Broad-scale acoustic telemetry reveals long-distance movements and large home ranges for invasive lionfish on Atlantic coral reefs

Stephanie J. Green[1,*], Jordan K. Matley[2], D. Elizabeth Smith[3], Bernard Castillo II[3], John L. Akins[4,5], Richard S. Nemeth[6], Clayton Pollock[7], Kynoch Reale-Munroe[3]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2R3, Canada
[2]Department of Aquatic Resources, St. Francis Xavier University, Antigonish, NS B2G 2W5, Canada
[3]College of Science & Mathematics, University of the Virgin Islands, RR1 Box 10 000, St. Croix, USVI 00850
[4]Reef Environmental Education Foundation, Key Largo, Florida 33037, USA
[5]Phillip and Patricia Frost Museum of Science, Miami, Florida 33132, USA
[6]Center for Marine and Environmental Studies, University of the Virgin Islands, 2 John Brewers Bay, St. Thomas, USVI 00802
[7]National Parks Service, Buck Island Reef National Monument, Christiansted, St. Croix, USVI 008020-4611

ABSTRACT: Tracking studies for invasive lionfish (*Pterois volitans* and *P. miles*) in the Western Atlantic can provide key information on habitat use to inform population control, but to date have likely underestimated home range size and movement due to constrained spatial and temporal scales. We tracked 35 acoustically tagged lionfish for >1 yr (March 2018–May 2019) within a 35 km^2 acoustic array in Buck Island Reef National Monument, St. Croix, US Virgin Islands (an area 10× larger than previous studies). Tracking lionfish at this scale revealed that home range size is 3–20 times larger than previously estimated and varies more than 8-fold across individuals (~48 000–379 000 m^2; average: 101 000 m^2), with estimates insensitive to assumptions about potential mortality for low-movement individuals. Lionfish move far greater distances than previously reported, with 37% of fish traveling >1 km from the initial tagging site toward deeper habitats, and 1 individual moving ~10 km during a 10 d period. Movement rates, home range size, and maximum distance traveled were not related to lionfish size (18–35 cm total length) or lunar phase. Lionfish movement was lowest at night and greatest during crepuscular periods, with fish acceleration (m s^{-2}) increasing with water temperature during these times. Our results help reconcile observed patterns of rapid recolonization following lionfish removal, and suggest complex drivers likely result in highly variable patterns of movement for similarly sized fish occupying the same habitat. Culling areas ≥ the average lionfish home range size identified here (i.e. ~10 ha) or habitat patches isolated by ≥ ~180 m (radius of average home range) may minimize subsequent recolonization. If the shallow–deep long-distance movements observed here are unidirectional, mesophotic habitats may require culling at relatively greater frequencies to counteract ongoing migration.

KEY WORDS: Animal movement · Home range size · Habitat use · Acoustic telemetry · Invasive species · Population control · Marine conservation

1. INTRODUCTION

Understanding patterns and drivers of animal movement is a fundamental pursuit in ecology with important conservation and management implications (Börger et al. 2008, van Beest et al. 2011). In particular, information on rates and patterns of movement can inform habitat conservation plans for populations of imperiled species (Hays et al. 2019), and guide population control and management activities for non-native species (Lennox et al. 2016). The invasion of Indo-Pacific lionfish (*Pterois volitans* and

P. miles) into coastal marine habitats in the Tropical Western Atlantic Ocean and Caribbean Sea represents a conservation issue for which information on the species' movement patterns and home range size is urgently needed to inform ongoing management. Lionfish represent the first successful introduction of marine fish from the Western Pacific Ocean to Atlantic waters (Whitfield et al. 2002, Sutherland et al. 2010), and were first reported in the Atlantic in the early 1980s, possibly as a result of aquarium releases (Semmens et al. 2004). By 2010, lionfish were established along the eastern coast of the USA throughout the Northern Caribbean region (Schofield 2010). Since then, the invasion has expanded to include the Gulf of Mexico and Southern Caribbean to the northern coast of South America (Schofield & Akins 2019, USGS 2019), with the rate and degree of spread greater than documented before in any marine system (Côté et al. 2013).

At high densities, invasive lionfish have detrimental ecological effects on coral reef ecosystems, highlighting the need for ongoing, targeted population management (reviews of the issue by Côté et al. 2013, Hixon et al. 2016, Côté & Smith 2018). Numerous studies have highlighted the localized effects of predation by lionfish on the recruitment, survival, biomass, and diversity of native fish species at high densities (e.g. Green et al. 2014, Albins 2015, Benkwitt 2015), as well as effects of competition with lionfish on the growth, behavior, and distribution of native reef predators (e.g. Albins 2013, Raymond et al. 2015). There are also concerns for the long-term effects of the invasion on key ecological services provided by impacted native taxa as well as on commercially important species (e.g. Lesser & Slattery 2011, Chagaris et al. 2017). To reduce local densities of lionfish and alleviate ecological effects on invaded habitats, culling programs (in the form of manual removal of the fish from invaded habitats using spears and nets, and increasingly via traps) are underway across the invaded region (Green & Grosholz 2021). While some work has assessed the frequency and timing of culling to maintain lionfish abundances below levels predicted to cause negative effects (e.g. Green et al. 2017, Kyne et al. 2020), relatively little work has focused on identifying the location and spatial scales at which culling is most effective. Information on patterns and drivers of lionfish movement in invaded habitats would help to identify the scale and frequency of culling required to meet management targets for suppression.

Previous studies of lionfish habitat use and movement have varied greatly in detection methods and

Table 1. Literature describing lionfish movement in terms of home range sizes and maximum distance traveled. Studies show variability in both home range size and maximum distance traveled by lionfish. USVI: US Virgin Islands

Location	Fish tagged (n)	Method	Study area (km²)	Study duration (d)	Home range (m²)	Maximum distance traveled (m)	Reference
St. Croix, USVI	35	Acoustic telemetry	35	2–244	48 373–379 163	129–4680	This study
Northern Gulf of Mexico	20	Acoustic telemetry	3.5	2–223	158–4051	2000	Dahl & Patterson (2020)
Florida Keys	14	Acoustic telemetry	4 sites ranging from 120 to 400 m in diameter	5–141	360–18812 (mean ± SE 3802 ± 1620)	24–116 (mean daily distance)	McCallister et al. (2018)
210 Rock, North Carolina	25	Acoustic telemetry	0.408 (estimated)	4–175	Estimated 1963–126000	<150 (daily)	Bacheler et al. (2015)
Eleuthera, Bahamas	79	Mark re-sighting	2	49	20–1340 (mean ± SD 552 ± 436.5)	1350	Tamburello & Côté (2015)
Loxahatchee River Estuary, Florida	55	Mark–recapture	60 (estimated)	56 ± 44 (mean total time at liberty)	28 m (mean linear range)	420 (at liberty)	Jud & Layman (2012)

sample sizes (Table 1), but taken together, they suggest the species exhibits high site fidelity (Jud & Layman 2012, Bacheler et al. 2015, Tamburello & Côté 2015, McCallister et al. 2018, Dahl & Patterson 2020). Tamburello & Côté (2015) estimated the average lionfish home range size to be 552 m^2 for 79 lionfish fitted with external visual streamer tags in the Bahamas tracked via daytime re-sighting over 7 wk across coral reef habitats distributed within a 2 km^2 area (Table 1). Bacheler et al. (2015) inferred lionfish home range to be between 1963 and 125 663 m^2 from detections of 25 acoustically tagged fish collected over 5 winter months from 9 receivers spaced ~300 m apart in coastal habitats off North Carolina, USA (Table 1). McCallister et al. (2018) estimated average home range size to be 3979 ± 1599 m^2 (mean ± 95% kernel utilization distribution [UD]) for 14 acoustically tagged lionfish tracked for up to 4 mo over 4 sites covering a <300 m diameter area in the Florida Keys (Table 1). Most recently, Dahl & Patterson (2020) estimated home range size to be between 159 and 4051 m^2 for 20 acoustically tagged fish tracked up to 9 mo across a 3.5 km^2 array of the Gulf Coast of Florida (Table 1).

Small home range sizes reported by these studies suggest that culling programs could be highly effective at controlling lionfish locally, with little movement of adult fish (i.e. post-settlement) from adjacent reef sites. However, high rates of recolonization have been reported in studies of lionfish removal on reefs that are larger than the majority of home range estimates (i.e. 2500 m^2; Green et al. 2015; Table 1) and spaced apart at distances greater than traveled by most lionfish (i.e. >500 m; Smith et al. 2017; Table 1). Moreover, allometric scaling relationships between marine fish body size and home range also suggest that large adult lionfish (≥1000 g mass) might have home range sizes in the range of ~150 000 m^2 (Tamburello & Côté 2015), which is above the upper limit of range size estimated from previous work. These observations suggest that the restricted spatial and temporal scale of previous work on lionfish movement, presumably due to logistical constraints, may underestimate home range sizes and movements across the seascape. In particular, studies that take place over small spatial scales are more likely to underestimate home range as individuals that move 'out of bounds' are excluded from analysis. Likewise, studies that take place over short temporal scales have a reduced likelihood that observations are taking place across the range of environmental factors and conditions that influence movement across the seascape, especially if the focal species undergoes shifts in habitat occupancy as a result of environmen-tal drivers (e.g. temperature, seasons, lunar phases) and biological processes (e.g. across ontogeny).

