

# Movement of invasive adult lionfish *Pterois volitans* using telemetry: importance of controls to estimate and explain variable detection probabilities

Nathan M. Bachele<sup>1,\*</sup>, Paula E. Whitfield<sup>2</sup>, Roldan C. Muñoz<sup>1</sup>, Brett B. Harrison<sup>2</sup>,  
Craig A. Harms<sup>3</sup>, Christine A. Buckel<sup>2</sup>

<sup>1</sup>Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

<sup>2</sup>Center for Coastal Fisheries and Habitat Research, NOAA, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

<sup>3</sup>Department of Clinical Sciences and Center for Marine Sciences and Technology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

**ABSTRACT:** The Indo-Pacific lionfish *Pterois volitans* has invaded western Atlantic Ocean coastal habitats over the past 2 decades and has the potential to cause major ecological changes in reef fish communities. While many aspects of lionfish ecology in their invaded range have been examined, there is a paucity of information on movements of lionfish, particularly adults. We surgically implanted ultrasonic transmitters into 25 lionfish at a natural hard bottom area off North Carolina (USA) in December 2008 and February 2009, and used an array of remote underwater receivers to monitor movements in the study area for up to 6 mo. We also affixed a control transmitter in the study area to assess changes in transmitter detection rate as a function of multiple variables, and used a generalized additive model to show that the control transmitter detection rate declined with time, increasing water temperature, and increasing wave period. Despite variable detection probabilities, we found that telemetered lionfish remaining in the study area displayed high site fidelity to areas no broader than 400 m in diameter; daily movements were nearly always <150 m. By estimating variable detection rates of transmitters and lionfish movements, we provided information that can be useful in understanding the spatial scale of lionfish impact and developing management or mitigation strategies for this invasive species.

**KEY WORDS:** Indo-Pacific lionfish · Invasive species · Acoustic tagging · Range test · Ultrasonic transmitter · Telemetry · Movements · Receiver array

—Resale or republication not permitted without written consent of the publisher—

## INTRODUCTION

The Indo-Pacific lionfish *Pterois volitans* is native to the Pacific and Indian Oceans, but is now a permanent resident of the western north Atlantic following their introduction into Florida coastal waters in the 1980s (Whitfield et al. 2002, Schofield 2009, Betancur-R. et al. 2011). They rapidly invaded the western Atlantic (Betancur-R. et al. 2011), and their overwintering distribution now extends from Cape Hatteras, North Carolina, southward throughout the Bahamas,

the Caribbean Sea, and the Gulf of Mexico (Kimball et al. 2004, Morris & Whitfield 2009, Schofield 2009, 2010). Lionfish have become a primary predator in many ecosystems in the western Atlantic, preying upon and causing significant population declines in numerous small fish species (Morris & Akins 2009, Muñoz et al. 2011, Green et al. 2012), and having the potential to substantially change western Atlantic reef ecosystems (Arias-González et al. 2011, Lesser & Slattery 2011). The increasing ecological threat posed by this rapidly expanding invader was identified as a

global conservation issue in 2011 (Sutherland et al. 2011), and has prompted local efforts to manage and control lionfish populations (Akins 2012).

While many aspects of lionfish ecology (e.g. their larval ecology, feeding behavior, and genetic structure) have been elucidated in the western Atlantic, there is a paucity of information on movements of lionfish. Movements of all life stages, however, must be described in order to fully understand the breadth of distribution, the population structure, and the connectivity of populations of invasive species over time (Turchin 1998). The success of control or eradication programs is also strongly dependent upon knowing how individuals move across habitats following their initial recruitment (Lapointe et al. 2010, Vrieze et al. 2011). Juvenile and adult lionfish are generally considered to have high site fidelity; for instance, Jud & Layman (2012) showed that 74 % of tagged juvenile lionfish moved <10 m from their release location in a Florida estuary over a time scale of weeks to a few months. Moreover, only 2 out of 55 juvenile lionfish were recaptured at >100 m from their tagging sites (Jud & Layman 2012). Lionfish have also displayed low movement rates during short-term foraging studies conducted over hours to days (Albins & Hixon 2008, Côté & Maljkovi 2010, Green et al. 2011); we are unaware of any studies examining adult lionfish movements over longer time scales.

Acoustic telemetry has become the leading technique for studying movement patterns of freshwater, estuarine, and marine fish species (Lucas & Baras 2000, Bacheler et al. 2009c, Topping & Szedlmayer 2011), and could be useful in examining lionfish movements. Telemetry can be used to quantify various aspects of a species' ecology such as site fidelity, home range size, migratory pathways and timing, and habitat preferences (White & Garrott 1990), while also being useful in understanding the efficacy of marine reserves (Farmer & Ault 2011) and quantifying natural and fishing mortality rates (Bacheler et al. 2009b, Topping & Szedlmayer 2013). Tracking movements of fish using automated acoustic receiver arrays has become particularly common, with receivers often being deployed in overlapping arrays throughout an area of interest (Heupel et al. 2006) so that accurate fish positions can be determined (Farmer et al. 2013). Fish positional data may be biased if receivers become fouled (Heupel et al. 2008), the spatial structure of the habitat is complex (Giacalone et al. 2005, Farmer et al. 2013), water moves due to tides (How & de Lestang 2012, Mathies et al. 2014), or water temperature varies (How & de Lestang 2012). These studies and others highlight the danger in interpreting fish

positions from receiver arrays in the absence of adequate controls (Payne et al. 2010).

