the level of handling stress experienced by the fish (Feeley et al. 2018). *In–situ* tagging also allows tagged fish to be released at the exact location of capture, minimizing changes in behavior associated with being released away from the original capture location.

During surgery, a lionfish was secured ventral side up and a 1–2 cm incision was made in the abdominal wall posterior to the pelvic girdle. An acoustic tag (Vemco V9–1H, 69 kHz, 100 to 180 s ping delay, estimated tag life of 116 days; Vemco Ltd.) was inserted into the abdominal cavity and the incision closed with 2 to 3 interrupted sutures. Sterile, synthetic, absorbable braided sutures (VICRYL Plus; Ethicon Inc., Somerville, NJ) with antibacterial coating and a size 0 reverse–cutting needle were used. An external tag (Floy FTSL–73 streamer tag or Floy FTF–69 fingerling tag; Floy Tag Inc., Seattle, WA) was placed on the caudal peduncle for external identification. Lionfish were then measured (total length [TL], cm) and released at the capture site. Following release, tagged lionfish were observed by divers to document post–tagging condition. Tagging, including collection, lasted approximately 2 minutes. Video of the capture and tagging process can be seen here: *https://youtu.be/ clGR–K7IU3U.*

Data Analysis

Acoustic detection data were managed using VUE Software v2.1.3 (Vemco Ltd.), and scanned for false detections using the VUE False Detection Analysis Tool. Detections flagged as questionable were examined using the acceptance criteria proposed by Pincock (2008), and those that failed to meet these criteria were excluded from the final data set. Detections during the first 24 h post–release were also removed prior to analysis to minimize any effects of unnatural post–tagging behavior (Farmer and Ault 2011). Additionally, only lionfish that were detected for a minimum of 5 days post tagging and had a minimum of 500 detections were included in statistical analyses. Tagged fish that did not meet these criteria were excluded from further analysis. This approach is a common practice in acoustic telemetry studies (i.e. Hartill et al. 2003, Campbell et al. 2012, La Mesa et al. 2013, Bacheler et al. 2015) and is intended to ensure that collected data are more likely to be indicative of natural behavior (Bridger and Booth 2003).

Range Testing and Array Performance

Due to the high variability in detection probability in coral reef habitat (Welch et al. 2012), range tests were conducted at each study site to measure the performance of the acoustic receivers (Kessel et al. 2014). A single V9 acoustic tag (see specifications above) was deployed at each site and left for about 2 months. Each acoustic signal transmitted from the V9 acoustic tag propagates in all directions throughout the acoustic array, where the probability of a receiver detecting the signal is influenced by several factors. Acoustic signals will decay over a certain distance based on the environmental conditions, and can also be obstructed by reef habitat (Welch et al. 2012) or obscured by ambient biological or environmental noise (Payne et al. 2010). A generalized linear mixed model (GLMM) with a binomial distribution was used to examine the range test data for each array (Farmer et al. 2013), with the detection rate as the response variable and time of day (day, night,

and twilight), distance (from the range test tag to the receiver), and obstruction used as explanatory variables and date used as a random effect. The detection rate for time of day for each acoustic receiver was calculated by dividing the total number of detections recorded by the maximum number of detections possible during each time of day for each day of the study. The distance from the source of the signal to the receiver, obstruction by reef habitat, and time of day were included as explanatory variables to estimate the acoustic signal decay. Stations with high–relief reef habitat (>1.5 m) between the acoustic receiver and transmitter were classified as "obstructed", whereas stations with low–relief reef or sand between receiver and transmitter was classified as "unobstructed." The obstruction explanatory variable was only used at one site (Site 4) because it was the only array that contained both reef habitat (obstructed) and sand habitat (unobstructed) between receivers. The receivers in the acoustic arrays at the other study sites were all equally obstructed by reef habitat, thus no obstruction parameter was needed. Time of day was included as an explanatory variable to determine if detecting an acoustic signal was similar throughout the day, or if it was influenced by daily changes in biological noise and environmental conditions. GLMM analysis was performed in R using the lme4 package (Bates et al. 2015). The best–fit model was selected for each array by comparing the Akaike Information Criterion (AIC) values for all combinations of explanatory variables. AIC was used to select the best–fit model because it uses a multi–model inference penalty for model complexity, so only explanatory variables that influence receiver detection rate are included. Pseudo r–squared values were calculated for each best–fit model using the method described by Nakagawa and Schilzeth (2013).