Here, we present a full year of tracking invasive lionfish using acoustic telemetry in Buck Island Reef National Monument (BIRNM) in the US Virgin Islands, covering 35 km^2 of coastal marine habitat. The scale and duration of the study should give a more complete picture of the range of variation in annual habitat use by this important invasive species. Tracking invasive lionfish across a full set of annual seasons and at a range of body size classes also allowed us to test several hypotheses about potential drivers of lionfish home range size and movement patterns.

First, studies suggest that the extent of a home range is set by the body size of the individual (Minns 1995), with home range estimates increasing significantly across fish species of increasing body size (Woolnough et al. 2009). We therefore hypothesized that lionfish body size influences movement, with larger lionfish using larger home ranges and traveling greater distances during the study period.

Second, many reef fishes, such as parrotfish and groupers, align reproductive behaviors with full moon phases and in some cases seek out particular habitats for spawning (Bolden 2000, Hamilton et al. 2008, Nemeth 2012, Rhodes et al. 2012). If the timing and location of lionfish reproduction coincides with lunar cycles, we hypothesized that lionfish would likely be more active (i.e. traveling greater distances) and show directional movement (i.e. towards particular locations) during particular lunar phases.

Third, studies of lionfish foraging behavior report periods of intense activity centered around crepuscular (dawn and dusk) periods, with periods of relative inactivity during day and night (Green et al. 2011, Cure et al. 2012). We hypothesized that rates of movement for lionfish in BIRNM will follow these diel cycles, but that this pattern may be mediated by variation in seasonal water temperature, with rates of activity lower in seasons where cooler temperatures result in lower metabolic demands.

Finally, acoustically tagged animals repeatedly detected on one or few adjacent receivers are typically assumed to represent mortality events (Klinard & Matley 2020). However, this method is not likely appropriate for lionfish because visual tagging studies have indicated that a single individual could be highly resident (i.e. <20 m movement from tagging site) for more than 6 mo (Akins et al. 2014). We therefore explored assumptions about mortality (vs. resident behavior) for individuals with highly localized detections on estimates of average home range size, rate of movement, and maximum distance traveled

for the species. We hypothesized that while maximum estimates of home range size and rates of movement will be unaffected by assumptions about mortality, average estimates for these properties may be higher when fish that might otherwise be assumed to represent mortality events (but could instead represent sedentary individuals) are included in our analyses.

2. MATERIALS AND METHODS

2.1. Study area

The study took place in BIRNM off of St. Croix, USVI (17° 47′ 11″ N, 64° 37′ 14″ W). The monument includes a relatively small (712 000 m²) and un-inhabited island approximately 2.4 km north of St. Croix, as well as 76.2 km² of coral reef, colonized pavement, seagrass, and sandy-bottom habitats where fishing, including for lionfish, is prohibited (Pittman et al. 2008). VR2W acoustic receivers (InnovaSea, formerly Vemco, 69 kHz) were installed throughout the park in depths between 5 and 60 m (N = 131 receivers) and covered an area of approximately 35 km². Lionfish collection and tagging were restricted to habitats near the center of the monument within a cluster of closely spaced receivers (N = 36) covering an area ~0.25 km² and located at depths of 5–8 m along the fringing reef and 12–18 m in patch reef areas south of Buck Island with a minimum of 100 m and maximum of 125 m between each (Fig. 1). The closely spaced cluster of receivers was designed as a fine-scale positioning system (FPS; formerly Vemco Positioning System) and located within the center of the broader array of 95 receivers covering 35 km². Range testing conducted by Selby et al. (2016) within this cluster of receivers (where tagging occurred) and throughout the broader array area indicated that a receiver–transmitter distance of 100 m resulted in 58.2% of transmissions being detected across all habitats.

2.2. Fish collection and tagging

In March 2018, 40 (of 42 sighted) lionfish were captured and tagged underwater by SCUBA divers from patch (n = 30) and continuous fringing reef (n = 10) habitats south of Buck Island (Fig. 1) following methods adapted from Akins et al. (2014). Captured fish were held, unanesthetized, by divers in clear vinyl
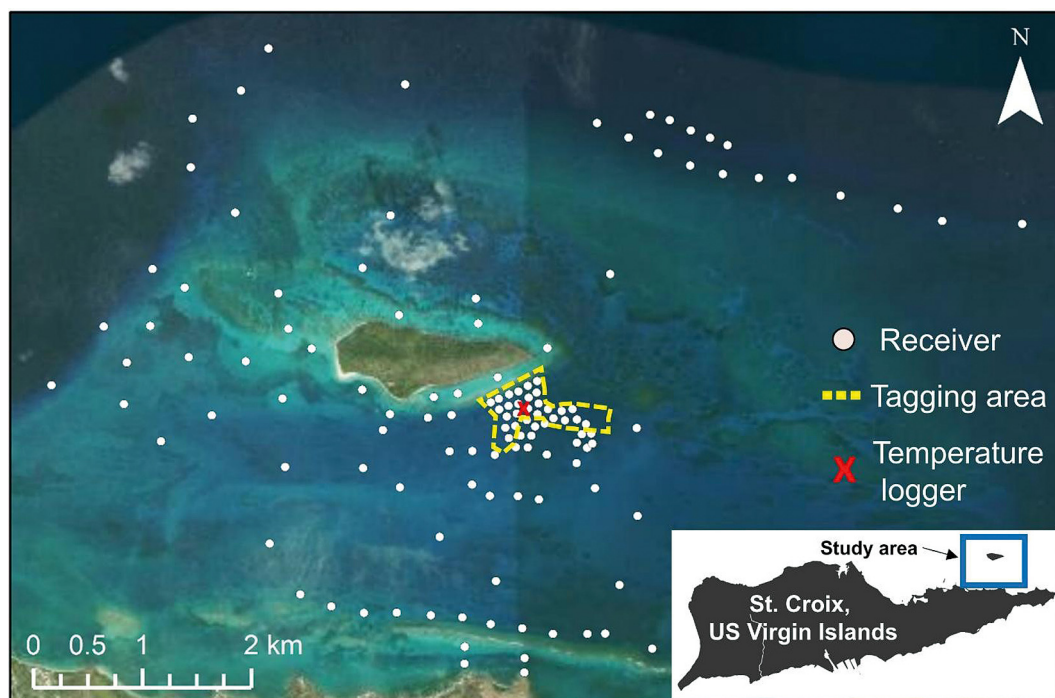

Fig. 1. Receiver array (N = 131) within the Buck Island Reef National Monument (BIRNM) off the northeast coast of St. Croix, US Virgin Islands (USVI; inset). Six receivers deployed ~20 km to the northeast of the tagging area did not record any detections and were omitted from the map

nets, and fish total length (TL, ±1 mm) was recorded. Fish >18 cm (n = 35) were implanted with an internal acoustic transmitter (InnovaSea, V9-2h, 110–250 s delay, 492 d battery life, 9 mm × 43 mm, 3.3 g in water) and fitted with an external streamer tag (Floy, FTSL-73). Seven transmitters (InnovaSea, V9AP-2h, 170–270 s delay, 365 d battery life, 9 mm × 48 mm, 3.6 g in water) also included acceleration and pressure sensors to provide additional movement information. Since V9AP tags were larger and heavier, they were implanted in the larger lionfish (>24 cm). Fish <18 cm TL (n = 5) were tagged exclusively with an external streamer tag. Acoustic transmitters were placed within the body cavity through a 1–2 cm incision anterior of the vent. The incision was closed with dissolvable sutures (Ethicon, 18 inches [45 cm]). To insert the external streamer tag, the fish was flipped dorsal side up, and was pierced through the upper portion of the caudal peduncle with an 18-gauge, 1.5 inch intravenous needle as a guide. The streamer tag was then inserted through the opening of the needle and pulled through the fish when the needle was removed. Each streamer tag was brightly colored and labeled to allow for rapid identification and contained a unique identification number. Surgeries took 7–9 min per fish. Immediately following surgery, each fish was returned by divers using hand nets to the exact site of capture and briefly observed for any adverse reactions to surgery. All fish appeared to make a successful recovery, as characterized by recovery and maintenance of buoyancy and active swimming within 2 min following release. Fish collections and surgeries were conducted under University of the Virgin Islands Institutional Animal Care and Use Committee permit 949107 and National Park Service research permits BUIS-00072 and BUIS-2016-SCI-0004.

