Home range and spawning migration patterns of queen triggerfish *Balistes vetula* in St. Croix, US Virgin Islands

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ABSTRACT: Queen triggerfish *Balistes vetula* are an ecologically and economically important species associated with coral reefs throughout the tropical Atlantic Ocean. To better understand spatial and temporal movement patterns and help determine the effectiveness of a no-take marine reserve (Buck Island Reef National Monument, BIRNM), 55 queen triggerfish were surgically implanted with acoustic transmitters and tracked for 434.6 ± 27.3 d (mean ± SE) within a large acoustic array in St. Croix, US Virgin Islands. Queen triggerfish displayed high site fidelity within the reserve during non-spawning months. Home range sizes, as measured by 95 % minimum convex polygons and kernel utilization distributions, averaged 2.44 ± 0.30 and 3.34 ± 0.17 km^2, respectively. High site fidelity was interrupted briefly during full moons from November to March (2015–2017), when 22 % of the tagged population (n = 12) undertook repeated migrations to a nesting area located approximately 12 km from BIRNM. During the same-season spawning periods, 5 other fish were exclusively detected at a receiver station within the reserve, indicating a possible local nesting area and resident (non-migratory) contingent of queen triggerfish. The high site fidelity of queen triggerfish during non-spawning months coupled with the discovery of a resident spawning population highlights the importance of BIRNM as a potential refuge from local fishing pressures. This study provides improved understanding of queen triggerfish movement ecology, an extremely valuable asset for the development of spatial management strategies throughout their range.

KEY WORDS: Movement ecology · Marine reserves · Partial migration · Fisheries management · Acoustic telemetry · Balistidae · Spawning aggregation

1. INTRODUCTION

An understanding of the temporal and spatial extent of reef fish movement patterns is paramount to successful design of spatial management strategies (Sale et al. 2005, Botsford et al. 2009, Grüss et al. 2011a). For example, the movement ecology of adult fish, including the location and size of home ranges, migratory pathways, and spawning areas, can influence the effectiveness of marine protected areas (Kramer & Chapman 1999, Crossin et al. 2017). Highly mobile fish with large home ranges and extensive

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migrations require larger protected areas to reduce exploitation in comparison to more sedentary species (Kramer & Chapman 1999). In recent years, acoustic tracking of reef fishes has provided great insight into the spatial connectivity within tropical coral reef ecosystems and has revealed species-specific differences in home ranges and the timing and extent of migratory movements (Farmer & Ault 2011, Hitt et al. 2011, Pittman et al. 2014a, Green et al. 2015, Hussey et al. 2015, Crisafulli et al. 2018). This information can be used in the design of marine reserves and to predict possible benefits of protected areas (Grüss et al. 2011a,b, Cornejo-Donoso et al. 2017, Weeks et al. 2017, Farmer & Ault 2018, Krueck et al. 2018).

Queen triggerfish *Balistes vetula* (Balistidae) are an important food fish targeted by commercial, recreational, and artisanal fishers throughout the tropical Atlantic (Tyler & Munroe 2015). Despite their wide geographic range and economic importance, queen triggerfish movement ecology is not well understood. Their reproductive strategy includes paired spawning, demersal eggs, territorial nests, and parental care (Kawase 2002, Clark et al. 2015). Queen triggerfish are sexually dimorphic, with 50% of males reaching sexual maturity at significantly smaller sizes (21.1 cm fork length, FL) than females (24.5 cm FL) (Hernández et al. 2019). In the Caribbean Sea, they are indeterminate batch spawners,

and females may spawn up to 5 times a year (Hernández et al. 2019). In the Gulf of Mexico, male gray triggerfish *B. capriscus* build, maintain, and guard demersal nests during a summer spawning period while females tend the eggs (Simmons & Szedlmayer 2012). Acoustic tracking and conventional tagging studies have indicated that gray triggerfish have high site fidelity and residency rates (Ingram & Patterson 2001, Herbig & Szedlmayer 2016). Anecdotal information also suggests that queen triggerfish aggregate at nesting sites where they reproduce (Kadison et al. 2009, Kobara et al. 2013, Hernández et al. 2019), but very little is known about their movement behaviors, including home range sizes, spawning activity, and migratory pathways.

St. Croix, United States Virgin Islands (USVI), is a relatively small, isolated, tropical island located in the northern Caribbean Sea, surrounded by coral reefs (Fig. 1). Overexploitation of local reef fish populations has been reported for decades, yet fishing remains an important economic activity on the island (Kadison et al. 2017). Queen triggerfish, which are still relatively common on the shallow reefs (Bryan et al. 2016), are a significant component of the local fishery with modest annual landings averaging 6750 kg on St. Croix and 20100 kg on St. Thomas and St. John (Sagarese et al. 2018). Sustainability status of queen triggerfish in the USVI and the effectiveness
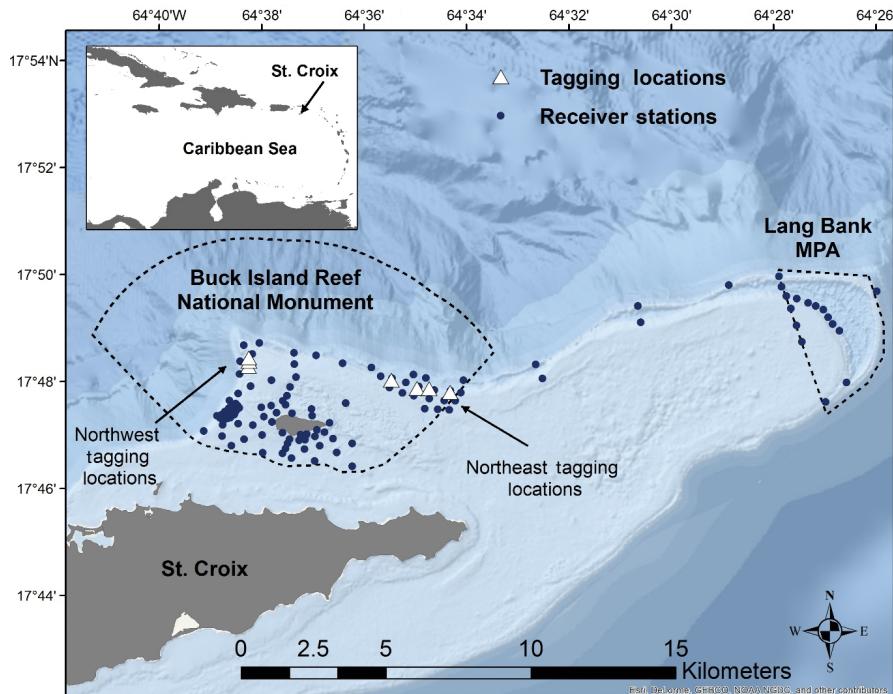

Fig. 1. East end of St. Croix, US Virgin Islands, including Buck Island Reef National Monument and the Lang Bank marine protected area (MPA) boundaries. Receiver stations are shown as dark blue circles and tagging locations as white triangles

of current catch limits are not well understood (Garcia-Moliner & Arnold 2013, Carruthers et al. 2014, Newman et al. 2015, Sagarese et al. 2018). However, in addition to catch limits, there is a large no-take marine reserve and several smaller seasonal area closures in St. Croix that could play an important role in sustaining reef fish stocks (Russ & Alcala 2004, Gaines et al. 2010, Ault et al. 2013, Pittman et al. 2014b). In this study, we used a large acoustic array to monitor the spatial and temporal movements of queen triggerfish within and among these marine reserves. Improved understanding of the movement patterns of queen triggerfish can help evaluate the efficacy of marine reserves in St. Croix and guide spatial management planning throughout their range.