Daily Activity Patterns

At each site, lionfish daily activity patterns were examined by grouping detection data from all receivers into hourly bins and summing the total number of detections in each bin throughout the duration of the study. The mean number of detections per hour and the mean number of unique stations that recorded a detection per hour were then calculated and plotted to provide a visual representation of lionfish activity over a 24–hour cycle. These metrics were used as a proxy for describing lionfish activity levels because lionfish behavior is likely to influence the probability of an acoustic tag being detected. Previous studies of lionfish behavior have found that lionfish were most active while foraging (Green and Akins 2011, Cure et al. 2012), and will rest or shelter under reef habitat or in crevices during periods of inactivity (Fishelson 1997, Green and Akins 2011). Thus, when a lionfish is sheltering the transmission range of its tag is likely to be reduced as a result of acoustic shadowing (Welch et al. 2012), but should increase when a lionfish is not sheltering. Based on these observations it was assumed that lionfish would have a greater number of detections per hour, and be detected on a greater number of receivers, during periods of increased activity than during periods of decreased activity. It is necessary to evaluate the mean number of detections per hour and mean number of unique stations with detections together, because an increased number of detections by itself could indicate that a lionfish is resting/sheltering in close proximity to a single receiver. An increase in the number of detections in conjunction with an increased number of receivers with detections, however, would suggest that lionfish are more exposed and likely moving around the acoustic array. Increased lionfish activity could also potentially result in a decrease in the number of receivers with a detection if a tagged lionfish moved outside of the array into the surrounding area. However, with the exception of site 4, the study sites were located on discrete habitat patches surrounded by open sand and seagrass habitat and the acoustic arrays in this study were designed to encompass the entire habitat patch. Thus, we would not expect lionfish to spend any significant amount of time in these surrounding areas.

TABLE 2. *Parameter estimates for the generalized linear mixed model used to estimate the detection range for each site. EDR = effective detection range.*

Site	Predictors	Intercept	Coefficient	Random Effect (SD)	Significance	Pseudo r²	50% EDR (m)
1	Distance	-0.010	-5.145	0.001	p<0.001	0.889	89.1
2	Distance	13.617	-9.749	0.001	p<0.001	0.621	164.1
3	Distance	2.002	-1.610	1.521	p=0.004	0.598	39.3
4 (No Obstruction)	Distance, Obstruction, Distance:Obstruction	6.688	-4.787	0.002	p<0.001	0.902	252.2
4 (Obstructed)	Distance, Obstruction, Distance:Obstruction	-0.443	-2.485	0.002	p<0.001	0.510	79.2

In order to examine the effect of time of day on lionfish activity, detection data for all lionfish were grouped into one of 3 diel time periods based on the receiver time stamp for each detection: day (30 minutes after sunrise until 30 minutes before sunset), night (30 minutes after sunset until 30 minutes before sunrise, and twilight (30 minutes before and after sunrise or sunset). Daily sunrise and sunset data were obtained from the U.S. Naval Observatory (Astronomical Applications Department, accessed 01/12/2015: http://aa.usno.navy.mil/). Prior to analysis, detection data were standardized by dividing the total number of detections in each time of day (ToD) by the total number of hours in that ToD, resulting in the number of detections per hour during each ToD for each day of the study. Raw data were assessed for normality, and the residuals were normally distributed and had homogenous variance. A generalized linear mixed effects model (PROC MIXED, SAS Enterprise Guide v.5.1) was used to determine if lionfish were more active during different diel periods: day, night, and twilight. Time of day was set as the fixed effect, and site and fish ID (nested within site) were set as random effects. Post—hoc pairwise comparisons between time periods were made using the studentized maximum modulus (SSM option) for PROC MIXED. Significance was set at α level of 0.05.

Lionfish Activity Centers

Short—term center—of—activity (COA) locations were es-timated for each tagged lionfish using the mean—position algorithm described by Simpfendorfer et al. (2002). These COAs represent an estimated position over a specified time interval, rather than an exact location at a single point in time. Lionfish COAs were calculated by binning detection data into each time of day, and also by daily 24 h time periods. The arithmetic means of receiver locations, weighted by the number of detections at each receiver, were then calculated for each time interval. Time of day COAs were used to evaluate diel changes in habitat use between day, night, and twilight. Daily COAs were used to evaluate daily shifts in habitat use within the array and migration to other habitat patches throughout the duration of the study. All COA position estimates were plotted in ArcGIS 10.3.

Home Range and Movements

Lionfish home ranges were estimated by calculating the 95% kernel utilization distribution (KUD) for each tagged fish from the diel COA position estimates. Kernel utilization distributions are probabilistic estimates of home range that highlight the area most frequently used by the animal (Wetherbee et al. 2004). For calculating the KUDs, the smoothing parameter (*h*) was calculated by the least squares cross validation (LSCV) method (Seaman and Powell 1996) using bivariate normal kernels. The LSCV approach was used because it was shown to perform better than other bandwidth selection methods when point distributions are