Here, we used ultrasonic telemetry paired with an underwater receiver array and a control transmitter to make inferences about the movements of lionfish at a natural hard bottom reef in North Carolina, USA. The objectives of this study were twofold. First, we determined the detection rate of a control transmitter in our study area during the time when telemetered lionfish were present, in order to relate that detection rate to environmental conditions. Second, we quantified variable transmitter detection rates in order to quantify movements of telemetered adult lionfish at a natural hard bottom reef in North Carolina near the northern limit of their overwintering range (Kimball et al. 2004). By determining variable detection rates, we were able to more accurately interpret lionfish movements, thus providing information that can be useful in developing management or control strategies for this invasive species.

## MATERIALS AND METHODS

### Study site

Our acoustic telemetry study was conducted at a temperate hard bottom reef known as '210 Rock', which is ~30 km south of Cape Lookout, North Carolina (Fig. 1). 210 Rock is an expansive area of calcium carbonate rock outcroppings and ledges located at ~30 m depth, with bathymetric relief of 0.5–3.0 m (Fig. 2). The rocky structure provides substrate for a wide variety of sessile invertebrate and algal species (Parker & Dixon 1998). Most reef fish associate with ledges and other reef habitats along the rock–sand interface due to the increased complexity of undercuts and overhangs (Whitfield et al. 2014). Lionfish were first reported at 210 Rock in 2004, but had been seen in nearby deeper water since 2000 (Whitfield et al. 2002, 2007). This site was chosen based on high year-round lionfish densities, the presence of an accurate and detailed bathymetric map, and known winter bottom water temperatures (Parker & Dixon 1998, Whitfield et al. 2014).

### Receiver and transmitter range tests

Vemco® V9-2H coded transmitters (9 mm diameter, 29 mm long, 4.7 g weight in air, operated on a frequency of 69 kHz, power output of 151 Db) were selected for lionfish in this study. Transmitters were

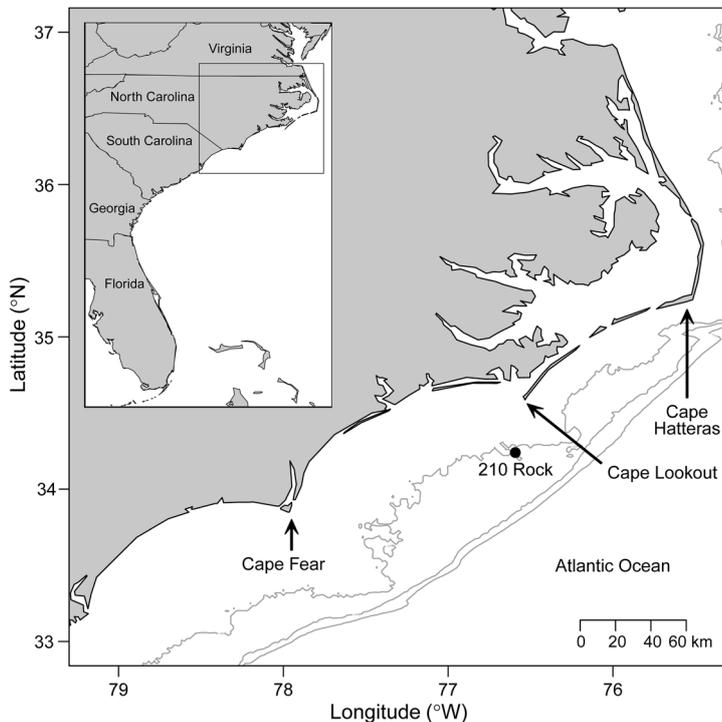


Fig. 1. Study area and location of 210 Rock (North Carolina) where lionfish *Pterois volitans* were tagged in 2008 – 2009. Bathymetry isobaths are 30, 50, and 100 m

programmed to transmit an acoustic ping approximately every 240 s (range: 170 – 310 s) and had a theoretical battery life of 348 d.

Two range tests were conducted within the study area to determine the optimal distance between receivers. The first range test (7 November 2008) used 2 Vemco VR2 receivers and 3 transmitters deployed in a single horizontal pathway for 4 d to estimate detection distances every 25 m between 50 and 150 m. The second range test used 2 transmitters at distances of 300 and 400 m away from a single receiver in a straight line for 4 h on 8 December 2008.

#### Receiver array and control transmitter

We deployed 9 VR2 receivers at 210 Rock on 8 December 2008 based on the methods of Domeier (2005), using sandbags as weights and subsurface floats to keep the receivers upright on a line. Receivers were attached to a line ~3 m above the bottom, with each hydrophone pointing upwards. Based on the results of range tests (see 'Results'), receivers were spaced ~300 m from one another so that nearly all of the hard bottom habitat in our study area could be acoustically monitored (Fig. 2). Acoustic detections by receivers in the array then provide information about the movements of lionfish throughout the study system. Also, a control V9-2H coded transmitter was placed in a fine mesh bag and attached to the mooring line of receiver #4 at ~1 m above the seafloor and 2 m below the receiver, on 8 December 2008. Three recei-