2. MATERIALS AND METHODS

2.1. Study site and receiver stations

Located off the northeast coast of St. Croix, USVI, Buck Island Reef National Monument (BIRNM) is a no-take marine reserve that encompasses 10% of the island's mapped coral reef habitat (Fig. 1). BIRNM contains a wide diversity of reefs ranging from shallow patch reefs to deep mesophotic ridges (Costa et al. 2012). To better understand habitat utilization and the potential connectivity of a broad range of marine taxa (e.g. sharks, conches, turtles, fishes), within and outside of BIRNM, the National Park Service, in collaboration with 11 partner agencies, established a relatively large acoustic array in 2014 that consisted of 111 stations equipped with VR2W® passive acoustic receivers (Vemco) located in a variety of habitats in depths ranging from 2 to 40 m (Becker et al. 2016, Selby et al. 2016) (Fig. 1). Thirty of the 111 stations were specifically located in the northwestern and northeastern regions of BIRNM, where queen triggerfish are common. In addition to the BIRNM acoustic array, from 2014 to 2017 researchers at the University of the Virgin Islands (UVI) also maintained a seasonal (November–April) array of 10 to 16 VR2W® receivers at Lang Bank in depths of 14–48 m. Lang Bank is a submerged hardbottom platform located 12 km east of BIRNM and is a known fish spawning aggregation site for queen triggerfish and red hind *Epinephelus guttatus* (Nemeth et al. 2007); this area is closed to all fishing from December 1 until February 28 each year and closed to trap fishing all year.

All receivers in the 2 arrays (BIRNM and Lang Bank) were anchored semi-permanently to the sea floor with either cement blocks or sand screws de-pending on the substrate type. Receivers at deeper stations (>15 m) were pointed downward and suspended 5 m off the bottom with a line attached to a buoy, whereas those at shallower stations (≤15 m) were placed 0.5 m off the bottom and pointed upward. During the course of the study, individual stations were visited every 6 mo to download the data recorded on the receiver, replace batteries, and to inspect and maintain the anchoring tackle.

2.2. Range testing

In 2016, we performed a range test on 6 receiver stations in the northwest and northeast regions of the BIRNM array, across a variety of habitat types (i.e. pavement, sand, rhodolith beds, and spur and groove) (Fig. 2). Range tests were conducted during daylight hours with typical weather conditions and sea state for BIRNM. Fixed delay V9-2L tags (Vemco) with 60 s intervals were used for the range testing. Each tag was placed 2 m off the bottom, to replicate the typical height queen triggerfish that were observed swimming off bottom, at 50 m increments up to 350 m from the targeted station and left for 1 h. A detection rate for each distance from the station was calculated by dividing the total number of observed detections by the expected number of detections based on the ping rate and the duration of the deployment. We modeled the detection rates at each station and distance combination with a logistic regression, specifically a generalized linear model with a binomial distribution and logit link function in R (Welsh et al. 2012, Farmer et al. 2013, R Core Team 2016). Estimates of the distances (m) for 50, 25, and 10% detection probabilities within the array were calculated.

2.3. Acoustic tags

To minimize handling and barotrauma stress and avoid unwanted bycatch, queen triggerfish were targeted with underwater hook-and-line methods and tagged *in situ*, which ensures a high survival rate (Tuohy et al. 2015). Fish were captured with small 1/0 circle hooks tied to 1 m of 30 lb fluorocarbon leader attached a spool of abrasion-resistant Dacron line. Hooks were baited with small sections of previously frozen ballyhoo *Hemiramphus brasiliensis*. At each tagging site, scuba divers attracted queen triggerfish into the area by spreading out pieces of chopped bait. Shortly after fish began to aggressively feed, a diver placed a baited hook into the area where fish
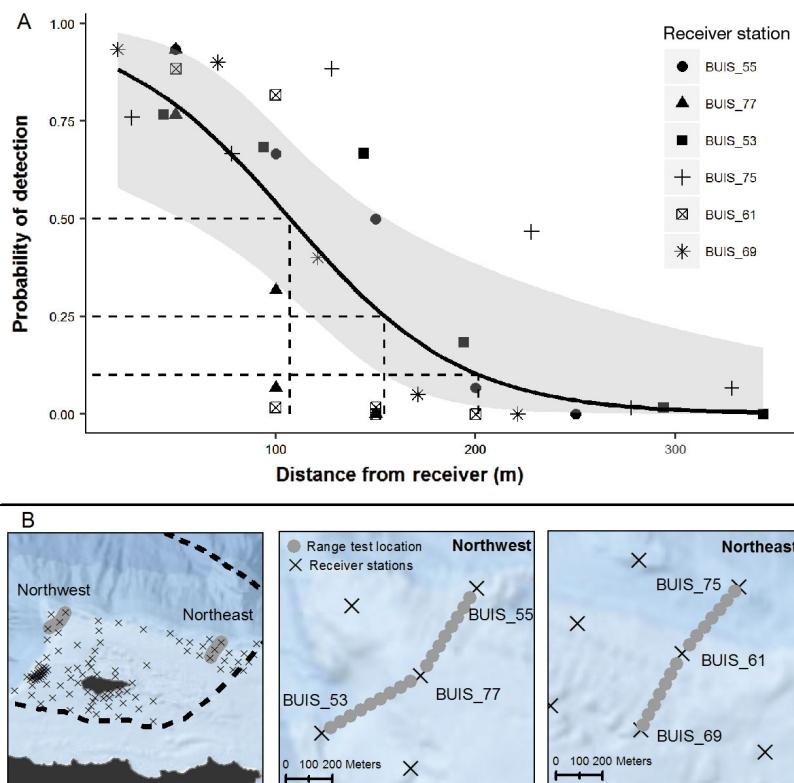
Fig. 2. (A) Probability of detection by distance for all range tests fit with a generalized linear model (black line). Gray shading represents the 95% confidence interval of the model predictions. Dashed lines indicate the predicted distance at 50% (107 m), 25% (154 m) and 10% (201 m) detection probabilities. (B) Location of range testing sites in the northwest and northeast regions of Buck Island Reef National Monument (dark dashed line)

Tagging locations were chosen based on habitat maps and known distributions of queen triggerfish; these were typically at 25 m depth. Tagging locations were divided into 2 general areas, the northwest and northeast regions of BIRNM (Fig. 1). Tagging took place in April 2015 and February and March 2016. Habitat in both locations was similar and consisted of low-relief reef pavement mixed with areas of unconsolidated sediments and rhodolith beds. In the northwest region, the reef had a patchy distribution with a high percent of soft coral coverage. In the northeast region, the reef was linear with minimal biotic cover.

2.4. Analyses

Acoustic detections from tagged fish were processed and summarized in the R programming environment (R Core Team 2016). An estimate of array fidelity within BIRNM was calculated by dividing the number of days that a fish was detected by the total number of days between the first and last detection. The analysis of queen triggerfish movement and home ranges was divided into non-spawning (2 April to 12 November) and spawning (13 November to 1 April) time periods based on post hoc movement analysis. The spawning season was defined as starting 1 wk prior to the first detection of a tagged fish at Lang Bank and ending 1 wk after the last detection at Lang Bank. Daily activity patterns during non-spawning months were calculated by averaging the proportion of daily movements between stations that each fish made by hour.

Hourly mean positions were calculated for each fish following the weighted arithmetic mean formula described by Simpfendorfer et al. (2002). Hourly mean positions were used to calculate the center of activity (COA) and to generate the home range estimates for each fish as described below (Udyawer et al. 2018). The COA was calculated by weighting the hourly mean positions by the number of hours at a position divided by the total number of hours detected. The maximum linear distance moved during the non-spawning season from the COA was calculated. In addition to the COA, a home station (station with maximum detections) was identified, and the

were feeding. All fish were hooked in the lip by slowly pulling in the line when fish began to feed on the bait. Once hooked, queen triggerfish were quickly pulled in and confined within a large nylon net where the surgery took place.

Due to their relatively small abdominal cavity, V9-2L coded transmitters (Vemco) with a 9 mm diameter and 29 mm length were used to tag all queen triggerfish. Transmitter power output was set to low, and each tag was programmed with a 90–180 s delay to provide an average battery life of 802 d.