TABLE 3. *Details of lionfish tagged at Florida Keys, FL.*

Site	Fish	TL (cm)	Tagging date	Last detection	# days detected	Total Detections	Mean detections/day
1	280	34	6/10/2014	7/28/2014	49	10,531	215
	282	36	6/10/2014	7/28/2014	49	2,845	58
	283	36	6/10/2014	6/19/2014	10	3,165	316
2	3774*	34	6/17/2014	6/17/2014	1	265	-
	3775	34	6/17/2014	10/30/2014	136	235,362	1,731
	3776	32	6/17/2014	6/21/2014	5	5,129	1,026
	3777	25	6/17/2014	10/30/2014	136	132,131	972
3	274	17	4/23/2014	9/10/2014	140	78,039	553
	275	17	4/23/2014	5/6/2014	9	3,779	420
	276	26	4/23/2014	5/1/2014	8	14,746	1,843
4	277*	18	5/23/2014	8/11/2014	24	150	6
	287*	23	5/5/2014	-	-	-	-
	288	20	6/19/2014	8/11/2014	12	9,626	802
	3778	30	6/19/2014	8/11/2014	7	6257	232

*Fish excluded from all analyses.

tightly clumped (Gitzen et al. 2006). All home range analyses were performed using the adehabitatHR (v. 0.4.15) package (Calenge 2006) in R 3.5.0 (R Development Core Team 2014) and ArcGIS 10.3 using the North American Datum 1983 (NAD83) Universe Trans Mercator (UTM) Zone 17N projection.

Mean and maximum daily distance moved were also calculated for each lionfish. The distance between COA positions from consecutive diel time periods for each day were summed to estimate the daily distance moved. The mean daily distance moved was then calculated by averaging the summed daily distances for each tagged lionfish through the duration of the study. Only days that had at least one detection within each time of day were used when calculating the daily distance moved. The maximum daily distance moved throughout the duration of the study for each lionfish was also calculated.

RESULTS

Range Test Model Performance

For each site, the best–fit model indicated a significant negative relationship between detection probability and distance from the receiver. Time of day did not improve the model fit for any site. These models were used to estimate the 50% detection probability for each site (Table 2). This is the distance from the receiver where the effective working range is 50% and is deemed to be biologically acceptable. Two detection probabilities were estimated for site 4 due to the inclusion of the obstruction parameter in the model. The probability of detection dropped at a faster rate if the signal traveled across the reef tract, compared to traveling along the edge of the reef tract over sand habitat.

Tagging Summary

Fourteen lionfish (size range, 17–36 cm TL; mean ± se, 27.3 ± 1.9 cm TL) were tagged across the 4 sites (Table 3). The total number of days tagged fish were detected ranged from 5–141 days, with 3 lionfish detected throughout the duration of the study. Of the 14 lionfish fitted with acoustic tags, 11 met the minimum detection criteria to be included in further statistical analyses.
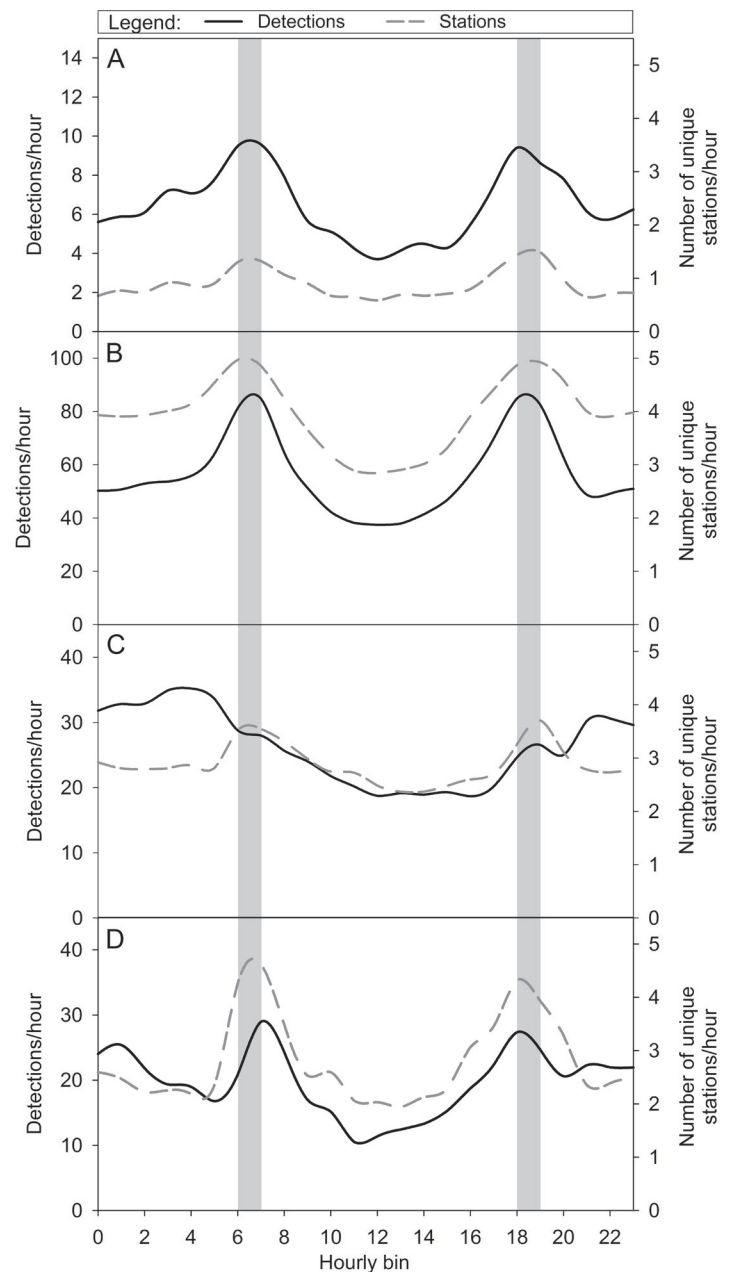
Daily Activity Patterns