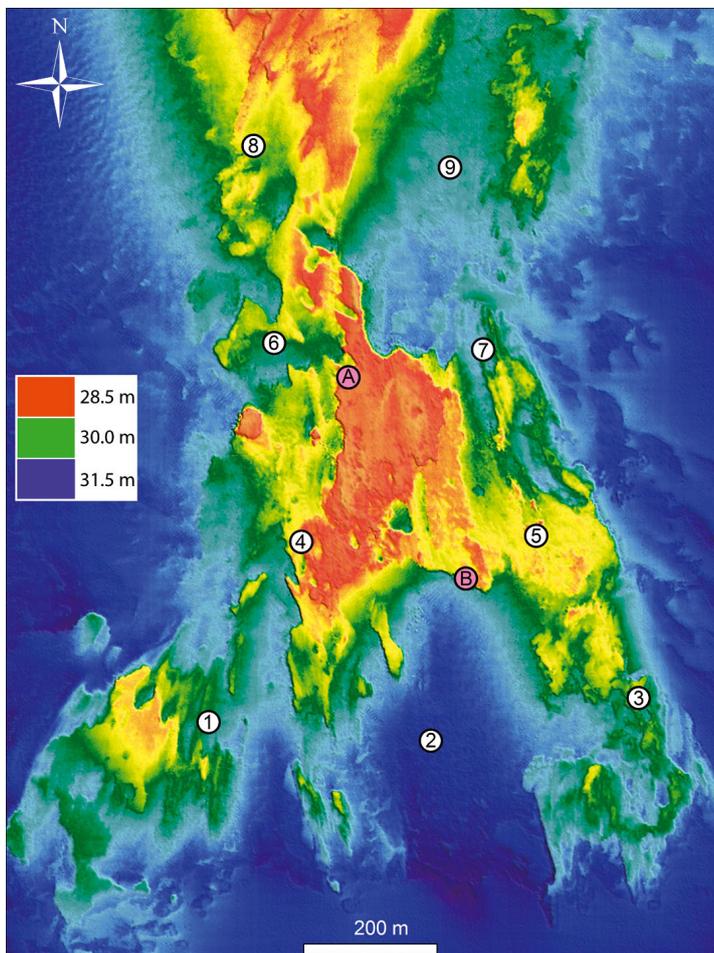


Fig. 2. Multibeam sonar bathymetry image of the study area (210 Rock) in North Carolina. Key shows water depth. White circles: locations of submersible receivers 1 to 9; pink circles: the 2 lionfish *Pterois volitans* tagging and release locations (A fish were tagged on 4 December 2008 and B fish were tagged on 6 February 2009). Receivers 2 and 9 were lost during the course of the study, all remaining receivers were replaced with clean receivers on 31 March 2009, and the control transmitter was attached to the line of receiver #4

vers were replaced on 31 March 2009 and 3 others on 1 June 2009 for cleaning; the control transmitter was not cleaned because the mesh bag and the transmitter had not accumulated any obvious biofouling.

### Transmitter retention and post-surgical survival experiment

A laboratory experiment was conducted before the field study in order to estimate transmitter retention and post-surgical survival. In early October 2008, 4 lionfish were captured in North Carolina by SCUBA divers using a hand net; the fish were then released into a 700 L flow-through tank in the laboratory. These 4 fish were fed twice per week and their behavior was frequently observed. On 16 October 2008, a 'dummy' V9 transmitter of the exact size and shape as those used in the field study was surgically implanted into each lionfish (using methods described below). Lionfish total lengths (mean = 240 mm; range = 195–305 mm) and weights (mean = 230 g; range = 102–456 g) were similar to those of fish tagged in the field study (described below). The tag weight to body weight ratio in air ranged from 1.0 to 4.6%. Transmitter retention and survival were monitored for the subsequent 9 mo.

### Field surgeries

Two groups of lionfish had transmitters surgically implanted at 210 Rock: 15 lionfish on 4 December 2008 (hereafter referred to as 'A' fish) and 10 lionfish on 6 February 2009 ('B' fish) (Fig. 2). All individuals were captured by SCUBA divers using hand nets and transferred to mesh bags underwater, and then slowly (9 m min<sup>-1</sup>) brought to the surface. Lionfish were placed in large coolers filled with ambient seawater until surgical implantation. Each fish was injected intramuscularly with 6 mg oxytetracycline (Liquamycin® LA-200®, 200 mg ml<sup>-1</sup>, Pfizer Animal Health) immediately after being brought on board for pre-surgery prophylaxis (Harms 2005) and to mark otoliths in case of future recapture. The oxytetracycline dose was back-calculated to approximate actual weight (when the boat was sufficiently stable to attempt weighing) or weight estimated from length (P. Whitfield, unpubl. data), and was a median of 15 mg kg<sup>-1</sup> (range: 7–47 mg kg<sup>-1</sup>). This dose range fell within the rather wide range of published oxytetracycline intramuscular doses in fish based on pharmacokinetic data (7–100 mg kg<sup>-1</sup>; Carpenter & Marion 2013).

Decompression of the swim bladder was achieved (when deemed necessary) by venting with a fresh sterile hypodermic needle (20 ga, 2.5 cm). All V9 transmitters were gas sterilized at a local hospital using ethylene oxide prior to implantation, and all surgical instruments were autoclaved, with a fresh pack used for each fish. Lionfish were anesthetized using 105–125 mg l<sup>-1</sup> tricaine methanesulfonate dissolved in seawater, with anesthesia water recirculating over the gills during surgery. Anesthetic concentration was adjusted between batches of fish to optimize induction and recovery times. Bottom water temperature was 16.1°C for A fish and 14.2°C for B fish. The surface water temperature (the starting point for holding tanks and anesthesia) was 17.2°C for A fish and 15.3°C for B fish, but the recirculating anesthesia water dropped to as low as 10.6°C at one point for B fish in cold air temperatures. Recirculating anesthesia water was changed multiple times to keep temperatures from dropping further.