Once confined within the nylon net, fish were positioned ventral side up to provide partial immobilization during surgery. The hook was carefully removed from their lip with a hemostat. A small (<2 cm) incision was made just to the side of the ventral axis, and the V9 tag was implanted into the abdominal cavity (Fig. 3). An absorbable vicryl suture (Ethicon) was used to evenly place 2 stiches along the incision. Surgery time was typically <5 min, after which the fish was turned upright and allowed to immediately swim away.

Fig. 3. Underwater surgery methods used for implanting transmitters. (A) Fish were carefully held upside down in a partially immobilized state within a large mesh net. (B) A small <2 cm incision was made on the side of the ventral axis allowing for the transmitter to be placed in the abdominal cavity. Incisions were closed with an absorbable vicryl suture using 2 stitches tied with an instrument surgeon knot. (C) Within 1 mo, one wound was found to have healed and the suture material had begun to dissolve

percentage of total detections at the home station was calculated. Home range estimates during the non-spawning season were made for fish that were detected at a minimum of 5 locations. Minimum convex polygon (MCP) and kernel density estimation of utilization distributions (KUD) were computed with the 'adehabitatHR' package in R (Calenge 2006). We removed 5% of the hourly locations furthest from the centroid to calculate 95% MCPs that were used as general estimations of normal home range. Estimates of core use (50% KUD) and overall use (95% KUD) were made with the bandwidth parameter set to 201 m, which was the distance of the 10% detection rate estimated from range tests performed within the array and likely a conservative estimate (Udyawer et al. 2018). Differences in array fidelity, the percent of detections at a home station, and home range size between fish tagged in the northwest region versus the northeast region were tested with a Mann-Whitney-Wilcoxon *U*-test. Differences in migration timing were tested with a Student's *t*-test. Swimming speed over ground during migrations was calculated by dividing the linear distance between the last station detected within BIRNM and the first station detected at Lang Bank by the timespan between detections. Mean values throughout are presented with ± standard error (SE).

3. RESULTS

3.1. Range test

Detection probabilities varied amongst receivers; for half of the stations, no detections were observed when the transmitters were 150 m away from the station, while at 1 station there was a 6% detection rate at 328 m (Fig. 2). Modeled detection probabilities suggested a 50% detection rate at a distance of 107 m, 25% at 154 m, and 10% at 201 m (Fig. 2). There was considerable variance associated with model predictions.

3.2. Home range

In total, 60 queen triggerfish were acoustically tagged in 2015 (n = 26) and 2016 (n = 34). Sizes ranged from 25.5 to 38.0 cm FL (mean: 32.4 ± 0.4 cm). Two tagged fish were never detected within the BIRNM array, and 3 fish were tracked for less than 60 d. These 5 fish were removed from further analyses. The average number of days between the first and last detection for the 55 fish used for this study was 434.6 ± 27.3 d (Table 1). Twenty-one fish were tagged in the northwest region, and 34 were tagged in the northeast

Table 1. Details of 55 queen triggerfish tracked with passive acoustic telemetry in St. Croix, US Virgin Islands, for more than 60 d between April 2015 and November 2017. Home station: station with maximum detections, COA: center of activity; MCP: minimum convex polygon; KUD: kernel density estimation of utilization distributions. MCP home range estimates were made for 19 fish that were detected at more than 5 locations; KUDs were estimated for 22 fish that were detected at a minimum of 5 stations and more than 100 total detections. –: insufficient data

Fish ID	Tag period	Tag location	Fork length (cm)	Total detections	Migration detected	Days between first and last detection	Total days detected	Array fidelity (%)	Detections at home station (%)	Maximum distance from COA (km)	Number of stations (non-spawning season)	95% MCP area (km²)	50% KUD area (km²)	95% KUD area (km²)
55223	Feb_2016	Northeast	27	8553	No	650	476	73.20	41.10	3.85	7	0.992	0.575	2.894
55230	Feb_2016	Northeast	27	1239	No	613	230	37.50	91.80	0	1			
55233	Feb_2016	Northeast	27	797	–	118	84	71.20	50.30	1.3	6	2.944	0.442	3.835
55231	Feb_2016	Northeast	28	2224	Yes	649	155	23.90	79.00	0.35	3			
59144	Apr_2015	Northeast	29	1194	Yes	364	51	14.00	98.80	0	1			
59155	Apr_2015	Northeast	29	3648	–	459	366	79.70	93.00	1.36	5		0.308	2.415
59171	Feb_2016	Northeast	29	8	–	243	5	2.10	25.00	0	1			
59556	Feb_2016	Northeast	30	4	–	243	4	1.60	50.00	0	1			
55225	Feb_2016	Northeast	30.5	5742	No	649	279	43.00	82.50	2.01	8	0.992	0.191	1.206
59137	Apr_2015	Northeast	30.5	50	Yes	347	15	4.30	34.00	0	1			
55229	Feb_2016	Northeast	31	1140	No	643	179	27.80	54.60	0.54	3			
59140	Apr_2015	Northeast	31	23873	No	874	739	84.60	95.50	0.46	4	0.103	0.175	0.777
59149	Apr_2015	Northeast	31	97	Yes	335	45	13.40	61.90	0.36	2			
59170	Feb_2016	Northeast	31.5	46	–	284	23	8.10	78.30	0	1			
59139	Apr_2015	Northeast	32	24834	–	230	231	100.00	99.70	3.64	5		0.167	0.853
59168	Feb_2016	Northeast	32	281	–	564	94	16.70	99.30	0.49	3			
59552	Apr_2015	Northeast	32	127	–	662	56	8.50	96.90	0.37	2			
55226	Feb_2016	Northeast	33	2527	No	440	302	68.60	99.10	0.5	3			
59148	Apr_2015	Northeast	33	46	–	277	16	5.80	97.80	0	1			
59156	Apr_2015	Northeast	33	294	Yes	384	62	16.10	81.60	0.36	2			
59554	Apr_2015	Northeast	33	6516	–	196	197	100.00	98.60	6.97	7	1.81	0.351	3.26
55227	Feb_2016	Northeast	34	1918	–	650	153	23.50	95.90	1.18	6	3.664	0.164	0.779
59138	Apr_2015	Northeast	34	115094	Yes	658	641	97.40	99.80	6.98	4			
59150	Apr_2015	Northeast	34.5	1366	Yes	349	250	71.60	89.10	3.63	2			
59141	Apr_2015	Northeast	35	789	Yes	729	158	21.70	55.90	1.27	10	1.282	0.35	4.201
59548	Apr_2015	Northeast	35	332	–	83	50	60.20	100.00	0	1			
59135	Apr_2015	Northeast	36	774	No	517	250	48.40	88.20	0.31	2			
59146	Apr_2015	Northeast	36	13376	Yes	241	230	95.40	99.70	7.95	5		0.167	0.784
59549	Apr_2015	Northeast	36.5	9	–	62	8	12.90	100.00	0	1			
55232	Feb_2016	Northeast	37	11510	Yes	615	286	46.50	96.20	3.69	7	3.692	0.275	2.095
59145	Apr_2015	Northeast	37	2012	–	653	136	20.80	99.70	0.37	2			
59136	Apr_2015	Northeast	37	15	–	87	4	4.60	33.30	0.67	5			
59553	Apr_2015	Northeast	38	626	–	187	140	74.90	35.60	0.73	6	1.695	0.678	3.695
55222	Feb_2016	Northeast	38.5	41247	No	646	430	66.60	78.00	4.6	28	4.605	0.188	1.358
55209	Mar_2016	Northwest	39	1521	No	411	82	20.00	97.40	0	1			
55212	Mar_2016	Northwest	25.5	4152	–	512	282	55.10	94.60	0.71	3			
55213	Mar_2016	Northwest	27	1333	No	356	200	56.20	99.60	0	1			
59173	Feb_2016	Northwest	27	436	Yes	350	116	33.10	48.40	0.69	3			
55210	Mar_2016	Northwest	28	184	No	546	58	10.60	57.10	0.39	2			
55208	Mar_2016	Northwest	29	3229	No	81	82	100.00	99.70	0.5	3			
55215	Mar_2016	Northwest	31	845	No	112	91	81.30	72.90	7.03	14	1.083	0.269	3.475
59161	Apr_2015	Northwest	31	15442	Partial	668	607	90.90	99.10	4.4	4			
55207	Mar_2016	Northwest	31	1371	–	142	126	88.70	89.80	0.79	6	0.887	0.216	2.063
55224	Mar_2016	Northwest	31.5	3876	–	506	321	63.40	99.70	0.42	3			
55217	Mar_2016	Northwest	31.5	510	No	483	47	9.70	78.20	0.45	2			
55205	Mar_2016	Northwest	32	3469	Partial	411	361	87.80	98.50	0.41	6			
55220	Feb_2016	Northwest	33	1640	–	596	254	42.60	78.90	1.47	4	3.4	0.358	3.632
55211	Mar_2016	Northwest	33.5	1403	Partial	585	162	27.70	42.60	0.59	4	1.813	0.424	2.286
55218	Feb_2016	Northwest	34	2671	No	635	171	26.90	88.10	0.77	3	0.928	0.521	2.948
59163	Apr_2015	Northwest	34	101	Partial	339	44	13.00	69.30	0.43	6			
55206	Mar_2016	Northwest	34	3557	–	324	285	88.00	63.60	1.02	3	2.406	0.405	2.494
59165	Feb_2016	Northwest	35	76	Partial	587	43	7.30	68.40	0.46	6			
55216	Mar_2016	Northwest	35	901	–	593	67	11.30	77.90	0.43	3	0.265	0.364	1.815
55219	Mar_2016	Northwest	36	4557	–	566	310	54.80	49.80	1.28	15	8.473	0.788	4.978
55214	Mar_2016	Northwest	37	330	Yes	397	59	14.90	35.50	6.68	12	5.288	0.564	6.087