2.3. Data analysis

2.3.1. Data filtering

Archived transmitter detection data were downloaded from all receivers in May 2018, November 2018, and May 2019 with VUE software (version 2.6.0). All following data organization and analyses were conducted using R version 3.6.1 (R Core Team 2019). Raw detections underwent several filtering steps prior to data analysis. First, false detections resulting in unknown tag IDs were removed from the dataset, as well as potential false detections arising from erroneous detections matching IDs of tagged

fish. Instances of the latter were identified as individual detections occurring remotely in space or time without demonstrating any sequential movement pathways (e.g. a singular detection observed several kms away from where the individual was routinely detected during the same period). Second, data from the first 24 h after tagging were removed from spatial analyses, unless stated otherwise, to allow for a recovery period from surgery where behavior may be unduly affected (Fig. 2). Third, data from individuals were excluded if they were detected on less than 8 unique days after tagging to avoid interpreting data from under-represented lionfish (Table 2, Fig. 2). Finally, we removed detection data from individuals that were associated with either a dropped tag or mortality event based on acceleration sensor values that were stagnant near zero through time. Of the 7 individuals tagged with sensor-enabled transmitters (i.e. tracking acceleration and depth), data from 5 individuals were dropped from analysis due to consistent acceleration values <0.1 m s^{-2} (i.e. at ~0 m s^{-2}) and limited depth variation, suggesting that these fish either expelled their tags, were consumed and the transmitter was dropped within detection range of receivers, or died by other means (Table 2, Fig. 2; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m673p117_supp.pdf).

2.3.2. Mortality scenarios

Initially, we considered that animals repeatedly detected on one or few adjacent receivers represented mortality events (Klinard & Matley 2020). However, this method is not likely appropriate for lionfish because visual tagging studies have indicated that a single individual could be resident on the same patch reef (i.e. <20 m movement from the tagging site) for more than 6 mo (Akins et al. 2014). Thus, individuals may be highly resident to small areas relative to the detection range of receivers, causing difficulty in distinguishing between ejected tags/mortalities and sedentary individuals. Because it was not always possible to confirm the fate of individuals in these instances, i.e. distinguish between a mortality event or highly resident behavior (hereafter referred to as 'highly restricted detections'), we investigated 2 scenarios (high survival and low survival) throughout this study, representing detection data from different numbers of individuals included in calculations of movement and home range. The high survival scenario represented the assumption that highly restricted detections originated from liv-

ing individuals with low movement rates, with all detection data (after initial filtering steps described above) incorporated in analyses. Conversely, the low survival scenario assumed that highly restricted detections were from ejected tags or dead individuals, with data from these individuals excluded from analyses (see next paragraph).

We identified highly restricted detections by first calculating the maximum distance a stationary tag could be detected in the array using detections from the 5 individuals equipped with both acoustic transmitters and acceleration sensors for which mortality events had occurred based on acceleration values consistently <0.1 m s^{-2}, which was estimated to be ~175 m. We then used this distance when evaluating transmitter location data at a weekly scale for all tagged fish. Specifically, during weeks when each animal's transmitter was detected on receivers greater than 175 m apart, the animal was deemed to be alive during that period (and thus included in all analyses; Fig. 2); alternatively, if the transmitter was only detected on receivers less than 175 m apart (i.e. a highly restricted detection), the animal was included in the high survival scenario, but excluded from the low survival scenario, due to the possibility of a mortality event (Fig. 2). Since these classifications were conducted weekly, all periods prior to the last week with detections >175 m apart were identified as 'living' and any following highly restricted detections were either incorporated (high survival scenario) or excluded (low survival scenario). We chose the described approach of identifying possible mortality events as opposed to setting distance limits by traditional range testing techniques (e.g. Kessel et al. 2014) because sentinel tags that were deployed within the array, as part of another study objective, were deployed relatively high in the water column. This led to overestimates of detection range when compared with tagged lionfish that remained near the substrate in rugose habitat where detection efficiency was reduced. Consequently, the use of dropped tags was more representative of lionfish locations, and although small shifts due to currents or tide are possi-

ble, the effect was minimal because designations were conducted weekly.

We then conducted all further analyses for both high and low survival scenarios, in order to help us to explore the effect of assumptions about the fate of animals (i.e. mortality events) versus animal behavior (i.e. sedentary habits) on patterns of movement and home range generated from telemetry data (Klinard & Matley 2020). In particular, the high survival scenario may underestimate the average home range size, rate of movement, and distance moved for this species, because fish that have died (and thus are not moving) may be included in the analysis. Conversely, the low survival scenario may overestimate the average home range size, rate of movement, and distance moved if resident fish are erroneously assumed to have died and removed from analyses.
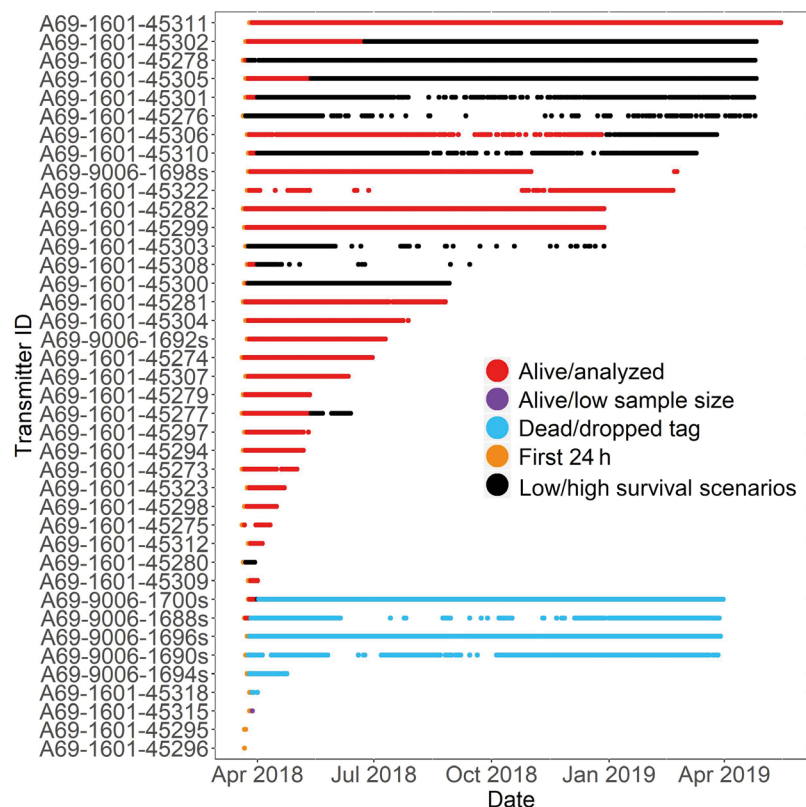

Fig. 2. Detections of acoustically tagged lionfish within the 35 km^2 BIRNM array off St. Croix, USVI, across the study period. Colors represent the various filtering stages applied to detection data prior to analysis of home range and movement. Detections collected for all fish <24 h from tagging (orange), from any evident mortality event based on acceleration sensor data (blue; acceleration <0.1 m s^{-2}), and for fish detected on fewer than 8 d after tagging (purple) were excluded from our analyses. Fish detected >175 m apart within 1 wk (red) were designated as living and were included in all analyses. Weekly detections <175 m apart (black) represented potential mortality events and were excluded in the low survival scenario but included in the high survival scenario of each analysis

Table 2. Summary of tagging, detection, and residency history of each tagged lionfish (denoted by transmitter number) within the Buck Island Reef National Monument array reported for both high and low survival scenarios. Transmitter codes ending in 's' indicate V9AP accelerometer tags. Asterisks (*) indicate individuals that made long-distance movements (>1 km from release site). FR: fringing reef; PR: patch reef; RI: residency index; TL: total length. Blank cells in the 'Low survival scenario' represent fish that were not identified as a possible mortality event, resulting in the same data used in both low and high survival scenarios. Cells with dashes indicate metrics that were not analyzed due to low sample size