Plots of both the mean number of detections per hour and the mean number of unique stations at which a fish was detected revealed distinct daily activity patterns. Lionfish at sites 1, 2, and 4 had a strong diel pattern with distinct peaks in the mean number of detections per hour during dawn and dusk (Figure 2A, 2B, and 2D). Site 3 had a strong diurnal pattern with mean detections per hour reaching a maximum at night and decreasing during the day (Figure 2C). The same patterns were also seen in the mean number of unique stations that recorded a detection during each hour at all 4 sites (Figure 2). Results of the generalized linear mixed–effects model indicated a significant effect of time

of day ($F_{2, 1720}$ = 117.31, p < 0.0001) on lionfish activity. Specifically, mean detections per hour were ~1.5 times greater during twilight ($\bar{x}$ = 50.2 ± 1.6 se) than during day ($\bar{x}$ = 34.3 ± 1.3 se) or night ($\bar{x}$ = 35.9 ± 1.1 se).
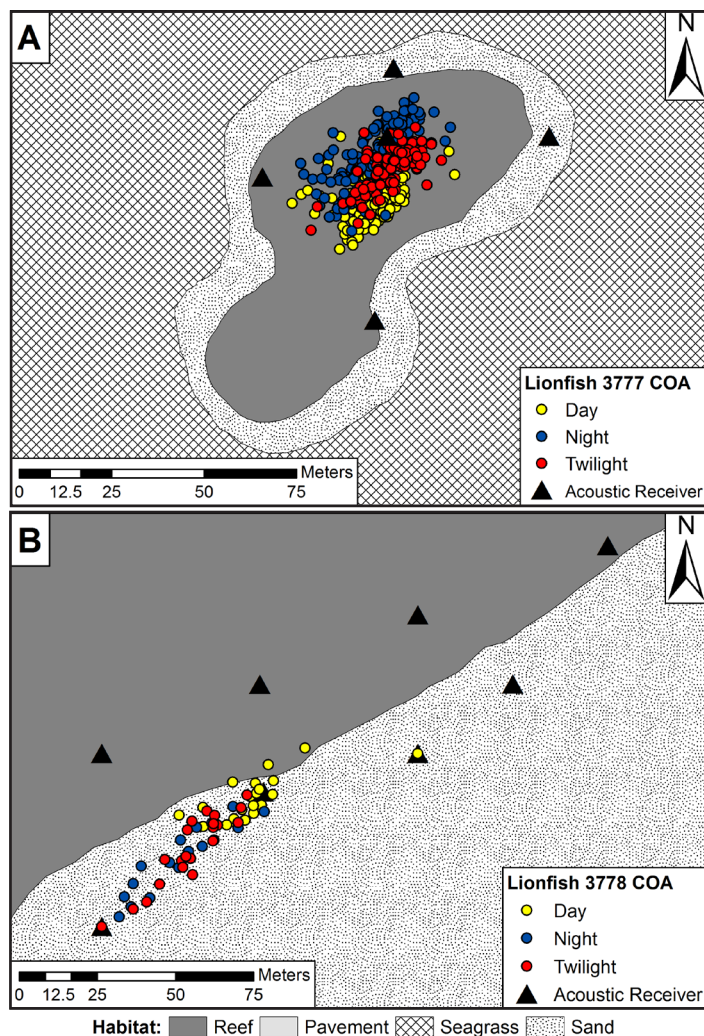
Lionfish Activity Centers

Distinct clustering of COA locations was apparent for 4 of the acoustically tagged lionfish. Diel COA locations for lionfish 3777 and 3778 formed apparent day, night, and twilight clusters (Figure 3). At site 2, position estimates for lionfish 3777 were grouped near the south side of the array during the day, the center of the array during twilight, and the north side of the array at night (Figure 3A). At site 4, position estimates for lionfish 3778 were clustered along

FIGURE 2. *Plot of mean lionfish daily activity patterns. A. Site 1. B. Site 2. C. Site 3. D. Site 4. Black line represents the mean detections per hour. Dashed line represents mean unique number of stations per hour. Shaded bars denote the twilight periods of dawn and dusk.*

the south edge of the array, with night and twilight clusters near the western most receiver (Figure 3B). Daily COA locations for lionfish 280 and 274 showed apparent shifts in habitat use over the duration of the study (Figure 4). At site 1, daily position estimates appear to show fish 280 moving between small habitat patches during June and July (Figure


FIGURE 3. *Calculated diel center-of-activity (COA) locations for lionfish. A. Fish 3777 at site 2. B. Fish 3778 at site 4. COAs calculated for day, night, and twilight for each day a tagged fish was detected. Triangles show the locations of acoustic receivers.*

4A). The most notable movement, however, was the emigration of fish 274 at site 3 from the primary habitat patch to a nearby patch. Daily position estimates were spread throughout the patch reef in April/May, and then concentrated in the southwest corner of the acoustic array in June/August before the emigration to the nearby patch reef in September (Figure 4B).