region of BIRNM. A total of 32 fish were detected for longer than 1 yr. The average array fidelity within BIRNM was 44.1 ± 4.4 % and was not significantly different between fish tagged in the northwest (46.4 %) and northeast (43.4 %) locations ($U = 324$, $p = 0.57$; Table 1). Queen triggerfish displayed strong site fidelity, and for most individuals, a majority of detections came from a single station. The average percentage of detections at a home station was 77.9 ± 3.1 %, and 21 fish had >95 % of their detections recorded at a single station (Table 1). Similar to array fidelity, there was no difference in the percentage of detections at a

home station between fish tagged in the northwest or northeast locations ($U = 401$, $p = 0.45$). Not only did the fish spend a majority of their time near a single station, but during non-spawning months (April 2 to November 12), they did not travel far (Fig. 4). The average maximum distance traveled from their COA was 1.5 ± 0.3 km, and 79 % of fish traveled less than 2 km. Movements between stations largely (87 %) took place between 06:00 and 18:00 h (Fig. 5).

MCP (95 %) home range estimates were made for 19 fish that were detected at more than 5 locations, after outlier locations were removed, during non-
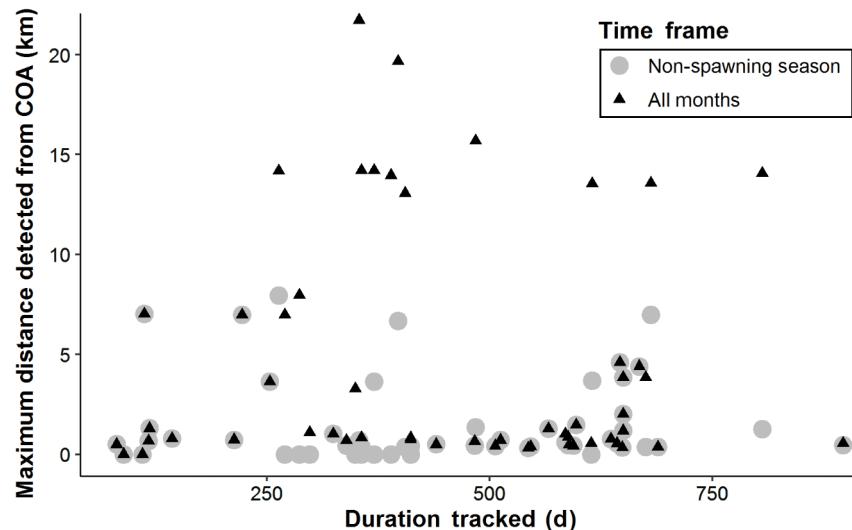
Fig. 4. Maximum linear distance (km) that queen triggerfish (n = 55) moved during the non-spawning season (grey circles) and all months (black triangles) from their center of activity (COA) compared to the number of days they were tracked
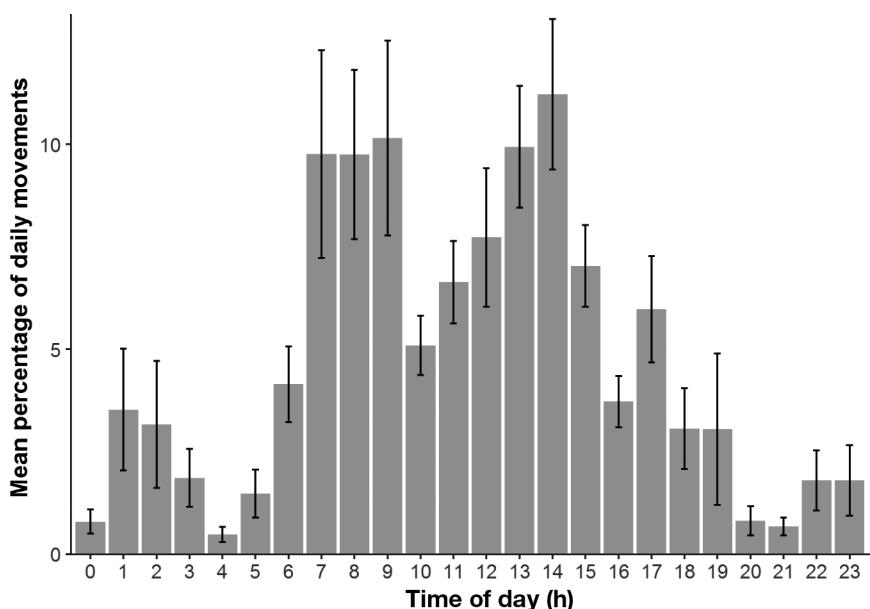
Fig. 5. Daily activity for queen triggerfish (n = 55) as measured by the mean percentage of movements by hour. Error bars = SE

spawning months (Table 1). The average 95% MCP was $2.44 ± 0.30$ km^2. Home range estimates using 50% and 95% KUDs were made for 22 fish that were detected at a minimum of 5 locations and more than 100 total detections, and the average 50% and 95% KUDs were $0.36 ± 0.02$ and $2.63 ± 0.19$ km^2, respectively (Table 1). There was no significant difference in home range estimates (MCP, 50% KUD, and 95% KUD) between fish tagged in the northwest location versus those tagged in the northeast location ($U = 70$, 30, and 35, p = 0.53, 0.06, and 0.12).