Transmitter	Habitat (at release)	TL (cm)	No. detections	No. receivers	High survival scenario						Low survival scenario		
					No. days detected	Detection period (d)	Max distance from release (m)	Detection RI	Tag-life RI	Analyzed?	Possible mortality?	No. days detected	Analyzed?
A69-1601-45311	PR	23.5	138231	49	416	416	3460*	1	0.99	Yes	Yes	93	Yes
A69-1601-45302	FR	19	62585	39	400	400	984	1	0.95	Yes	Yes	51	Yes
A69-1601-45305	PR	27	91634	30	400	400	467	1	0.95	Yes	Yes	4	No
A69-1601-45278	PR	26	135264	29	398	401	263	0.99	0.95	Yes	Yes	9	Yes
A69-1601-45301	PR	19	35370	43	301	398	972	0.76	0.72	Yes	Yes	278	Yes
A69-1601-45306	PR	20	12614	13	287	368	364	0.78	0.68	Yes			
A69-1601-45282	PR	25	108720	43	283	283	2519*	1	0.67	Yes			
A69-1601-45299	PR	19	106666	42	282	282	2224*	1	0.67	Yes			
A69-1601-45310	PR	24	38889	45	275	351	972	0.78	0.65	Yes	Yes	7	No
A69-9006-1698s	PR	28	115154	51	221	336	4725*	0.66	0.61	Yes			
A69-1601-45300	PR	25.5	38291	36	161	161	342	1	0.38	Yes	Yes	3	No
A69-1601-45281	PR	23	61591	51	152	159	4009*	0.96	0.36	Yes			
A69-1601-45276	PR	20.5	4589	25	149	401	333	0.37	0.35	Yes	Yes	0	No
A69-1601-45322	FR	19	7868	38	140	334	511	0.42	0.33	Yes			
A69-1601-45304	PR	19	22112	24	125	128	588	0.98	0.3	Yes			
A69-9006-1692s	PR	26	36118	34	109	109	883	1	0.3	Yes			
A69-1601-45274	PR	21.2	54361	39	102	103	4603*	0.99	0.24	Yes	Yes	2	No
A69-1601-45303	FR	21	2044	18	99	281	409	0.35	0.24	Yes			
A69-1601-45307	PR	21.5	38565	45	80	81	4473*	0.99	0.19	Yes	Yes	54	Yes
A69-1601-45277	PR	23.6	52562	39	79	86	662	0.92	0.19	Yes			
A69-1601-45279	PR	30.3	102889	48	53	53	2476*	1	0.13	Yes			
A69-1601-45294	PR	25.5	53628	38	48	48	2489*	1	0.11	Yes			
A69-1601-45297	PR	22	22067	39	46	51	3880*	0.9	0.11	Yes			
A69-1601-45273	PR	20.5	14826	36	38	44	3098*	0.86	0.09	Yes	Yes	7	No
A69-1601-45308	FR	20	6491	30	34	175	898	0.19	0.08	Yes			
A69-1601-45323	PR	21.5	22615	36	30	30	1617*	1	0.07	Yes			
A69-1601-45298	PR	23	9830	38	25	26	2624*	0.96	0.06	Yes			
A69-1601-45275	PR	21.5	1222	32	14	23	964	0.61	0.03	Yes			
A69-1601-45312	PR	18	1572	12	12	12	470	1	0.03	Yes			
A69-1601-45280	PR	18.2	1086	17	10	10	349	1	0.02	Yes	Yes	0	No
A69-9006-1700s	FR	25.5	10247	32	8	8	893	1	0.02	Yes	Yes	7	No
A69-1601-45309	PR	24.5	7994	30	8	8	726	1	0.02	Yes			
A69-9006-1688s	FR	24	459	33	5	5	–	–	–	No	Yes	5	No
A69-1601-45315	PR	23	599	19	3	3	–	–	–	No	Yes	0	No
A69-1601-45318	FR	20.5	14	4	2	2	–	–	–	No	Yes	0	No
A69-9006-1690s	FR	35	139	11	2	2	–	–	–	No	Yes	2	No
A69-9006-1694s	FR	24.5	408	12	2	2	–	–	–	No	Yes	2	No
A69-9006-1696s	FR	26.5	501	38	2	2	–	–	–	No	Yes	2	No
A69-1601-45295	PR	19	369	30	2	2	–	–	–	No			
A69-1601-45296	PR	25	89	12	1	1	–	–	–	No	Yes	0	No

2.3.3. Residency

For both scenarios (i.e. high survival and low survival) we calculated 2 different residency indices (RIs) to indicate individual presence within the receiver array (i.e. study area) through time. The first, hereafter referred to as the 'detection RI', was defined as the number of unique days with detections (including the release day) divided by the number of days between the first and last detection. The second RI was referred to as the 'tag-life RI' and was calculated as the number of unique days detected divided by either the number of days expected in the battery life of the tag (e.g. 365 d for sensor tags), the number of days in the study period (e.g. the study period was 420 d, i.e. shorter than the battery life of non-sensor tags), or number of days until the tag was deemed dead/dropped, whichever option was shorter in duration. Both indices required at least 2 detections in a day to be considered present to reduce the possible inclusion of false detections (Simpfendorfer et al. 2015). Two RIs were used because they provide different representations of presence within the array; for example, detection RI provides information relating to presence only during the period in which an individual is using areas with receivers, whereas tag-life RI incorporates absence after the animal was last detected within the array area.

2.3.4. Long-distance movements

We evaluated the relationship between lionfish size (TL) and maximum distance moved (i.e. from release location) via linear regression. We also summarized spatial trends in the timing and location of movements for fish that traveled ≥1 km from their release location (considered 'long-distance movement' based on existing knowledge of lionfish movement patterns). These movements were examined qualitatively in relation to time of year and lunar phases to explore the possibility of spawning- (or feeding)-related movement cues tied to moon phase, as for other reef fishes (Nemeth 2009). We calculated speed during these movements based on the sum of distances between the last position before a long-distance movement and the first position in the new area of detection (divided by the sum of durations between the long-distance detections). As the pathway of movement between receivers is unclear, this rate, calculated as a straight line, likely reflects the minimum speed that individuals traveled. This metric was also used to explore possible predation

events of tagged lionfish (i.e. long-distance movements faster than expected for this species).

2.3.5. Rates and drivers of movement

For lionfish detected on 8 or more days at any time following release, we estimated activity levels, quantified as rates of movement. Rates of movement were calculated as the speed ($m s^{-1}$) of movements over the course of at least 1 h when detected consecutively at 10 min intervals (i.e. at least 6 intervals of 10 min had to be included). To calculate speed, we first estimated average location for each fish every 10 min as centers of activity (COAs; Simpfendorfer et al. 2002). COAs are calculated by taking the mean position of all detections from receiver locations during a specified time interval, providing an estimated location during each period which helps account for receivers with overlapping detection ranges (i.e. pseudo-replication from multiple receivers detecting singular transmissions) and drift in receiver clocks. The distances (in m) between each consecutive COA location (every 10 min) were then added together and the sum was divided by the total time and converted to $m s^{-1}$. Acceleration values from the 2 transmitters with acceptable acceleration data (i.e. registering >0.1 $m s^{-2}$, indicative of movement of live fish; Fig. S1 in the Supplement) were averaged each 10 min to compare with rates of movement estimated from COA positions over time, although it should be noted that these metrics represent different aspects of activity (e.g. longer-term speed [rates of movement] vs. shorter-term acceleration).

Next, we created 2 linear mixed effects models (LMMs; i.e. with Gaussian distributions) to determine whether rates of movement were influenced by biological and environmental factors: one model for rate of movement under the low survival scenario and a second model for movement under the high survival scenario. We checked our response data (rates of movement) for each model for normal distribution and homogeneity of residuals prior to analysis, and log-transformed when necessary. We included in each model the following explanatory variables, which were all present in model selection explorations (i.e. present in at least 1 model with the difference in corrected Akaike's information criterion ΔAICc <2): diel period (dawn, day, dusk, night), moon phase (new, waxing, full, waning), capture location (fringing or patch reef), TL of the individual, and water temperature. Dawn and dusk diel periods were defined as the hourly periods on each side of sunrise and sunset, re-

spectively, which were calculated locally using the R package 'maptools' (Bivand & Lewin-Koh 2019). Day and night diel periods consisted of the time post-sunrise/pre-sunset and post-sunset/pre-sunrise, respectively. Rate of movement estimates were only retained for analysis when they occurred fully within a diel period (i.e. not between 2 different diel periods). Moon phases were designated using the R package 'lunar' (Lazaridis 2014). Water temperature was measured hourly within the center of the tagging area (16 m depth; U22-001 HOBO® Water Temp Pro v2; Onset Computer; Fig. 1), and all measurements were averaged during each corresponding period in which rates of movement were estimated. The R package 'nlme' (Pinheiro et al. 2019) was used to run LMMs with transmitter ID as a random variable and a first-order auto-correlation structure built in to account for serially auto-correlated data. Correlation among explanatory variables was tested using variance inflation factors (R package 'car'; Fox & Weisberg 2019), which indicated no issues (i.e. variance inflation factor ≤3). We also included an interaction effect between diel period and water temperature because we predicted temperature may influence rates of movement differentially depending on the activities lionfish conduct (i.e. crepuscular feeding vs. mid-day resting) and after preliminary data exploration indicated it was contributory. We also conducted a similar LMM with the 10 min mean acceleration sensor data (excluding size and habitat because there were only 2 individuals) for comparison. Differences were considered significant when $p < 0.05$.