The surgical site was prepared with a single swipe of dilute chlorhexidine (Nolvasan®, Fort Dodge Animal Health) over the incision site with a sterile cotton-tipped applicator, and the surgery field was covered with a sheet of cling-type plastic wrap as a surgery drape. Transmitters were inserted into the abdominal cavity of lionfish through a 1 cm incision that was made 3 cm caudal to the pelvic girdle on the ventral midline. The incision was closed with a 4-0 polydioxanone suture (PDS®II, Ethicon), using 4 throws of a simple continuous or interrupted pattern. After initial uses, each of 3 sutures was rotated through a disinfectant bath of dilute chlorhexidine and used on every third fish (to allow at least 15 min of contact time for disinfection between fish) until expended. Fresh nitrile examination gloves or sterile latex surgery gloves were donned for each surgery. A triple antibiotic ointment was applied to each incision site after the surgery. All fish were held in on board tanks until full recovery, after which they were brought back down to the bottom and released by a SCUBA diver. Tagged fish were released at the locations where they were captured: site A for fish tagged on 4 December 2008 and site B for those tagged on 6 February 2009 (Fig. 2).

### Transmitter detections

We first examined the patterns of transmitter detections in the study system over the course of this study. In our first analysis, we summed the total number of detections for all receivers within each day for A fish, B fish, and the control transmitter separately,

and plotted these detections along with *in situ* bottom temperatures as measured by a bottom temperature sensor (HOBO® water temperature Pro v2 data logger, Onset). Next, to determine whether there were diel differences in receiver detections (Stocks et al. 2014), we summed transmitter detections for A fish, B fish, and the control transmitter separately across all receivers and days within 30 min daily bins. In order to make each group of transmitters comparable, we divided the total number of detections within each 30 min period by the maximum number of detections in any 30 min period for each group of transmitters separately, and then multiplied those values by 100; the standardized detection rate was then plotted for A fish, B fish, and the control transmitter separately over the diel period. For all analyses, we examined the period between 8 December 2008 and 10 June 2009, after which there were very few detections of any fish or the control transmitter. All receivers and the control transmitter were removed from the system on 19 August 2009.

### Detection rate of control transmitter

The introduction of a control transmitter into the study system for the duration of the study allowed us to calculate a control transmitter rate of detection, and then relate that detection rate to environmental conditions. The daily detection rate (%) for the control tag was calculated as:

$$\text{Daily detection rate} = \frac{\text{\#of daily detections}}{\text{maximum\#of daily detections}} \times 100 \quad (1)$$

We then related the daily detection rate to environmental conditions. Daily bottom water temperature (°C) was provided by the HOBO data logger deployed at 210 Rock for the duration of the study, and mean daily wave height (m), wave period (s), and barometric pressure (hPa) were available from buoy 41036 (National Data Buoy Center, NOAA), which was located ~30 km west of the study site.

We used a generalized additive model (GAM) to relate the daily detection rate of the control transmitter to daily environmental conditions in the area. GAMs use nonparametric smoothing functions to account for nonlinearities that may exist between response and predictor variables (Hastie & Tibshirani 1990, Bachelier et al. 2009a). GAMs extend traditional additive models by allowing for alternative distributions of underlying random variation, just as generalized linear models allow for alternative distributions in linear models (Wood 2006).

Before developing GAMs, multicollinearity among predictor variables was examined because its presence can cause erratic model behavior and should be avoided (Zar 1999). We assessed the severity of multicollinearity among predictor variables by calculating the variance inflation factor (VIF) for each variable; VIF measures the amount of variance that is inflated for each variable due to its collinearity with other predictor variables (library 'HH' in R version 3.1.1; R Core Team 2014). The VIF for all predictor variables was <2.0, which is well below the level generally acknowledged to be problematic (5 – 10; Neter et al. 1989), thus indicating no significant multicollinearity among predictor variables in our dataset. We coded our base GAM as:

$$dr^{0.25} = a + g_1(t) + g_2(wp) + g_3(wh) + g_4(p) + e, \quad (2)$$

where  $dr^{0.25}$  is the 4th root transformed daily detection rate of the control transmitter,  $a$  is the intercept,  $t$  is bottom temperature,  $wp$  is wave period,  $wh$  is wave height,  $p$  is barometric pressure,  $g_s$  are non-parametric smoothing spline functions, and  $e$  is random error. We compared multiple response variable transformations (i.e. 4th root, log, arcsin), and the 4th root transformation performed best based on model diagnostic plots and the Akaike Information Criterion (AIC; Burnham & Anderson 2002). AIC was calculated as:

$$\text{AIC} = -2\log[L(\hat{\theta}|y)] + 2K \quad (3)$$

where  $[L(\hat{\theta}|y)]$  is the log-likelihood and  $K$  is the number of parameters for each model. The model with the lowest AIC score was considered to be the best model in the model set.

We compared our base model with various reduced models that had one or more predictor variables removed. The predictor variables included in the best model were plotted in response space (at average values of all other predictor variables in the model) to show their predicted relationship with daily detection rate. GAMs were coded and analyzed using the *mgcv* library (version 1.8-3; Wood 2004) in R version 3.1.1 using the Gaussian family model (R Core Team 2014). The *gam.check* function of the *mgcv* library was used to verify that the final model met the assumptions of constant variance and normal residuals.