3.3. Migration

Several queen triggerfish had reduced site fidelity during the late fall and winter, when they were detected at Lang Bank (Fig. 6). A total of 38 migrations to Lang Bank were observed for 12 individual fish during the winters of 2015/16 and 2016/17. Ten of these individuals were tagged in the northeast region of BIRNM, and 2 were tagged in the northwest region. The earliest detection of a queen triggerfish at Lang Bank was November 19 and the latest
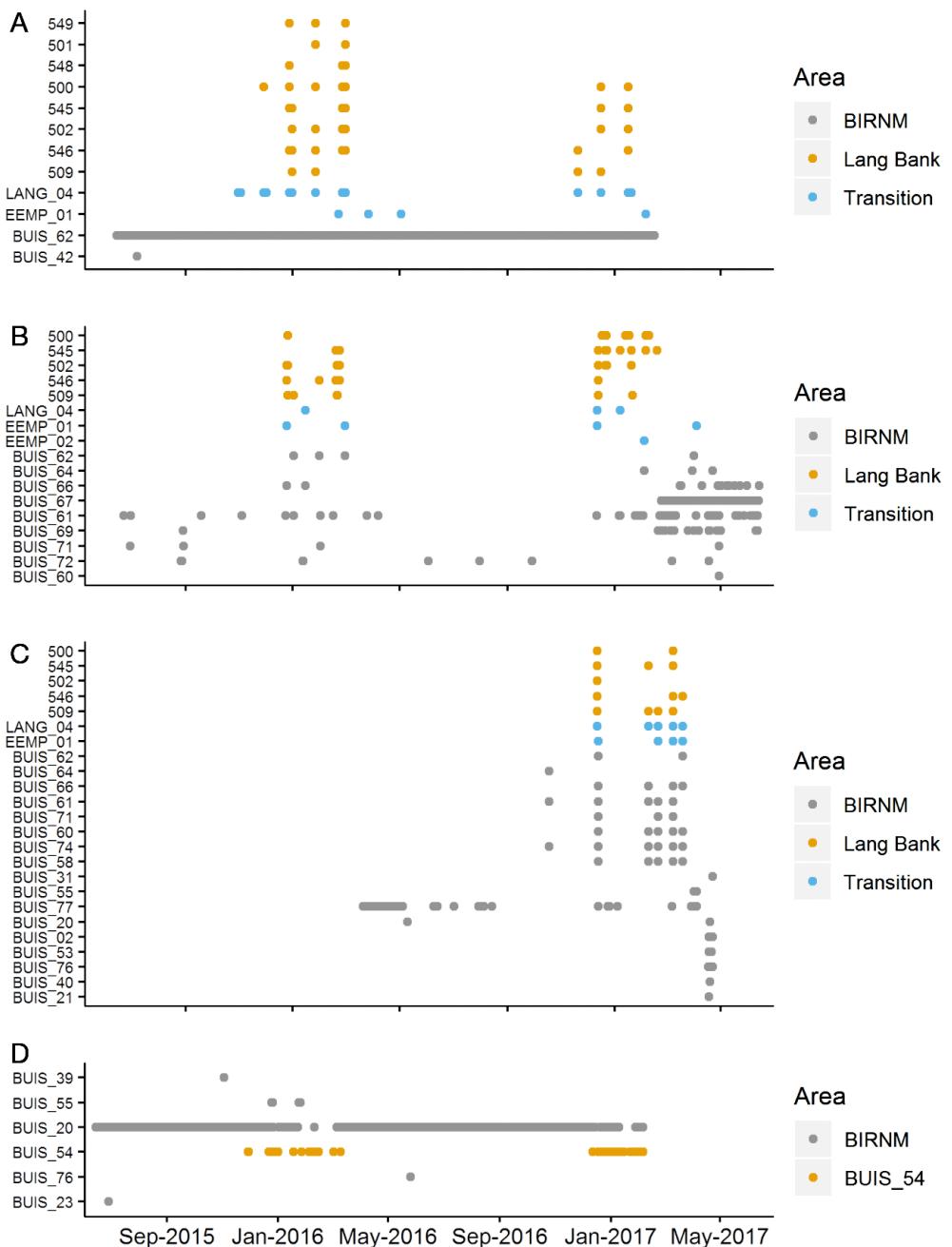
Fig. 6. Daily station locations of 4 queen triggerfish for 2 yr (June 15, 2015 – June 15, 2017) with stations ordered from west on bottom to east on top and color coded by area. Transition stations (in blue) are those outside of Buck Island Reef National Monument (BIRNM) along the northeastern reef edge of St. Croix. (A) Fish 59138 was tagged in the northeast region and had 99.8% of non-spawning season detections at its home station (BUIS_62). (B) Fish 59141 was also tagged in the northeast region, but it had a much larger home range (9 stations). (C) Fish 55214 was tagged in the northwest region, but migrated to Lang Bank through the northeast region and then followed the same pathway as other fish that were tagged in the northeast. (D) Fish 59161 was tagged in the northwest region and had very high site fidelity during most of the year, but during spawning months it visited Stn BUIS_54, a possible nesting site

detection was March 25. In 2015/16, the greatest number of detections at Lang Bank occurred during 3 full moons in late December, late January, and late February. Detections during November and March were limited to 2 fish with only 16 total detections. In 2016/2017, the greatest number of detections at Lang Bank was during the full moon in mid-December, mid-January, and mid-February. Similar to 2015/16, detections during November and March were also limited to 2 fish with only 11 detections. We recorded 1 fish making 4 migrations to Lang Bank, but the mode for all fish was 3 migrations. Of the fish that made migrations to Lang Bank, 60% were detected along the northern reef edge after leaving BIRNM and 42% were detected along this same path on their return to BIRNM (Fig. 7). Lang Bank Stn 500, located in 32 m depth just off the reef ridge in an area of colonized reef pavement near the center of the MPA, was the center of spawning activity for queen triggerfish (R. Nemeth & D. Bryan unpubl. data). The average linear distance between COAs in BIRNM and Stn 500 in Lang Bank was 15.09 ± 0.64 km (Fig. 4). The time between the last detection in BIRNM and

first detection at Lang Bank varied, but 42% of migrations to the spawning site and 36% of homeward migrations took place in less than 12 h. The average time between BIRNM and Lang Bank for this subset of fish was 6.74 ± 0.40 h and required a swimming speed of 1.96 ± 0.08 km h^{-1}. The average time for these swims was not significantly different from homeward trips, which took 6.34 ± 0.34 h, with an average swimming speed of 2.05 ± 0.09 km h^{-1}. Both fish that migrated from the northwest region of BIRNM to Lang Bank were also detected in the northeast region of the array during their migration to and from Lang Bank (Figs. 6 & 7). Fish 55214 was detected at the same stations during repeated outward and homeward migrations at the same time of day (±2 h).