Home Range and Movements

Home range estimates for acoustically tagged lionfish were mostly confined to the reef habitat within the boundaries of their respective acoustic arrays (Figure 5), but total home range size varied among tagged individuals. The 95% KUDs
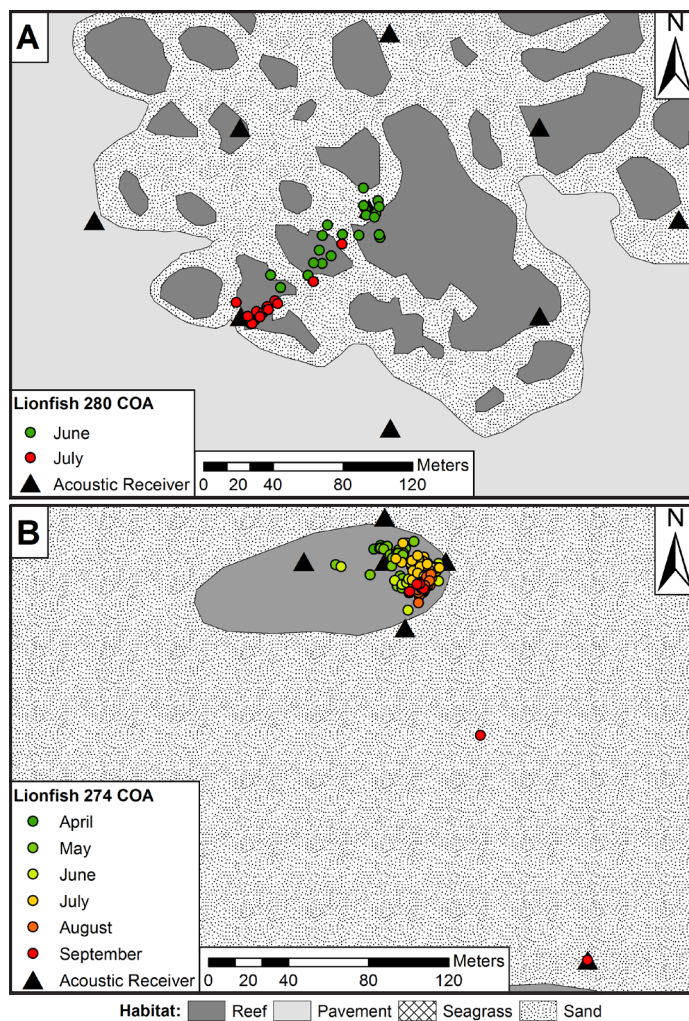
FIGURE 4. *Daily center-of-activity locations depicting the extent of spatial movement over the duration the study. A. Lionfish 280 at site 1. B. Lionfish 274 at site 3. Triangles show the locations of acoustic receivers.*

ranged from 360–18,812 m^2 (mean ± se = 3,802 ± 1,620 m^2; Table 4). Mean daily distance moved ranged from 24–117 m (Table 4), with grand mean daily distance moved of 56 ± 9 m. Only one lionfish had a mean daily distance moved > 100 m. By comparison, the maximum daily distance moved by lionfish ranged from 31–427 m (Table 4). Three lionfish had a maximum daily distance moved > 200 m and one had a maximum daily distance moved > 400 m.

Discussion

This study is the first to describe lionfish daily activity patterns, home range estimates, and daily movements on a coral reef ecosystem in the tropical western Atlantic utilizing acoustic telemetry. Lionfish in this study exhibited distinct diel activity patterns, with peaks in activity during twilight periods (dawn and dusk). These twilight activity peaks are contradictory to findings by Bacheler et al. (2015), who reported the lowest percentage of detections for acoustically tagged lionfish during dawn and dusk and the highest dur-

ing the day off North Carolina. Their results were attributed to increased biological noise at dawn and dusk, as well as changing environmental conditions (i.e., waves, wind) throughout the day, which have been shown to interfere with acoustic detections and the interpretation of diel activity patterns (Payne et al. 2010). In the present study, however, performance tests of the array indicated that time of day had no effect on the detectability of tags at any of the study sites. Thus, it is not likely that biological noise influenced the diel activity patterns observed in this study, and it can be assumed that these patterns were natural. The contrasting patterns in lionfish daily activity between this study and the study by Bacheler et al. (2015) may also be attributed to regional differences in habitat and environmental conditions. The present study was done on a coral reef system in the Florida Keys during summer, whereas the previous study was conducted on a hard–bottom reef system off North Carolina during winter.