### Lionfish movements

We used 2 analytical approaches to make inferences about lionfish movements in our study area. First, we quantified the proportion of pings from each

transmitter being detected by each receiver each day, and plotted those proportions over the duration of the study. Visualizing the daily detections by receiver for each lionfish was intended to provide insights into space use and movements at 210 Rock; the same visualization for the control tag provides a sense of how much a transmitter at a fixed site may appear to move among receivers due to highly variable detection ranges. Individual telemetered lionfish were only included in this and subsequent movement analyses if at least 500 total detections were recorded by the receiver array ( $N = 14$  fish and the control transmitter).

For the second analysis, we estimated the daily centers of activity for each telemetered lionfish and the control transmitter. Simpfendorfer et al. (2002) showed that transmitter presence and absence data from an underwater receiver array can be converted to position estimates based on the weighted means of the number of signal detections at each receiver over a specified time period. Lionfish center-of-activity longitudes were estimated as:

$$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n R_i X_i}{\sum_{i=1}^n R_i} \quad (4)$$

where  $\bar{X}$  is the mean position during time interval  $\Delta t$ ,  $n$  is the number of receivers in the array,  $R_i$  is the number of receiver detections by the  $i$ th receiver during  $\Delta t$ , and  $X_i$  is the longitude of the  $i$ th receiver. Mean latitude for each transmitter was calculated using the same equation as for longitude except that  $Y$  (latitude) was substituted for  $X$  in Eq. (4). These center-of-activity location estimates thus tend to be a mean position for each day rather than a precise location at a certain point during the day, and can be useful when quantifying long-term movements, space use patterns, and home range size (Simpfendorfer et al. 2002). The downside is that mean positions underestimate the total distance moved compared to active tracking (Simpfendorfer et al. 2002). Mean positions over the course of the study were plotted for a variety of telemetered lionfish and the control transmitter, highlighting the core space use patterns of lionfish at 210 Rock.

Lastly, we calculated the distance moved by lionfish as the linear distance between the mean position estimates over consecutive days. Distance moved was only calculated when mean position estimates existed for 2 consecutive days, and mean distance moved was calculated separately for A fish, B fish, and the control tag. Mean daily distance moved provides a lower-bound approximation of the movements and space use patterns of lionfish in the study area.

## RESULTS

### Range tests and holding tank experiment

Detection rates of V9 transmitters were 100% between 50 and 150 m, but 0% at 300 and 400 m, indicating that the actual range of detection of V9 transmitters was  $>150$  m but  $<300$  m. Throughout the course of the study, however, the control transmitter was periodically detected by some receivers  $>300$  m away. Therefore, receivers were placed 300–350 m apart to minimize coverage overlap between receivers while covering most of the hard bottom habitat at 210 Rock (Fig. 2). All 4 of the lionfish that were surgically implanted with V9 transmitters and held in the laboratory for 9 mo remained healthy and suffered no apparent adverse effects from the transmitter implantation. These fish were subsequently donated to the North Carolina Aquarium at Pine Knoll Shores, where they were on display and survived for many years.

### Field surgeries

A total of 25 lionfish was surgically implanted and released at 210 Rock: 15 on 4 December 2008 (A fish) and 10 on 6 February 2009 (B fish) (Table 1). The total length (mean = 300 mm; range = 210–400 mm), weight (mean = 456 g; range = 126–860 g), and tag weight to body weight ratio (mean = 1.3%; range = 0.6–3.7%) of released lionfish were similar to those of fish surgically implanted and retained in the laboratory.

### Transmitter detection probabilities

Daily transmitter detections from A fish, B fish, and the control transmitter by the receiver array generally declined over time (Fig. 3). Mean number of detections was higher for B fish (mean = 382 detections  $\text{fish}^{-1} \text{d}^{-1}$ ; range = 0–3580 detections  $\text{fish}^{-1} \text{d}^{-1}$ ) than for A fish (mean = 290 detections  $\text{fish}^{-1} \text{d}^{-1}$ ; range = 0–1481 detections  $\text{fish}^{-1} \text{d}^{-1}$ ) or the control tag (mean = 122 detections  $\text{d}^{-1}$ ; range = 0–758 detections  $\text{d}^{-1}$ ). Detections generally declined when the bottom water temperature began warming in March 2009 (Fig. 3).

We found a consistent diel pattern in transmitter detections for A fish, B fish, and the control (Fig. 4). Standardized detection rates were generally highest during the day ( $>80\%$ ), lowest at sunrise ( $<60\%$ ),

Table 1. Summary information for the 25 lionfish *Pterois volitans* tagged at 210 Rock, North Carolina, 2008–2009, as well as a control transmitter placed in the study area for the duration of the study. Dates are mm/dd/yyyy. Underwater receivers were first deployed on 8 December 2008 and retrieved on 19 August 2009. NA: not applicable