On average, fish were first detected at Lang Bank 1.3 ± 0.5 d after the full moon and were last detected 5.3 ± 0.4 d after the full moon (Fig. 8). The arrival pathway for most fish was past Stns 509 and 546 at the northern end of Lang Bank (Fig. 7). Fish that were recorded during multiple migrations and that were first detected at these stations showed a consis-
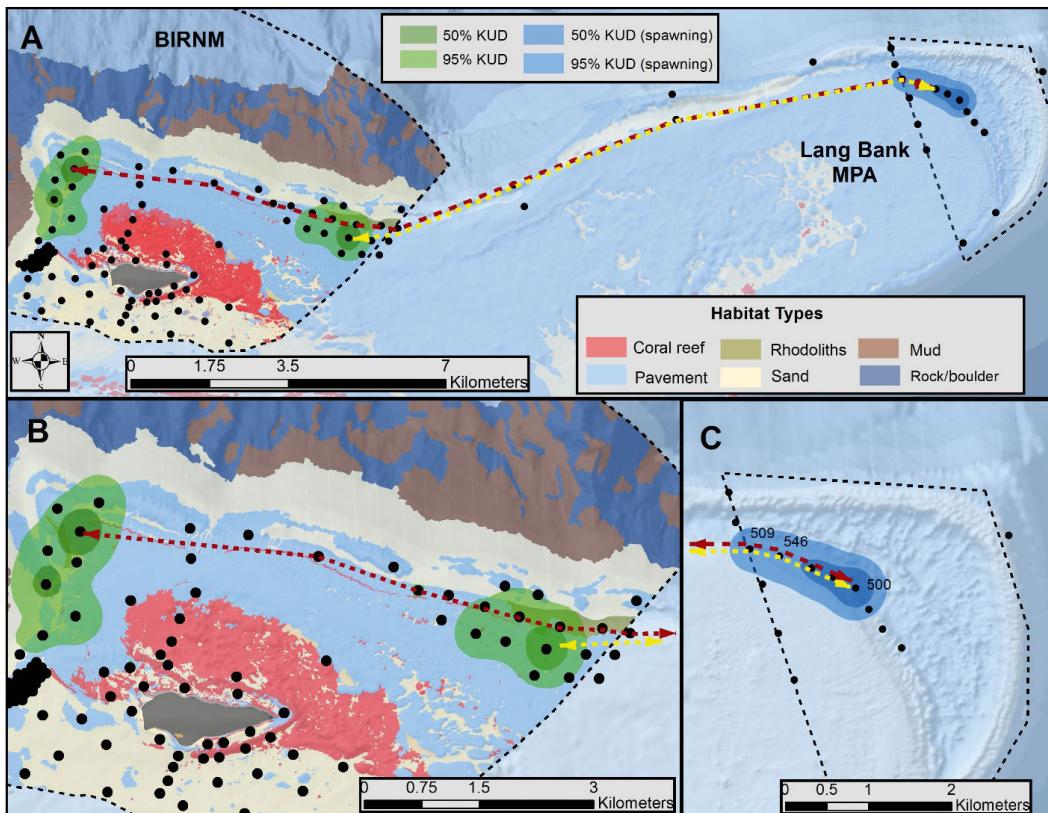

Fig. 7. (A,B) Resident home ranges (50 and 95% kernel density estimation of utilization distributions, KUDs) of Fish 55214 in northwest Buck Island Reef National Monument (BIRNM) and Fish 59141 in northeast BIRNM. The migration and return pathway for Fish 55214 is shown with a red dashed line and Fish 59141 with a yellow dashed line. (C) Combined spawning areas (50 and 95% KUDs) for Fish 55214 and 59141 and the pathway used by both fish when entering and exiting the spawning area. MPA: marine protected area

tent preference for the timing of their arrival at Lang Bank. A majority of fish first arrived at Lang Bank between 13:00 and 16:00 h in the afternoon. The precise timing of departure was more difficult to determine, as the last station at which fish were detected was often neither Stn 509 nor 546. For those fish that were last detected at these stations, the majority left Lang Bank between 08:00 and 10:00 h in the morning. Individual fish that were tracked at least once to Lang Bank made an average of 2.5 ± 0.21 trips per season. During their time at Lang Bank, fish had an average residence time of 4.0 ± 0.7 d, and individuals were detected on average at 3.0 ± 0.4 stations.

Two fish (59138 and 59141) that were tagged in the northeast region and tracked for 658 and 729 d, respectively, returned to Lang Bank in consecutive years (Fig. 6). Fish 59138 had extremely high site fidelity in BIRNM, with 99.8% of resident detections occurring at a single station. Fish 59141 was detected at a greater number of stations during the non-spawning season in BIRNM, but similar to 59138, returned to the same area within BIRNM after migrating to Lang Bank. At Lank Bank, Fish 59141 entered the area near Stn 509 and then swam towards Stn 500, where it typically spent most of its time. Most queen triggerfish followed a similar spatial pattern during their migration to Lang Bank and their time spent at Lang Bank (R. Nemeth & D. Bryan unpubl. data).

Despite the detection of several spawning migrations to Lang Bank from both the northeast and northwest region of BIRNM, a majority (79%) of queen triggerfish were never detected at Lang Bank. In the northwest region of BIRNM, 5 fish were exclusively detected at Stn BUIS_54, located on the northwestern corner of the array in 28 m depth, during the same time of the year when fish were detected at Lang Bank. The earliest detection was on November 29 and the latest detection was on March 26. Nineteen trips to Stn BUIS_54 were detected for these 5 fish during this time period. On average, these fish were first detected at this station 0.4 ± 1.0 d prior to the full moon and were last detected 4.3 ± 0.9 d after (Fig. 6). The average duration of a trip to Stn BUIS_54 was 4.7 ± 1.4 d. The average number of detections during these trips was low (7 ± 2.5), and 7 trips con-

sisted of only a single detection. This indicates that some fish passed Stn BUIS_54 and likely spawned nearby, but in an area that was not within our detection range. The fish made an average of 2.5 trips yr^{-1} to Stn BUIS_54. There was no significant difference in the average time of arrival or departure in relation to the full moon at Stn BUIS_54 when compared to arrival and departure times at Lang Bank (t = 1.47, p = 0.15 and t = 0.94, p = 0.35, respectively). Stn BUIS_54 was very close to the home ranges of these fish, and the average linear distance from their COAs to Stn BUIS_54 was only 0.7 ± 0.03 km (Fig. 9). Seven other fish that were tagged in the northwest region were also detected at Stn BUIS_54 during the spawning season, but they had home ranges that included this station, so it was not possible to categorize those detections explicitly as an indication of spawning movements.

3.4. Tag recovery

Two fish that had been tagged in February of 2016 were reported captured by a local fisherman in March and April of 2018 at Lang Bank with fish traps. One fish (55227) had been tracked for 650 d in the northeastern portion of BIRNM and had never been detected on Lang Bank. The other fish (59167), was 1 of 2 that had never been detected within the BIRNM
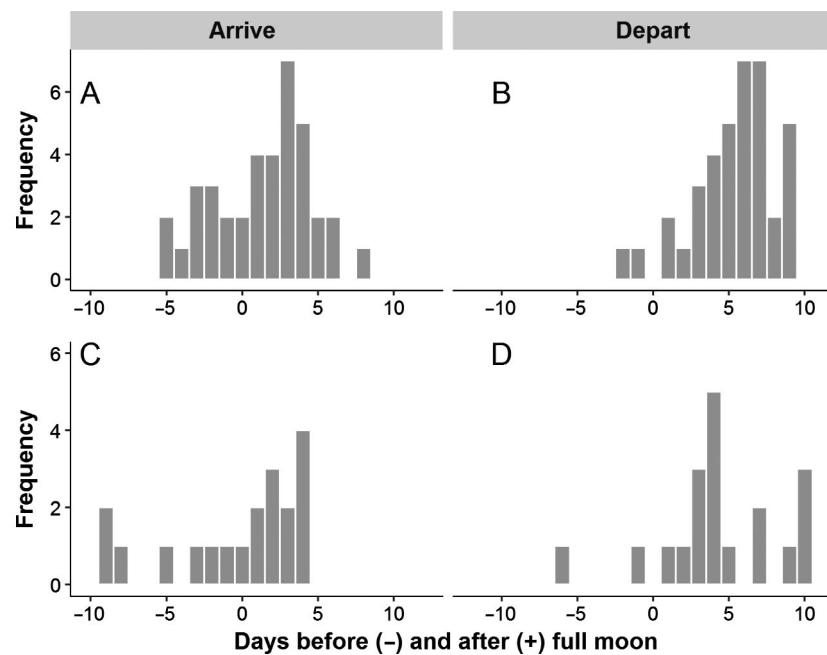