The significant effect of time of day on lionfish diel activity patterns was not unexpected. Increased activity dur-

TABLE 4. *Home range estimates, maximum, and mean daily distances moved for tagged lionfish at each study site in the Florida Keys, FL. KUD = kernel utilization distribution.*

Site	Lionfish	95% KUD (m²)	Max Daily Distance (m)	Mean ± se Daily Distance (m)
1	280	6,544	251	72 ± 10
	282	18,812	427	117 ± 49
	283	1,854	75	25 ± 9
2	3775	518	64	33 ± 1
	3776	1,561	77	59 ± 13
	3777	963	90	54 ± 1
3	274	1316	215	51 ± 3
	275	1,199	31	27 ± 2
	276	360	38	24 ± 4
4	288	5,527	101	60 ± 11
	3778	3,171	155	98 ± 8
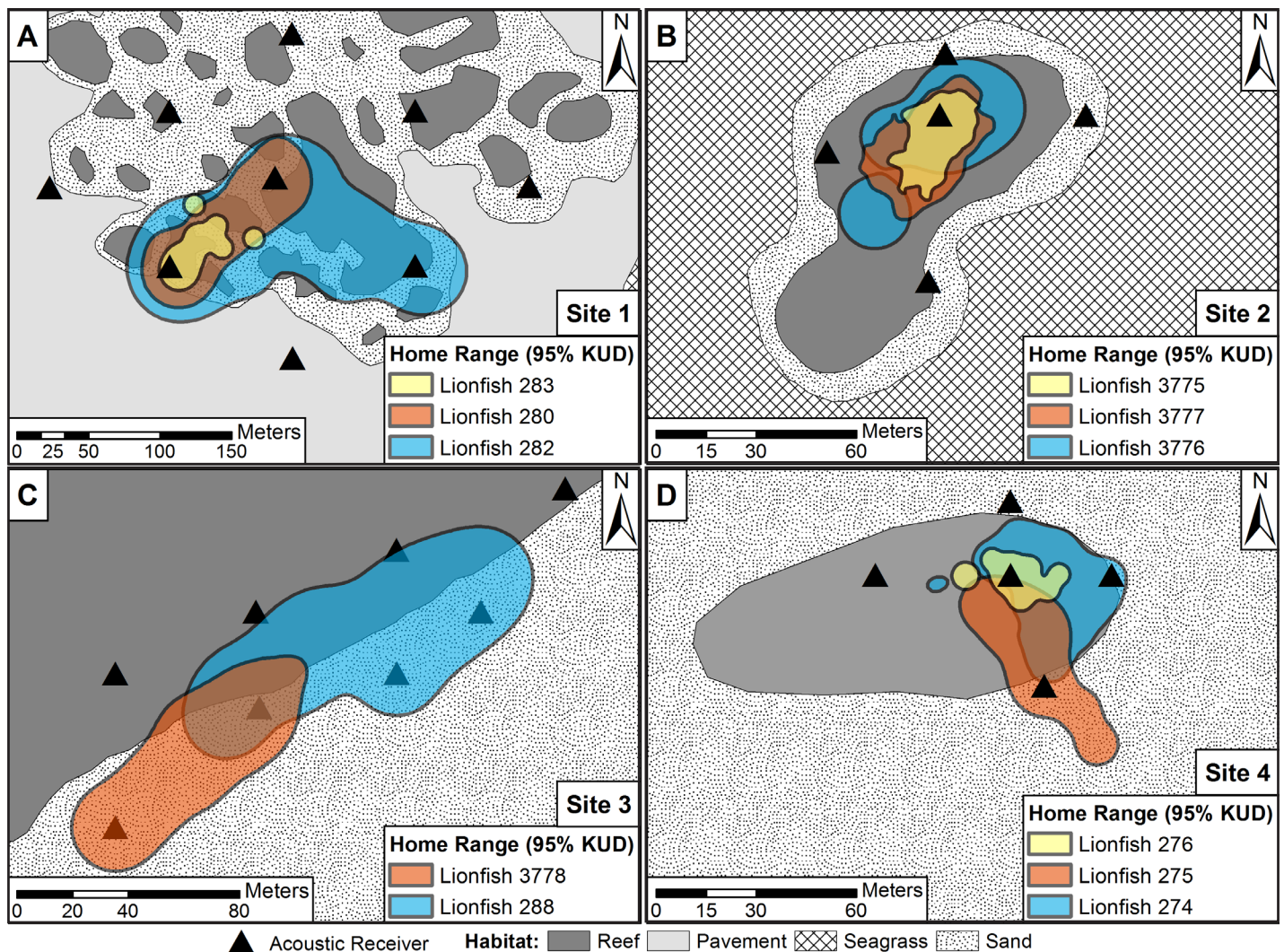
FIGURE 5. 95% kernel utilization distributions for tagged lionfish. A. Site 1. B. Site 2. C. Site 3. D. Site 4. Triangles show the locations of acoustic receivers.