Tagging date	Fish number	Time on surface (h:mm)	Weight (g)	Total length (mm)	Tag weight to body weight ratio	Date detections began	Date detections ended	Total days detected	Total number of detections	Included in movement analyses?
12/4/2008	A1	3:19	400	270	1.2	–	–	0	0	No
12/4/2008	A2	3:19	800	380	0.6	12/14/2008	12/20/2008	7	33	No
12/4/2008	A3	3:19	375	275	1.3	–	–	0	0	No
12/4/2008	A4	3:19	790	325	0.6	12/8/2008	4/1/2009	115	11624	Yes
12/4/2008	A5	3:19	350	240	1.3	–	–	0	0	No
12/4/2008	A6	3:19	550	310	0.9	12/8/2008	3/25/2009	108	8041	Yes
12/4/2008	A7	2:30	250	265	1.9	12/8/2008	5/31/2009	175	19101	Yes
12/4/2008	A8	2:30	550	265	0.9	–	–	0	0	No
12/4/2008	A9	2:30	360	280	1.3	12/8/2008	5/12/2009	156	7972	Yes
12/4/2008	A10	2:11	225	240	2.1	–	–	0	0	No
12/4/2008	A11	2:11	175	230	2.7	12/8/2008	12/13/2009	6	106	No
12/4/2008	A12	2:11	400	400	1.2	12/8/2008	4/11/2009	125	851	Yes
12/4/2008	A13	2:11	285	280	1.7	12/8/2008	12/13/2009	6	87	No
12/4/2008	A14	2:11	600	360	0.8	12/8/2008	2/12/2009	67	522	Yes
12/4/2008	A15	2:11	230	250	2.0	12/8/2008	5/15/2009	159	5909	Yes
2/6/2009	B1	2:46	436	303	1.1	2/6/2009	3/22/2009	45	7434	Yes
2/6/2009	B2	2:46	699	355	0.7	2/6/2009	4/16/2009	70	5284	Yes
2/6/2009	B3	2:46	340	280	1.4	2/6/2009	5/2/2009	86	13604	Yes
2/6/2009	B4	2:46	574	332	0.8	2/6/2009	2/10/2009	5	430	No
2/6/2009	B5	2:46	860	382	0.6	2/6/2009	6/10/2009	125	10816	Yes
2/6/2009	B6	2:46	332	278	1.4	2/6/2009	4/14/2009	68	3621	Yes
2/6/2009	B7	2:46	727	360	0.6	2/6/2009	4/1/2009	4	188	No
2/6/2009	B8	2:46	693	354	0.7	2/6/2009	3/17/2009	40	1109	Yes
2/6/2009	B9	2:46	285	265	1.6	2/6/2009	4/3/2009	57	5005	Yes
2/6/2009	B10	1:47	126	210	3.7	2/6/2009	2/9/2009	4	269	No
12/8/2008	Control	NA	NA	NA	NA	12/8/2008	6/10/2009	185	22603	Yes

and moderate during the night (60–80%) for all transmitters (Fig. 4).

Detection rate of the control transmitter was generally high but variable through March 2009, and declined markedly thereafter (Fig. 5). Bottom temperature followed an expected seasonal pattern of decline from December 2008 through March 2009,

subsequently warming throughout the spring. Wave height, wave period, and barometric pressure all varied in ways that are likely related to the periodicity of frontal systems and storms (Fig. 5).

Using the GAM, environmental conditions explained 37.8% of the deviance in daily detection rate (Table 2). All 4 environmental predictor variables

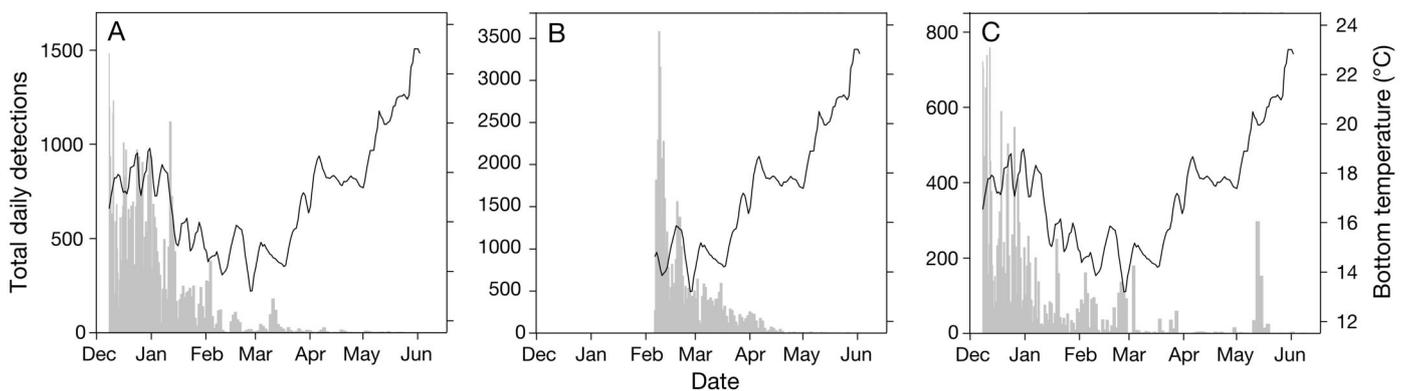


Fig. 3. Total daily detections for lionfish *Pterois volitans* (gray bars, y-axis) tagged on (A) 4 December 2008 (A fish) or (B) 6 February 2009 (B fish), and (C) the control tag related to bottom temperature (black line, 2nd y-axis) at 210 Rock, North Carolina, 2008–2009