Fig. 8. Frequency of the time of arrival (first detection) and departure (last detection) of queen triggerfish compared to the full moon, during their migrations to (A,B) Lang Bank and (C,D) Stn BUIS_54
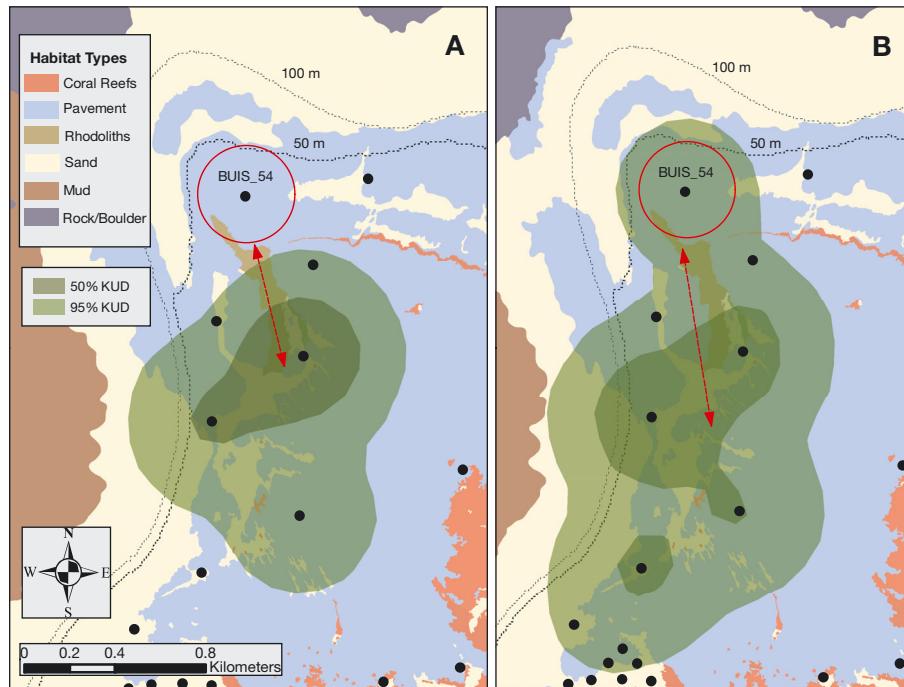
Fig. 9. Home range estimates (50 and 95% kernel density estimation of utilization distributions, KUDs) for queen triggerfish (A) 55211 and (B) 55219 during the non-spawning seasons from April 2016 until November 2017 that were tagged in the northwest region of BIRNM. Fish 55211 was only detected at Stn BUIS_54 (circled in solid red; 201 m radius represents the predicted distance for a 10% detection probability) during the spawning season. Fish 55219 was also detected at Stn BUIS_54 during the spawning season, but the station was within its overall use area (95% KUD). Red dashed line indicates pathway from center of activity to potential spawning location. Dark dashed lines represent 50 and 100 m depth contours

or Lang Bank acoustic arrays. The capture of these fish represents a minimum 2 yr fishing mortality rate of 3.3% for all tagged fish (n = 60) and a much higher 14.3% fishing mortality rate for queen triggerfish known to have migrated to Lang Bank during the study period (n = 14 [12 tracked plus 2 captured]).

4. DISCUSSION

Queen triggerfish displayed persistent and high site fidelity along with relatively small home ranges during non-spawning months. For part of the tagged population, this movement pattern was interrupted briefly by repeated spawning migrations from late fall through the winter to a transient nesting site. High site fidelity is common to many species of reef fish (Popple & Hunte 2005, Meyer et al. 2010, Topping & Szedlmayer 2011) and has also been observed in gray triggerfish (Ingram & Patterson 2001, Herbig & Szedlmayer 2016). Home range sizes vary among reef fish (Green et al. 2015), but the 95% KUD (0.77–6.09 km^2) of queen triggerfish was comparable to that of other similarly sized benthic carnivores (March et al. 2010, Farmer & Ault 2011, Currey et al.

2014, Feeley et al. 2018). High food abundance and the availability of shelter has been hypothesized as the reason for high site fidelity and small resident home ranges for reef fish (Kramer & Chapman 1999, Grüss et al. 2011a, Green et al. 2015). The interface between reef pavement and rhodoliths, along the edge of the reefs near our tagging stations, may provide ideal habitat for queen triggerfish. After the die-off of long-spined sea urchins *Diadema antillarum*, which were once a main food item, queen triggerfish have been reported to feed on a range of organisms including crabs, chitons, polychaetes, and other echinoids (Randall 1967, Reinthal et al. 1984, Turingan et al. 1995). These prey items are likely abundant in the diverse and productive rhodolith beds (James 2000, Berlandi et al. 2012), and we observed queen triggerfish tipping over loose rhodoliths, presumably looking for food. Almost 90% of the movements between stations took place between 06:00 and 18:00 h, suggesting that they are diurnal foragers (Turingan et al. 1995). Queen triggerfish are also reported to prey upon Caribbean spiny lobsters *Panulirus argus* (Weiss et al. 2006), which we observed in the small ledges and crevices in the adjacent reef pavement. These small spaces may also provide nighttime shelters

for queen triggerfish. Although it is possible that the sharp decrease in movement among stations at night is a result of fish moving outside of the range of acoustic array, we did not observe any consistent movements either away from or towards their COA during crepuscular hours. The close proximity of foraging grounds and sheltering areas likely explains the limited movement patterns of the fish during non-spawning months.

The queen triggerfish within BIRNM appeared to exhibit a partial migration strategy, in which both resident and migratory contingents exist within the population (Kerr & Secor 2012). In the migratory contingent, fish with typical high site fidelity migrated to Lang Bank several times from November until March around the full moon. *In situ* observation of queen triggerfish nests at Lang Bank (R. Nemeth unpubl. data) suggests that these movements represent spawning migrations. Furthermore, an examination of queen triggerfish gonads by Hernández et al. (2019) in St. Croix indicated a potential spawning season from November to August, with the highest proportion of spawning-capable females in February.

Hernández et al. (2019) also found that spawning activity was associated with the full moon, but their sampling design did not allow them to determine the specific timing. The correlation of migration with the lunar cycle, and in particular, with the full moon, is common among a large number of Caribbean reef fishes (Colin 1992, Starr et al. 2007, Heyman & Kjerfve 2008, Schärer et al. 2012, Feeley et al. 2018). In the USVI, cubera snapper *Lutjanus cyanopterus*, dog snapper *L. jocu*, Nassau grouper *Epinephelus striatus*, red hind *E. guttatus*, and yellowfin grouper *Mycteroperca venenosa* have all exhibited peak spawning activity directly following a full moon (Kadison et al. 2006, Nemeth et al. 2007, Rowell et al. 2015, Biggs & Nemeth 2016). Interestingly, all of the spawning migrations reported above have been for fish with a broadcast spawning reproduction strategy. In contrast, Balistidae spawn in pairs and deposit demersal eggs that are guarded by either a single or both parents and typically hatch during the first evening or within 24 h (Fricke 1980, Lobel & Johannes 1980, Kawase 2002, Simmons & Szedlmayer 2012, Clark et al. 2015). Despite this difference in reproductive strategy, queen triggerfish also time their spawning migrations with the full moon. Similar to other reef fishes, they make multiple spawning migrations each year (Kobara et al. 2013). We recorded 1 individual making 4 migrations to Lang Bank, but the mode for all fish was 3 migrations per year. This is similar to the estimate by Hernández et al. (2019) that female

queen triggerfish could spawn 4–5 times a year. In both the 2015/16 and 2016/17 spawning seasons, December, January, and February appeared to be the most active months for our tagged fish at Lang Bank, with few detections in November and March. The monthly and lunar timing of peak migration and spawning of queen triggerfish matches very closely with the red hind (*E. guttatus*) and seem to aggregate adjacent to red hind spawning sites, but in deeper sand and rubble habitats suitable for nest building (Nemeth et al. 2007, Kadison et al. 2009).