ing twilight periods is a typical pattern for lionfish in both their native and nonnative ranges (Cure et al. 2012). This increased activity most likely corresponds with more frequent foraging at those times. In the Bahamas, lionfish activity levels closely matched daily light cycles, with the proportion of time spent active and hunting both greater at dawn and dusk than during mid—day (Green and Akins 2011). Similarly, the majority of foraging activity for lionfish in the Red Sea also occurred around sunset (McTee and Grubich 2014). Although these studies described lionfish activity during day and twilight, the surveys in these studies were only conducted from sunrise to sunset. As a result, they were not able to characterize lionfish activity at night. By using acoustic telemetry, the present study was able to quantify lionfish activity throughout the entire 24—hour cycle and improve our understanding of lionfish activity during periods of darkness. Since direct observation of lionfish behavior at night was not possible, we can only speculate on why lionfish activity is reduced at night. However, lionfish activity levels at night were similar to those seen during the day, and previous studies have shown that lionfish spend more time sheltering during the day (Green and Akins 2011). Similar patterns in detections during day and night suggest that lionfish may exhibit similar behavior during those times; possibly resting or sheltering. Reduced detections at night could also be attributed to lionfish moving outside of the array and into surrounding areas to forage (Benkwitt 2016a). However, night COA estimates located on habitat within the confines of the arrays suggest this is less likely, although a more extensive acoustic array with additional receivers in the surrounding areas would be needed to address this fully.

While peaks in lionfish activity corresponded closely with dawn and dusk, the timing of these peaks differed slightly among sites. As depth increased (from sites 1 to 4), the activity peaks at dawn occurred 15–30 minutes later and activity peaks at dusk occurred 15–30 minutes earlier. This suggests that changes in ambient light levels (due to increasing depth) may affect lionfish behavior. Côté and Maljkovic (2010) found that lionfish predation rates increased during overcast days, supporting the notion that changes in ambient light levels may influence lionfish behavior.

Estimated COA locations for day, night, and twilight provide further evidence of lionfish diel activity patterns. Center—of—activity locations for 2 lionfish formed clusters during day, night, and twilight periods, suggesting that these fish may have used different microhabitats within the patch reef at different times of the day. Since lionfish are most active and likely feeding at dawn and dusk (Green and Akins 2011), clusters at twilight could represent foraging areas, while day and night clusters may represent areas that provide shelter. For instance, fish 3777 was caught and tagged in a small coral cave on the southwest side of a patch reef, where the daytime center of activity locations formed a clus-

ter. Twilight center of activity locations formed a cluster in the center of the patch reef where a large coral head with a high abundance of juvenile fish was located (M. McCallister, personal observations). However, the COA estimates within the different acoustic arrays do not provide the spatial resolution needed to determine if a tagged lionfish is located on a specific feature.

Quantitative measures of lionfish home ranges represent a considerable knowledge gap in the lionfish literature, with only one prior study providing an estimate of lionfish home range. Lionfish home ranges reported in the current study were considerably larger (mean 95% KUD = 3,979 ± 1,599 m^2) than the mean home range estimate of 552 m^2 reported by Tamburello and Côté (2015) on coral reefs in the Bahamas. However, they note that their mean home range size is most likely an underestimate because it was based on relocations of tagged lionfish during daylight hours only. In contrast, lionfish home range sizes in this study are more similar in size to home ranges reported for 2 sympatric native mesopredators; Red Hind, *Epinephelus guttatus* (range = 112–5,636 m^2, Shapiro et al. 1994) and Graysby, *Cephalopholis cruentata* (mean = 2,120 m^2, Popple and Hunte 2005). The rapid increase in lionfish abundance in the Gulf of Mexico (Dahl and Patterson 2014), Atlantic (Ruttenberg et al. 2012), and Caribbean (Green et al. 2012) throughout the past decade could result in more competition between lionfish and other native mesopredators. In Biscayne National Park, Florida, Curtis et al. (2017) found that lionfish and Graysby isotopic niches overlapped 67%, and that Graysby isotopic niches were 34% smaller in areas of high lionfish abundance. In addition, although lionfish and other similar sized mesopredators may occupy similar areas, their influence on local reef fish communities is not equivalent. Albins (2013) found that lionfish had a stronger effect on local fish communities than Coney Grouper (*Cephalopholis fulva*) and caused a greater reduction in the abundance and species richness of smaller native reef fishes.

This study represents the first time that lionfish home ranges have been estimated using acoustic telemetry. Although using this technique provides more robust home range estimates than previous studies, they should still be interpreted carefully. Home range estimates are more accurate when the tagged animals reside in the center of the array, thus reducing "edge effects" which can bias home range calculations (Farmer and Ault 2013). The areal extent of the acoustic array and location of receivers are also important when estimating home range. The acoustic arrays in this study were designed so that lionfish could be detected anywhere on the habitat patch, which resulted in a high degree of overlap between receivers. Although the acoustic arrays in this study were well suited for detecting lionfish movements, a fine—scale array is needed to provide more precise measures of home range. Despite these caveats, the home

ranges reported in this study add to our current knowledge of lionfish behavior and provide a baseline for comparison in future studies examining lionfish home ranges.