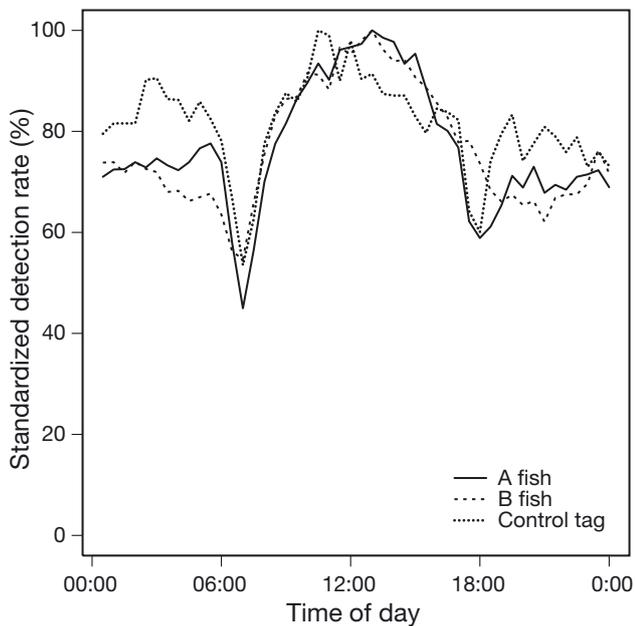


Fig. 4. Standardized detection rates of A lionfish *Pterois volitans* (tagged on 4 December 2008), B lionfish (tagged on 6 February 2009), and the control transmitter at 210 Rock, North Carolina, over a diel period (Eastern Standard Time). Detections were summed by 30 min bins and divided by the maximum number of detections in a 30 min period for each group separately

were included in the final model, which had a much lower AIC compared to the next best model that excluded barometric pressure (Table 2). Daily detection rate declined as bottom temperature and wave period increased, but appeared to increase (with much less confidence) as wave height and barometric pressure increased (Fig. 6).

### Lionfish movements

Excluding 5 telemetered lionfish that were never detected by the receiver array (all from the A release), the total number of days telemetered lionfish were detected ranged between 4 and 175 d (mean = 71.4 d), with 18 to 19101 detections per fish (mean = 5100; Table 1). Three lionfish were detected by the receiver array as late as the end of May or early June. Only fish with at least 500 detections ( $N = 14$ ) were included in subsequent movement analyses. The control tag was detected on 156 of 185 d (84%) of the study and had 22 603 total detections.

Telemetered lionfish displayed affinities for particular areas at 210 Rock, based on the low observed movements by lionfish among receivers

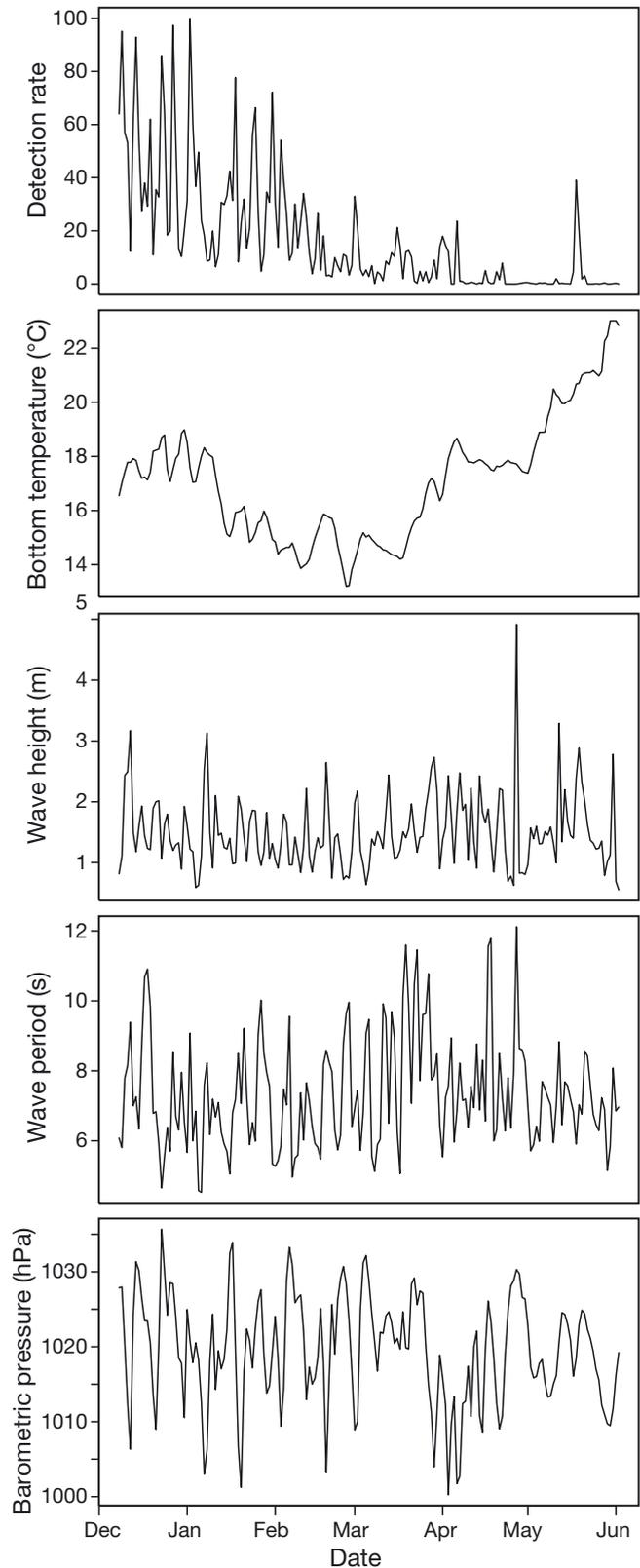


Fig. 5. Daily detection rate of the control transmitter and environmental conditions at 210 Rock, North Carolina, from 8 December 2008 to 10 June 2009