2.3.6. Home range size

We quantified home ranges by kernel density estimates (KDEs) using the package 'adehabitatHR' (Calenge 2006) for both high and low survival scenarios. The KDE approach was selected over others such as Brownian bridge movement models, which incorporate movement corridors in space use estimates (e.g. Becker et al. 2016), because the majority of receivers were located south of Buck Island in a relatively small area with overlapping detection ranges, negating the utility of movement corridors. The remaining receivers were sparsely arranged over a large area, which also made it difficult to identify pathways between receivers, especially when time differences were large. In general, we found the KDE approach to be more robust to uncertainty in lionfish locations between detections and also more readily comparable to other lionfish studies (e.g. Dahl & Pat-

terson 2020), which typically used the same approach to estimate home range sizes. The locations used for KDEs were estimated from 30 min COAs, which represent the average location where individuals were present every 30 min (Simpfendorfer et al. 2002). We selected UDs at 50 and 95% to represent the core use areas and extent of space use, respectively. We selected a smoothing factor (h) of 50 for UD estimates after fitting different smoothers to visually optimize contour levels (e.g. values that were too high overestimated receiver detection ranges as demonstrated by overlapping with adjacent 'unused' receivers; values that were too low underestimated expected detection ranges and resulted in highly disjointed polygons) as suggested by Calenge (2006). We used a paired t-test to test for differences between the home range size for each individual generated from the high survival and low survival scenarios for 50 and 95% UDs separately. We also constructed separate general linear models (GLMs) for high survival and low survival scenarios to test if the TL (in cm) of lionfish and the number of days each fish was detected (2 explanatory variables) affected home range size as estimated by the size of 50 and 95% UDs separately (response variables). Data were assessed for normality and homoscedasticity as described above. Finally, we plotted UDs to show specific areas used, as well as overlap among individuals.

3. RESULTS

We tracked 35 tagged lionfish ranging in size from 18 to 35 cm TL (23.07 ± 3.62 cm TL; mean ± SD) from 20 March 2018 to 15 May 2019 (14 mo) over an area of approximately 35.6 km² (Table 2, Fig. 2). Fish with V9 tags were 22.1 ± 2.91 cm TL (range = 18–30.3 cm TL) and fish with V9AP tags were 27.1 ± 3.74 cm TL (range = 24–35 cm TL) (Table 1). After initial data filtering, the high survival scenario included 1 417 695 detections from 32 individuals (27 initially tagged on patch reefs and 5 on fringing reefs), and the low survival scenario included 1 005 667 detections from 24 individuals (21 tagged on patch reefs and 3 on fringing reefs; Table 2). The mean (±SD) water temperature within the main receiver cluster was 27.6 ± 0.9°C (range: 26.0–29.4°C)

3.1. Residency and long-distance movements

Lionfish were highly resident within the BIRNM array during their detection periods (i.e. number of days between first and last detection), with a mean

detection RI of 0.86 (SD: 0.23; range: 0.19–1) for the high survival scenario, and with individuals being detected for up to 416 d (Table 2). The mean tag-life RI (i.e. detection days relative to expected duration of tag battery life, study period, or period that the individual was deemed alive) was 0.36 (SD: 0.31; range: 0.02–0.99) for the high survival scenario (Table 2). Nineteen of the 32 individuals (59%) for the high survival scenario remained within the primary tagging area throughout their detection periods, while the remaining 13 fish (41%) moved into other adjacent habitats or made long-distance movements within the BIRNM array.

Maximum distances traveled varied greatly among tagged fish, with 22 individuals (63%) moving <1 km from their tagging locations, while 13 individuals (37%) were detected making long-distance movements >1 km from the main study array to several different locations within the greater BIRNM array (mean ± SD long-distance movement: 3.4 ± 2.3 km; Fig. 3). The maximum distance any fish traveled within the BIRNM array from the location of tagging was ~10 km, which occurred during an 11 d period (Fig. 3; ID 45297). Of the 13 individuals making long-distance movements, 9 individuals traveled up to 3 km after leaving the primary tagging area, 2 traveled between 3 and 5 km, and 2 traveled >5 km (Fig. 3). Long-distance movements occurred in a variety of directions; 6 individuals exhibited westward movements, 2 moved to the southwest, 4 individuals moved to the northeast of the BIRNM array, and 1 traveled to the southeast (Fig. 3). The majority of these movements were towards receiver locations along the insular shelf edge in northern St. Croix

representing mesophotic reef habitats >40 m depth. There was no discernible pattern of drivers for these movements relative to time of year, although almost half of these movements (6 of 13 fish; Fig. 4) occurred during the waning phase of the moon and during summer months (7 of 13 fish from May to September; Fig. 4). Among individuals that made long distance movements (>1 km from tagging site), we estimated maximum average speed to be 0.26 m s^{-1} during a 2 h period (ID 45279), which is within the range observed from visual observations of the species while in transit between habitats (Green et al. 2011). There was no relationship between maximum distance detected from the release location and lionfish size (TL; linear regression: $r^2 = 0.03$, $p = 0.301$).

3.2. Rates and drivers of movement

Tagged lionfish movement speeds averaged ~0.051 m s^{-1} (high survival) and ~0.063 m s^{-1} (low survival; Table 3) across the study period; these rates differed significantly among diel periods (high survival: $F_{3,10741} = 399.4$, $p < 0.001$; low survival: $F_{3,8475} = 426.0$, $p < 0.001$) and were highest during dawn (high: mean ± SD: 0.091 ± 0.047 m s^{-1}, low: 0.098 ± 0.045 m s^{-1}) and dusk (high: 0.074 ± 0.043 m s^{-1}, low: 0.081 ± 0.041 m s^{-1}) compared to day (high: 0.069 ± 0.052 m s^{-1}, low: 0.077 ± 0.053 m s^{-1}) and night (high: 0.052 ± 0.036 m s^{-1}, low: 0.057 ± 0.037 m s^{-1}) in both survival scenarios (Fig. 4). Additionally, temperature interacted with diel periods (high survival: $F_{3,10741} = 40.4$, $p < 0.001$; low survival: $F_{3,8475} = 12.6$, $p < 0.001$), in which rates of movement at night decreased with temperature,
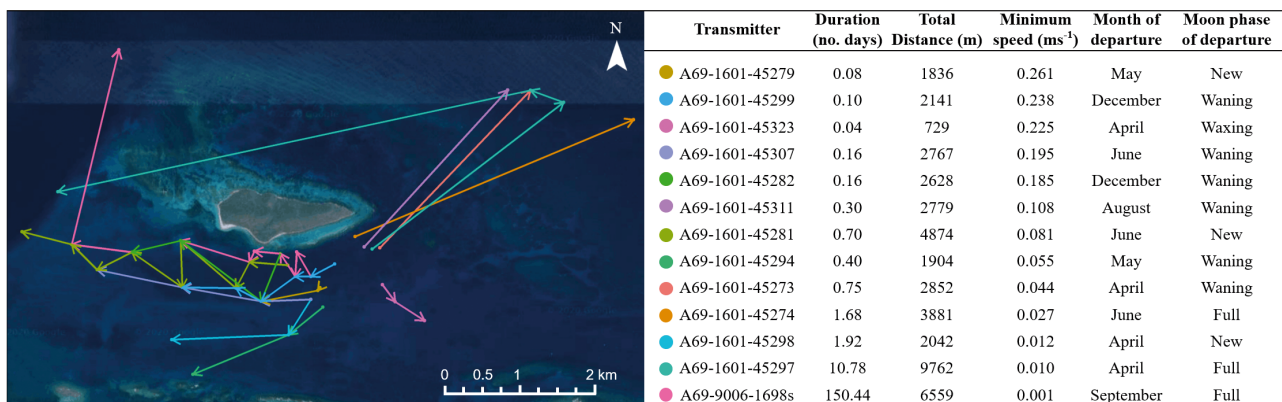

Transmitter	Duration (no. days)	Total Distance (m)	Minimum speed (ms^{-1})	Month of departure	Moon phase of departure
A69-1601-45279	0.08	1836	0.261	May	New
A69-1601-45299	0.10	2141	0.238	December	Waning
A69-1601-45323	0.04	729	0.225	April	Waxing
A69-1601-45307	0.16	2767	0.195	June	Waning
A69-1601-45282	0.16	2628	0.185	December	Waning
A69-1601-45311	0.30	2779	0.108	August	Waning
A69-1601-45281	0.70	4874	0.081	June	New
A69-1601-45294	0.40	1904	0.055	May	Waning
A69-1601-45273	0.75	2852	0.044	April	Waning
A69-1601-45274	1.68	3881	0.027	June	Full
A69-1601-45298	1.92	2042	0.012	April	New
A69-1601-45297	10.78	9762	0.010	April	Full
A69-9006-1698s	150.44	6559	0.001	September	Full