Migrating queen triggerfish appear to have a distinct pathway along the northern edge of the reef, and the majority of fish arrive at Lang Bank in the same area at the same time during each migration. Their migratory swimming speeds (1.98 km h^{-1}) are similar to measurements made from acoustic telemetry for other reef fish during migrations. These include coral trout *Plectropomus leopardus* (0.66 km h^{-1}, Zeller 1998), mutton snapper *L. analis* (2.2 km h^{-1}, Feeley et al. 2018), Nassau grouper (1.69–1.96 km h^{-1}, Starr et al. 2007, Rowell et al. 2015, Stump et al. 2017), and yellowfin grouper (2.03 km h^{-1}, Rowell et al. 2015). The 2 fish that migrated from the northwest region of BIRNM also had a very distinct pathway through BIRNM in which certain stations were passed at the same time of day, within a few hours, on repeated migrations. Distinct migratory corridors have been noted for other reef species (Mazeroll & Montgomery 1998, Rhodes et al. 2012, Biggs & Nemeth 2016). The knowledge of predictable movement patterns can be exploited by fishers to increase their efficiency (Claro et al. 2001, Sadovy de Mitcheson & Erisman 2012). However, this knowledge can also be beneficial if incorporated into spatial management (Erisman et al. 2017).

A number of individuals that were consistently tracked were not detected at Lang Bank during the spawning season. Three possible explanations are: (1) not all tagged fish were sexually mature; (2) not all tagged fish that migrated to Lang Bank were detected; and (3) Lang Bank is not the only nesting site for queen triggerfish that reside in BIRNM. All of our fish were above the size at 50% sexual maturity reported by Hernández et al. (2019) in St. Croix. However, those authors found that 100% sexual maturity for females did not occur until 35.1–37.5 cm FL. This was close to the size of our largest fish (38.0 cm), and thus it is probable that some of our tagged fish were immature females. The presence of immature females in our study would help explain the lack of migrations for some individuals. We also know that at least 2 tagged fish, which were caught

by a local fisherman, had made the migration to Lang Bank but were not detected by our acoustic array. The spatial extent of the nesting grounds at Lang Bank is unknown, and given the limited number of receivers at Lang Bank and their relatively small detection range, it is highly likely that other fish also had made the migration but were undetected. It is also unlikely that Lang Bank is the only queen triggerfish nesting site on the St. Croix shelf. Within BIRNM, we found 5 fish that were only detected at a station (BUIS_54) near their COAs during the late fall and early winter. The timing of detections and the temporal movement patterns of these fish were not significantly different from those of fish that underwent spawning migrations to Lang Bank. We believe that the area around this station represents a local nesting site and that the fish that visited this area during the spawning season make up a resident contingent of queen triggerfish that do not migrate outside the BIRNM to spawn. The location of Stn BUIS_54 in the northwest corner of the reef tract is close to a significant depth drop-off that has been considered a possible reef spawning aggregation site for other species (Weber & Brown 2009, Kobara et al. 2013). Furthermore, the positions of the other receivers and the frequency of detections for some fish make it unlikely that queen triggerfish were using this area as a pathway for a longer migration. In addition to the fish that were only detected at Stn BUIS_54 during the spawning season, 7 other fish were also detected at the station during the spawning season; however, since the area was part of their home range, it was not possible to definitively classify those detections as spawning related. Interestingly, no fish that were tagged in the northeast region of BIRNM migrated to the west through our array during the spawning season. The distance from the northeast region to Stn BUIS_54 is roughly 6 km, which is half the distance to Lang Bank. Instead of migrating west, it is possible that there is also a local nesting site in the northwest region of BIRNM that was either not covered by our receivers or was near a station that was encompassed by their home ranges and could not be separated from daily detections.

An important aspect of determining residency and home range sizes is the accuracy of an acoustic telemetry array. Range tests revealed highly variable detection probabilities across 6 receivers in our array during typical weather conditions in St. Croix. These results are similar to other acoustic studies on tropical reefs in the USVI where environmental factors such as depth, current, bottom topography, and temperature all influence the detection of acoustic signals

(Selby et al. 2016, Jossart et al. 2017). The predicted distance (107 m) at a 50% detection probability is similar to extensive work done by Selby et al. (2016) within the same BIRNM array (58% detection probability at 100 m) and that of Kendall et al. (2016) in St. John, USVI (50% detection probability at 125 m). Detection ranges can also have diurnal and seasonal variations which we were not able to incorporate into our study due to a lack of standardized controls (Payne et al. 2010, Mathies et al. 2014). Variation in detection ranges has the potential to introduce a bias into the analysis or cause the misinterpretation of results (Payne et al. 2010). The increase of fish movements during daylight hours, which we have associated with foraging behavior, has the potential to be an artifact of differences in detection rates. However, Selby et al. (2016) looked at temporal changes in detection rate within the same array in BIRNM and found mixed results; at one station, detections decreased at night, at another they increased, and at 2 stations they were the same. They concluded that the temporal variability in detection range may not be uniform across BIRNM. Thus, we believe that on average, detection probabilities across the BIRNM array are similar during the day and night and that the increase in movement during the day was genuine.

Fisheries management strives for sustainable harvest of fish stocks through size, effort, and catch limits while simultaneously protecting vulnerable life stages and essential habitats (Botsford et al. 1997). In regions where harvest control rules are weak to non-existent, additional protection through no-take marine reserves can be beneficial (Lauck et al. 1998, Hilborn et al. 2004, Ault et al. 2013). However, for marine reserves to work, closed areas must match with spatial distributions and movement patterns of fish (Kramer & Chapman 1999, Cornejo-Donoso et al. 2017, Weeks et al. 2017). The discovery of both a resident and migratory contingent of queen triggerfish has interesting implications for their management throughout their range and is very beneficial for the population around St. Croix. Partial migratory populations have been described for a number of fish (Chapman et al. 2012a,b), and as more studies take advantage of new technologies to conduct long-term monitoring of fish, the number of species reported to use this tactic may increase (Papastamatiou et al. 2013, Espinoza et al. 2016, Reid et al. 2018). In St. Croix, the large BIRNM no-take reserve (20 km^2) and the Lang Bank seasonal closed area together provide a comprehensive level of protection potential for queen triggerfish if there is adequate enforcement of spatial regulations and compliance by fishers (Ken-

dall et al. 2017). Migratory queen triggerfish with home ranges within BIRNM are potentially only exposed to fishing pressure along their migration pathway to Lang Bank and in the spawning months prior to and after the December 1 to February 28 closure. The migration between BIRNM and Lang Bank appears to be direct for a majority of individuals and constitutes a minimal amount of time exposed to fishing mortality, since most fish arrive at Lang Bank within 6 h. However, migratory queen triggerfish may make multiple migrations each year, and fish traps, which are commonly used to capture queen triggerfish, are often placed along this pathway. During our study period, 1 out of 12 fish that migrated to Lang Bank did not return to its COA, which could indicate fishing mortality. In addition, 2 of our original 60 tagged fish were caught by a local fisherman in Lang Bank during spawning months but after the seasonal closure was lifted. The capture of these fish highlights the potential risks encountered by queen triggerfish that migrate outside of BIRNM to a known spawning site. Combined, the capture of these 2 fish and the potential capture of the tracked fish that was not detected after leaving Lang Bank represents a 21% fishing mortality rate over 2 yr for the fish known to have left BIRNM (n = 14), but only a 5% fishing mortality rate for the entire tagged BIRNM population.

In contrast to the migratory spawners, a majority of the queen triggerfish that we tagged remained within BIRNM during the duration of the study. Some of these fish may have been immature, but others likely used local nesting sites to reproduce. Little is known of the pelagic larval phase of queen triggerfish post hatch, but increment analysis of 70 otoliths collected in April from newly settled juveniles in Panama revealed that these fish were between 66 and 86 d old (Robertson 1988). Recruitment patterns in St. Croix are likely driven by wake flow eddies created as the northward circulation of the Caribbean Sea comes in contact with the island (Chérubin & Garavelli 2016). The creation of these eddies, which could influence the local retention of recruits, is seasonally variable, and it is unclear how the conditions during the winter months would affect the local retention of queen triggerfish from various spawning sites (Chérubin & Garavelli 2016). It is possible that the larvae of resident queen triggerfish that spawn in BIRNM settle outside of the reserve boundaries and provide an important source of recruits for the fishery. Thus, the protection of mature fish within BIRNM is key to supporting a sustainable local fishery.

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