Mean daily distances moved for lionfish in this study ranged from 24–117 m, which is consistent with the 0—139 m daily distance movements that were observed for acoustically tagged lionfish in North Carolina (Bacheler et al. 2015). Our findings were also consistent with previous conventional tagging studies which found that lionfish tend to make short daily movements around habitat patches. In Florida, 73% of tagged lionfish were recaptured < 10 m from where they were tagged (Jud and Layman 2012). In the Bahamas, short distance movements between re—sightings of tagged lionfish were most common (Tamburello and Côté 2015). Three tagged lionfish had maximum daily distances moved > 200 m. Though infrequent, similar long—distance movements were seen by Bacheler et al. (2015) and Tamburello and Côté (2015). Notably, Tamburello and Côté found that lionfish on patch reefs had the greatest distances moved (up to 800 m), because they would move across narrow sand channels to other nearby patch reefs. Similarly, the 3 lionfish in this study with the largest maximum daily distances moved (lionfish 274, 280, and 282), were all tagged on patch reefs.

In a study examining the effect of lionfish densities on foraging behavior, Benkwitt (2016b) observed density—dependent changes in behavior due to intra—specific competition. Specifically, lionfish at higher densities were more active and made more frequent movements between coral patches than lionfish at lower densities. These changes in behavior, in particular the increased movements between patch reefs, could explain the large—scale movements (> 200 m) made by lionfish in coral reef habitats. Indeed, lionfish on patch reefs in the Bahamas were more likely to move to a new patch reef if the destination reef had a lower density of lionfish than the initial reef (Tamburello and Côté 2015). Interestingly, one such movement was observed in this study. Daily COA position estimates for lionfish 274 provided strong evidence that during the last week of detections this fish moved from the patch where it was initially tagged, and spent the first 5 months of the study, to an adjacent patch reef of similar size; a movement of ~200 m across an exposed seagrass area. These two patch reefs were part of a concurrent study examining the effects of control efforts on lionfish recolonization rates. The original patch reef where lionfish 274 was tagged did not undergo monthly lionfish removals, and diver surveys found 7 lionfish at the beginning of this tagging study. The patch reef that lionfish 274 emigrated to underwent monthly lionfish removals, and diver surveys recorded zero lionfish on this patch at the beginning of this tagging study (Binder et al. 2015). This is also consistent with findings that frequent culling of lionfish creates low—density patches that may be preferred by relocating lionfish (Smith et al. 2017).

The study by Tamburello and Côté (2015) also noted that the distance between patches determined how far a lionfish would move, with lionfish moving farther when patches where spaced closer together. This could explain the larger maximum daily distances moved by lionfish 280 and 288 at site 1, which was a large patch reef comprised of multiple smaller habitat patches.

Understanding temporal and spatial movement patterns is crucial to understanding the spread of invasive marine species. This is essential for the development of effective management plans and population control measures for lionfish (Akins et al. 2010). Acoustic data collected in this study offer valuable insight into the daily activity patterns and movements of lionfish that had previously only been described through observations made during foraging or conventional tagging studies. The distinct diel activity patterns observed in this study have increased our understanding of lionfish behavior in a coral reef system. This information can be used to improve invasive lionfish control and management efforts. With little evidence of biological control of lionfish in their invaded range (Albins and Hixon 2013), most management plans include directed removal efforts aimed at reducing local abundance (Morris and Whitfield 2009). These removals are typically performed by divers as part of ongoing removal efforts or during planned lionfish derbies and usually occur during the day (Akins 2012, Green et al. 2014a). Although effective (Ali 2014, Green et al. 2014b), our results indicate these efforts could be more effective if applied during twilight. Similarly, conducting visual surveys for lionfish during daylight hours may result in an underestimate of lionfish abundance. Future studies incorporating this technique should consider conducting surveys during twilight periods, when lionfish appear to be most active.

Although this study has furthered our understanding of lionfish activity patterns and how to study them using acoustic telemetry techniques, these results should not be seen as representative of all lionfish across all habitats. More work is needed to provide a complete understanding of lionfish movement ecology and the implications it could have on the future of the lionfish invasion. For instance, differences in diel activity and movement patterns between the current study and the study by Bacheler et al. (2015) suggest that lionfish may behave differently in different habitats and under different environmental conditions. Thus, additional studies across multiple habitats are needed to examine differences in activity, movement patterns, and home ranges on different types of reef habitat (i.e., shallow vs. deep, patch vs. continuous reefs, natural vs. artificial). Future work should also incorporate more advanced acoustic telemetry techniques, such as those that can provide fine—scale position estimates in a 3—dimensional space. This would provide more precise home range and movement data at a higher resolution than was possible in this study, in particular regarding how

lionfish may use different microhabitats. Such data would provide significant insight into the ways in which lionfish interact with their environment and would be invaluable to fisheries management groups throughout the invaded range.

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