Fig. 3. Summary of long-distance movements (>1 km from location of tagging) by invasive lionfish tracked within the 35 km^2 BIRNM acoustic array off St. Croix, USVI. Arrows indicate the direction of travel, as well as different areas in which individuals were detected during these movements. These data did not include detections on adjacent receivers <200 m for simplification. Minimum speed was calculated based on the sum of distances and durations between each movement segment (i.e. each line/arrow combination)
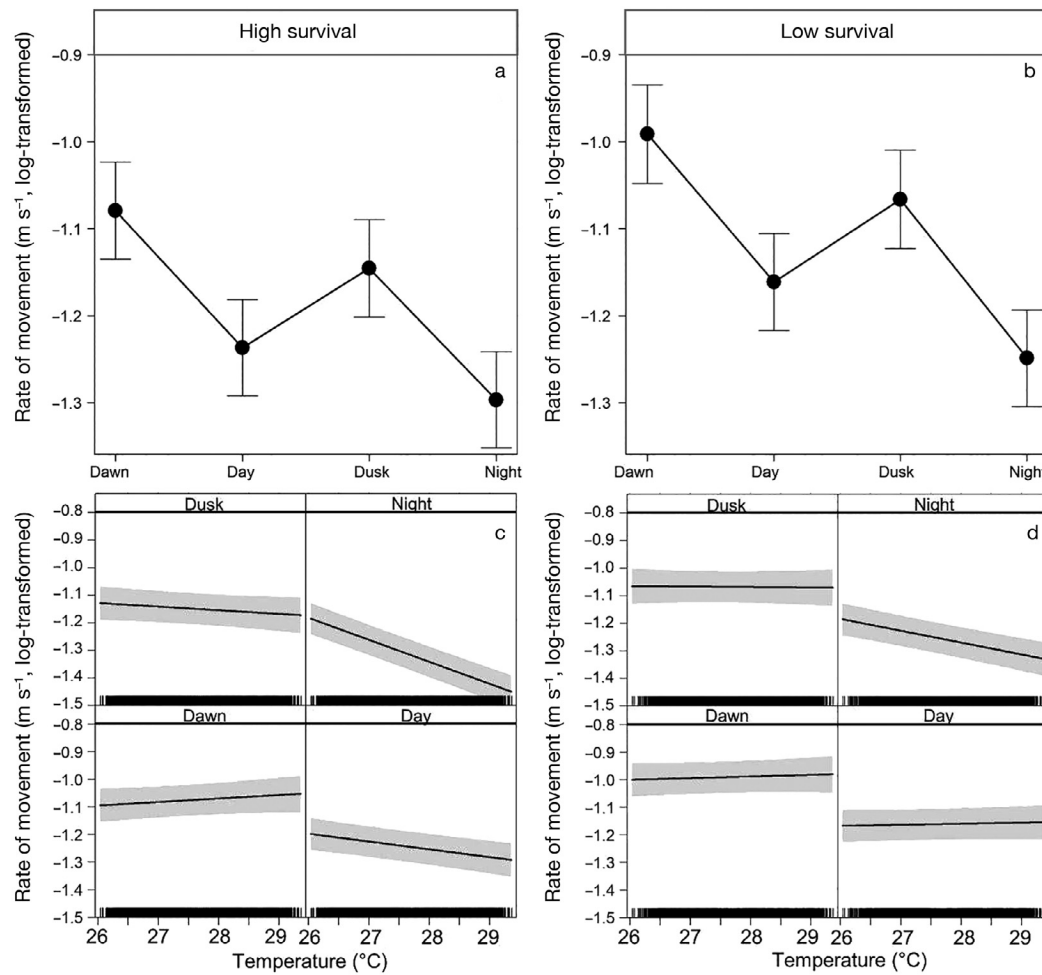
Fig. 4. Effects of (a,b) time of day and (c,d) temperature by time of day on mean rates of movement for high (a,c) and low (b,d) survival scenarios for invasive lionfish tracked within the 35 km² BIRNM acoustic array off St. Croix, USVI. Black lines surrounded by shaded areas (continuous variables) and points with error bars (discrete variables) represent the pointwise 95% confidence band of fitted values based on standard errors, respectively, from LMMs. Vertical lines (rug-plot) above *x*-axis (in c and d) represent observations recorded at different temperatures

whereas other periods typically remained consistent (Fig. 4). While limited to only 2 individuals with sensors, diel acceleration trends were similar to rates of movement identified above (i.e. activity highest at dawn/dusk, lowest at night). Also, night activity levels remained constant across water temperatures, unlike other diel periods in which water temperature was positively associated with acceleration (Fig. S2 in the Supplement). Interestingly, lionfish size, habitat type, and moon phase were not significant drivers of rates of movement ($p > 0.05$; Fig. S3).

3.3. Home range size

Home range size and location varied greatly among lionfish, but was far greater than observed previously,

with home range extent (i.e. 95% UDs) ranging from 48 373 to 379 163 m² and 50 164 to 379 163 m² for the high and low survival scenarios, respectively (Table 1). Mean home range estimates were larger for the low survival scenario (95% UD mean ± SD: 121 512 ± 67 037 m²; 50% UD: 23 848 ± 10 293 m²) relative to the high survival scenario (95% UD mean ± SD: 105 588 ± 66 398 m²; 50% UD: 21 320 ± 10 459 m²; Fig. 5, Table 3); however, estimates for the 2 scenarios were not significantly different from one another (95% UD: $t = 0.59$, df = 24, $p = 0.56$; 50% UD: $t = 0.49$, df = 24, $p = 0.63$). Most individuals remained near where they were tagged and released, as demonstrated by the high overlap in home range in the primary tagging area (e.g. up to 22 individuals within overlapping 95% UDs of high survival scenario; Fig. 6). Estimates of 50 and 95% UD were highly cor-

Table 3. Summary of rates of movement (m s^{-1}) and 50 and 95% home range sizes for individual lionfish reported for both high and low survival scenarios. UD: utilization distribution; COA: center of activity. Metrics for low survival scenarios were not calculated for some individuals (i.e. blank cells) because of low sample size

| Transmitter | Rate of movement | | | | 50% UD (m²) | | | | 95% UD (m²) | |
| | High survival | | Low survival | | High survival | | Low survival | | High UD | Low UD |
	No. consecutive movements	Rate	No. consecutive movements	Rate	No. COA locations	UD	No. COA locations	UD		
A69-1601-45311	1555	0.087	1555	0.087	14041	61669	14041	61669	379163	379163
A69-1601-45302	1310	0.020	383	0.050	16407	11435	3923	13326	52647	66516
A69-1601-45305	1710	0.009	129	0.083	16370	11448	1251	20383	53905	87098
A69-1601-45278	2019	0.007			17083	11245			49646	
A69-1601-45301	400	0.043	42	0.086	5666	13435	365	15073	64734	92219
A69-1601-45306	195	0.029	195	0.029	4017	13835	3433	14448	65512	66868
A69-1601-45282	1283	0.056	1283	0.056	9840	15831	9840	15831	82228	82228
A69-1601-45299	1213	0.060	1213	0.060	10531	25406	10531	25406	117322	117322
A69-1601-45310	430	0.064			5673	14944			65094	
A69-9006-1698s	904	0.041	904	0.041	7661	36619	7661	36619	211269	211269
A69-1601-45300	801	0.010			6964	11028			48373	
A69-1601-45281	469	0.071	469	0.071	3971	30537	3971	30537	188651	188651
A69-1601-45276	40	0.055			1574	21690			81009	
A69-1601-45322	56	0.048	56	0.048	1690	14111	1690	14111	68629	68629
A69-1601-45304	264	0.054	264	0.054	3177	17251	3177	17251	74378	74378
A69-9006-1692s	432	0.039	432	0.039	4232	30810	4232	30810	182679	182679
A69-1601-45274	529	0.075	529	0.075	4017	28380	4017	28380	125835	125835
A69-1601-45303	13	0.030			1091	12683			57931	
A69-1601-45307	376	0.095	376	0.095	3076	25323	3076	25323	125911	125911
A69-1601-45277	343	0.060	337	0.060	2926	29144	2439	21950	147554	107770
A69-1601-45279	304	0.086	304	0.086	2427	19535	2427	19535	86980	86980
A69-1601-45294	296	0.081	296	0.081	2084	27527	2084	27527	117299	117299
A69-1601-45297	230	0.082	230	0.082	1597	22161	1597	22161	99526	99526
A69-1601-45273	125	0.076	125	0.076	1025	33302	1025	33302	163916	163916
A69-1601-45308	111	0.049			966	12835			62171	
A69-1601-45323	159	0.085	159	0.085	1301	22793	1301	22793	118580	118580
A69-1601-45298	108	0.088	108	0.088	942	25013	942	25013	111363	111363
A69-1601-45275	5	0.000	5	0.000	191	10960	191	10960	50164	50164
A69-1601-45312	24	0.014	24	0.014	335	22601	335	22601	108430	108430
A69-1601-45280	13	0.047			93	18769			76599	
A69-9006-1700s	40	0.046			270	13310			61367	
A69-1601-45309	47	0.070	47	0.070	310	16615	358	17343	79980	83495
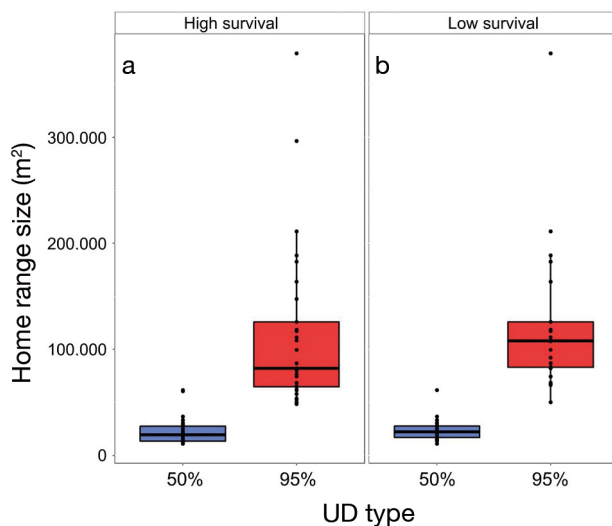
related in both low and high survival scenarios (>0.97 Pearson correlation coefficient); we therefore only tested for differences in 95% UD as a function of lionfish size and the time (days) spent within the array. For the high survival scenario, neither size nor time in the array significantly explained differences in 95%

Fig. 5. Summaries of home range size (50 and 95% utilization distributions [UDs]) reported for (a) high and (b) low lionfish survival scenarios. Black points represent estimates for each individual. The distal ends of boxplot whiskers represent the smallest and largest values that are 1.5 times the inter-quartile range, the hinges (i.e. ends of boxes) represent the 25th and 75th percentiles, and the inner horizontal line represents the median. There were no statistically significant differences between the 2 scenarios for both UD levels
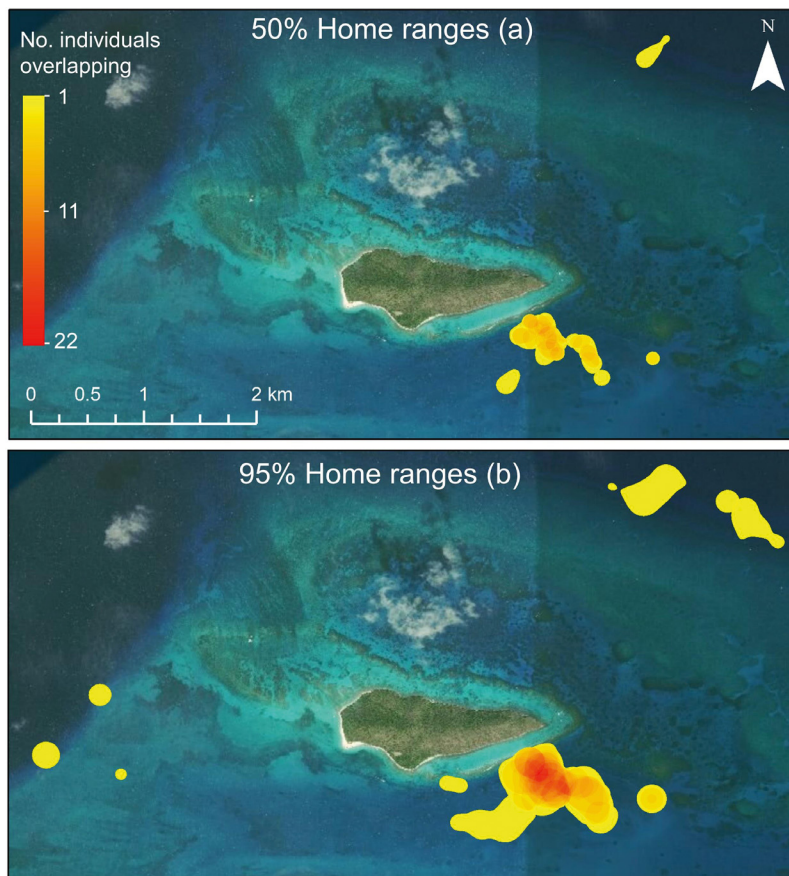
Fig. 6. Estimated (a) 50% and (b) 95% home ranges (utilization distributions) for individual lionfish tracked within BIRNM off St. Croix, USVI, based on the high survival scenario. The color gradient represents the number of individuals with overlapping home ranges

UD size, whereas the size of 95% UDs was positively associated with a greater number of days detected in the array for the low survival scenario ($F_{1,24}$ = 2.519, p = 0.020; Fig. S4 in the Supplement).

4. DISCUSSION

Our study reveals that while home range size and maximum distance traveled by invasive lionfish can vary greatly among individuals, it is at least 3 times larger than the largest home range previously reported for the species (here, 0.379 versus 0.126 km² of Bacheler et al. 2015; Table 1). Moreover, we found that lionfish travel greater distances than previously recorded. For example, Dahl & Patterson (2020) found that the maximum distance traveled by lionfish across reef environments did not exceed 2 km (the spatial limit of their array), while we documented ~40% of lionfish traveling >1 km from their initial capture location during periods up to

150 d, and with a maximum cumulative distance of approximately 10 km. Our results suggest that lionfish movement has been largely underestimated by past studies, likely due to constraints on the area over which previous visual tagging and acoustic studies have taken place, and the duration over which detections have been collected. The presence of a large acoustic array in BIRNM covering more than 35 km² allowed us to complete the largest-scale examination of lionfish movement to date. Indeed, the full scale of a species' movement is only revealed by studying an area that exceeds its home range size over a period that captures important ontogenetic or seasonal shifts in habitat use, indicating the importance of maintaining large acoustic arrays. A growing number of telemetry studies are taking advantage of this array to study the movement ecology of species with varied life histories and trophic roles, including sea turtles, sharks, and barracuda. We suggest that future studies that incorporate native predators with similar ecologies to lionfish (e.g. groupers and moray eels) could shed additional light on the extent of spatial overlap and potential mechanisms governing competition with this invasive taxon.

Several features of our data and analyses increase our confidence that the long-distance movements we observed are attributed to lionfish movement, as opposed to movements by lionfish predators (i.e. a tagged fish being ingested and tag retained by predator). First, there is no evidence that average speeds (interpreted as the minimum distance traveled) during the movements exceeded estimates of lionfish swimming speed from previous work (e.g. Green et al. 2011). Second, we expect that transmitters would pass through the digestive system of a predator or be regurgitated relatively quickly. For example, Brunnschweiler (2009) estimated retention of hand-fed tags (placed inside a dead fish) larger than those used in this study to be between 0 and 17 d (mean ~8 d) in 7 bull sharks *Carcharinus leucas*. Further, complete evacuation of food items from the stomach is estimated to take <41 h in lemon sharks *Negaprion brevirostris* (Wetherbee et al. 1990). Yet following the

long-distance movements observed in our study, we observed subsequent movements that extended past a 10 d period for at least 6 individuals, indicating that these tags were not stationary/expelled and were likely not within the gut of a predator. As described above, Dahl & Patterson (2020) observed movements from tagged lionfish up to 2 km from tagging locations which showed no patterns of being predated. Incorporating transmitters with additional predation sensors (Weinz et al. 2020) would allow future studies to concretely distinguish between migration and predation events.

Van Beest et al. (2011) suggested factors that affect intraspecific home range variation included body mass, age, reproductive status, resource availability (e.g. for foraging), and temperature. Typically, home range size depends upon body mass as a function of metabolic rate, with larger individuals maintaining larger home ranges (Ofstad et al. 2016). In this study, fish size (TL) was not related to home range size or maximum distance traveled. However, our transmitters were limited to lionfish >18 cm TL. Reproductive size for Caribbean lionfish is 10 cm TL for males and 18.9–19 cm TL for females (Morris 2009, Gardner et al. 2015). Given that all lionfish in our study were above this size, we may not have captured general differences in movement and home range between reproductive and immature portions of the population.

However, it is possible that the long-distance movements we observed are linked to individuals engaging in reproductive behavior, which can be sustained throughout the year in regions (such as St. Croix) when environmental conditions are favorable (Morris & Whitfield 2009, Morris et al. 2011). In particular, cues for and constraints on reproduction related to variation in water temperature and day length across seasons are greatly dampened in lower latitude regions like the US Virgin Islands compared with sub-tropical reef environments occupied by the species in the Bahamas, Northern Gulf of Mexico, and US Atlantic coast. Reduced environmental variation (e.g. in terms of seawater temperature; range: 26.0–29.4°C) in our study region may explain why we did not observe clear seasonal or lunar patterns relative to long-distance movements. Alternatively, it may be that the venomous dorsal spines of lionfish afford protection to size classes that would otherwise be more vulnerable to predation, reducing the potential for ontogenetic shifts in home range size seen in other reef fish species. Additional studies of movement involving similar large-scale, long-term tracking in higher latitude regions with greater seasonal environmental variation and in the species' home

ranges, and advances in acoustic tagging technology facilitating inclusion of smaller individuals in tracking studies, would help us to begin testing these alternative hypotheses.

Variation in home range sizes and long-distance movements among lionfish may be partially explained by differences in the quality and structure of the habitat types used (Nemtzov 1997, Saïd et al. 2009). In other species, habitat quality has been shown to directly affect the size of an animal's home range, due to factors such as availability and competition for food resources (e.g. McLoughlin et al. 2000, Schradin et al. 2010). Approximately 60% of the fish tracked in this study were only detected in the main tagging area, and those that did move into adjacent habitats or made long-distance movements within the BIRNM array (Fig. 3) typically did so after several months of high residency. The continued use of this relatively large area (~0.5 km^2), often with high spatial overlap (e.g. up to 22 individuals, 95% UDs), suggests that adequate resources were available. Nevertheless, many individuals were not detected throughout the battery life of the transmitters, indicating either movements to areas outside the range of the receivers or mortality/predation events (see below). Therefore, there are likely additional drivers influencing habitat use in this study.

The majority of lionfish were tagged within patch reefs, which likely represent smaller pockets of high-quality habitat (i.e. access to prey and shelter from predators) surrounded by unsuitable sandy habitat. Compared to continuous reef habitat, individuals inhabiting patch reefs may need to travel greater distances to access resources over time as they become limiting (Tamburello & Côté 2015). The relatively low number of lionfish tagged on the fringing reef habitat with sufficient data to be included in the study (3 and 5 fish within low and high survival scenarios, respectively) compared to patch reefs (21 and 27 fish, respectively) precluded a thorough comparison of movement between the 2 groups. Nevertheless, home ranges (50% UD, high survival) and rates of movement (high survival) were typically larger on patch reefs (mean values, respectively: 22 884 m^2 and 0.055 m s^{-1}) compared to continuous reefs (mean values, respectively: 12 874 m^2 and 0.039 m s^{-1}) supporting the possibility of limited resources on patch reefs.

Goodbody-Gringley et al. (2019) found a strong positive correlation, albeit influenced by water temperature, between lionfish density on mesophotic reefs and prey fish density and biomass. As a result, movement patterns may be driven more by prey abundance than competition and may also help explain why

some individuals made long-distance movements towards the insular shelf and mesophotic reefs around BIRNM. Lionfish making these long-distance journeys either west or east around Buck Island to the insular shelf edge (Fig. 3) would pass through a variety of habitat types including seagrass meadows interspersed with sandy barrens, patch reef, hardbottom habitat dominated by large sponges, and high-profile patch reef. Further work is needed to quantify fine-scale habitat selection in this study area, as well as drivers of habitat connectivity and the mechanisms influencing large-scale movements.

Despite uncertainty in specific drivers of home range size and long-distance movements, there were clear patterns influencing lionfish activity. Rates of movement and acceleration estimates were highest during dawn and dusk periods. These periods often afford the greatest access to food (i.e. increased foraging activity) or may represent transitioning periods between resting and foraging locations (Green et al. 2011, Benkwitt 2016). McCallister et al. (2018) similarly found that acoustically tracked lionfish in the Florida Keys were most active during crepuscular periods. Lionfish are relatively inactive unless foraging (Green et al. 2011, Cure et al. 2012); therefore, increased activity during these periods is most likely due to peak foraging behavior. Diurnal and nocturnal locations are often different (McCallister et al. 2018, Dahl & Patterson 2020), indicating that fish may transition between habitats, as a result of foraging bouts.

Water temperature also influenced activity patterns in this study, as demonstrated by its interaction with diel periods. Night activity trends relative to water temperature were often distinct from other diel periods; specifically, there appeared to be no influence of temperature on acceleration estimates and a negative influence of temperature on rates of movement. We hypothesize that these differences reflect the relative inactivity of lionfish during the night, resulting in less thermally coupled behaviors (Seymour 1982). By contrast, during periods when lionfish were more active (dawn, day, dusk), water temperature influenced physiological mechanisms and energetic budgeting of lionfish to a greater extent (e.g. Scott et al. 2017), leading to, for example, a positive relationship between acceleration estimates and water temperatures. More research investigating fine-scale space

use patterns is needed to further understand the specific cues driving activity patterns.

We incorporated the possibility of tagged lionfish suffering a mortality event (or shed tag) via the low survival scenario to explore whether differences in interpretation of behavior resulted. This is a common concern in acoustic telemetry research, since ~50% of recent studies did not consider the possibility of mortality, although it is estimated to occur on average in at least 11% of tagged individuals (Klinard & Matley 2020). Despite shorter detection periods for several individuals in the low survival scenario, comparisons of home range, rates of movement, and long-distance movements between scenarios typically only differed by small amounts (Table 4). This is not surprising given that individuals demonstrating restricted movements were consistently resident in the same area (i.e. high survival detections/individuals were not more mobile than low survival detections/individuals). We assumed that the high survival scenario would provide lower estimates of home range size and rates of movement since highly sedentary transmitters (potential shed tags or dead individuals) were included in the movement analyses. This trend was consistent with our prediction, but the differences were limited due to the reason explained above. Again, it is not clear which scenario best represented the detection history of living individuals, due to the resident nature of at least part of the lionfish population (Tamburello & Côté 2015, Dahl & Patterson 2020), as well as the relatively high detection range in the study area. However, estimates of high and low survival scenarios for more mobile species might produce

Table 4. Comparison of high and low survival scenarios for the home range and movement metrics quantified in this study; ns: not statistically significant at $\alpha = 0.05$. ROM: rate of movement; UD: utilization distribution

Variable	High survival	Low survival	High vs. Low result
Number of fish	32	23	H > L
Number of detections	1417695	1005667	H > L
Mean residency index	0.86 ± 0.23	0.92 ± 0.16	H < L
Mean rate of movement (m s^{-1})	0.051 ± 0.027	0.063 ± 0.025	H < L
Effect of diel period on ROM	p < 0.001	p < 0.001	H = L
Effect of temperature on ROM	p < 0.001	p < 0.001	H = L
50% UD Home range (min; m^2)	10959	10959	H = L
50% UD Home range (max; m^2)	61668	61668	H = L
50% UD home range (mean; m^2)	21320	23848	H < L, ns
95% UD Home range (min; m^2)	48373	50164	H < L
95% UD Home range (max; m^2)	379163	379163	H = L
95% UD Home range (mean; m^2)	105588	121512	H < L, ns
Effect of fish size on 95% UD	ns	ns	H = L
Effect of no. days on 95% UD	ns	p < 0.02	H < L

more distinct differences among survival scenarios. Regardless, these estimates provide lower and upper ranges in values for ecologically relevant behavioral metrics for future comparison, and do not bias findings of long-distance movements.

We suggest that lionfish control programs could benefit substantially from accounting for maximum lionfish home range size, movement rates, and patterns of directional movement in identifying the location and spatial coverage of target areas for culling. In particular, high rates of recolonization have been reported in studies of lionfish removal on reefs that are larger than the majority of previous home range estimates (i.e. 2500 m^2; Green et al. 2015) and spaced apart at distances greater than early estimates of movement for the species (i.e. >500 m; Smith et al. 2017). Our study shows that lionfish home range is highly variable, but likely far greater than estimated previously, confirming that local management (in terms of culling) is likely to be affected by recolonization from adjacent reefs. Thus, considering the spatial arrangement and size of focal habitats could assist in limiting recolonization following population control, for example by targeting culling activities over priority areas that are least the size of the mean home range estimated in our study (i.e. 101 000 m^2 or ~10 ha), or at sites that are isolated from other habitats by the radius of circular home range of this size (i.e. ~180 m). The relatively common occurrence of long-distance dispersal by mature lionfish of up to 10 km within a 10 d period also highlights additional management obstacles, as new habitats appear to be readily explored by at least a portion of individuals occupying a region. Most long-distance movements by lionfish in this study represent transit from shallow reef tagging areas to deeper sites at the edge of the continental shelf and mesophotic reefs in BIRNM, with no evidence of individuals moving back into shallow areas over the 14 mo study period. While we are not able to ascertain whether fish also move from deep habitats into shallow areas, net movement from deep to shallow would suggest that culling frequency may need to be even higher to sufficiently suppress densities in these areas as a result of migration from other habitats.

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