Table 2. Summary information for the 6 best generalized additive models relating control tag detection rate at 210 Rock, North Carolina, to environmental conditions, 2008–2009. Estimated degrees of freedom are shown for each term; (\*) significance: \*\* $\alpha = 0.05$ , \*\*\* $\alpha = 0.01$ ; AIC: Akaike Information Criterion; ex: variable excluded from the model. For base model see Eq. (2) in ‘Materials and methods’

Model	AIC	Deviance explained	Bottom temp (t)	Wave period (wp)	Wave height (wh)	Pressure (p)
Base	395.8	37.8	4.2***	1.0***	2.5**	3.9
Base – p	400.0	32.2	3.0***	1.0***	2.0	ex
Base – p – wh	402.9	29.2	2.6***	1.0***	ex	ex
Base – wh	404.0	30.1	2.7***	1.0***	ex	1.7
Base – wp	408.0	31.9	2.8***	ex	2.7**	4.1
Base – wp – p	410.3	27.0	2.3***	ex	2.4	ex

in the array (Fig. 7). Most telemetered lionfish were generally detected by a single receiver in the array. For instance, fish A4, A6, A9, and A14 were primarily detected by receiver #7, while fish A7, A12, and B1 were primarily detected by receiver #6 (Fig. 7). In contrast, some lionfish were consistently detected by multiple receivers over the course of the study (e.g. A15: 7 receivers, B5: 6 receivers, and B6: 5 receivers). The control transmitter was initially detected by multiple receivers early in the study, but by March or April 2009, receiver #4 was the primary receiver detecting the transmitter (Fig. 7); recall that the control transmitter was attached to the line of receiver #4 throughout the

study. Overall, 79% of the detections of the control tag were recorded by receiver #4. Moreover, compared to the control transmitter that was detected consistently over the course of the study, many telemetered lionfish were detected inconsistently over time. Some telemetered lionfish were not detected by receivers for short periods of 1–2 d, while other lionfish had periods of >10 d during which they were not detected by any receivers (Fig. 7).

Daily center-of-activity positions indicated that lionfish movements were generally limited during the 6 mo of the study (Fig. 8). All telemetered

lionfish (including the 8 ind. shown in Fig. 8) displayed fairly small clusters of mean positions during the 6 mo of this study, with no 2 points separated by >400 m for any fish. Some fish appeared to move <200 m throughout the study (e.g. A6, A7, A12, B1, B3), while others (A4, A15, B5) moved up to 400 m. The control transmitter also appeared to move up to ~200 m due to the variable detection rates associated with variability in detection range during the study (Fig. 8).

Estimated daily distances moved were similar for A fish (mean = 20 m; range = 0–139 m), B fish (mean = 23 m; range = 0–112 m), and the control transmitter (mean = 29 m; range = 0–125 m) (Fig. 9). In addition,

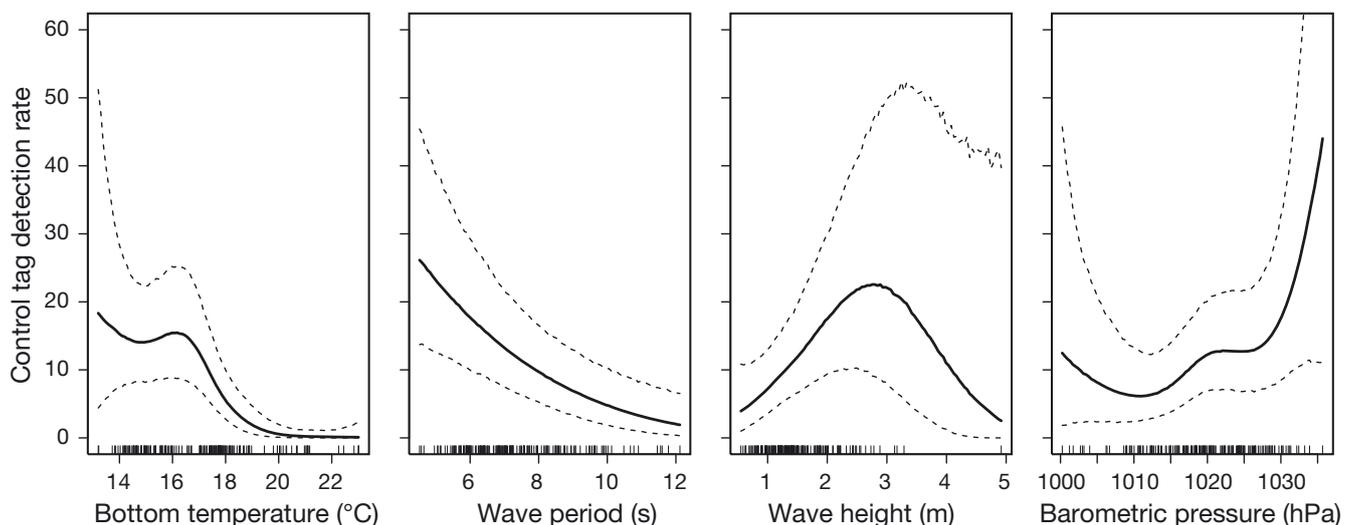


Fig. 6. Relationship between the control tag detection rate and bottom temperature (°C), wave period (s), wave height (m), and barometric pressure (hPa) as estimated by a generalized additive model at 210 Rock, 2008–2009. (Solid line) Mean prediction at average values of all other model covariates, (dashed lines) 95% CIs. Tick marks on x-axis indicate predictor variable data included in the generalized additive model

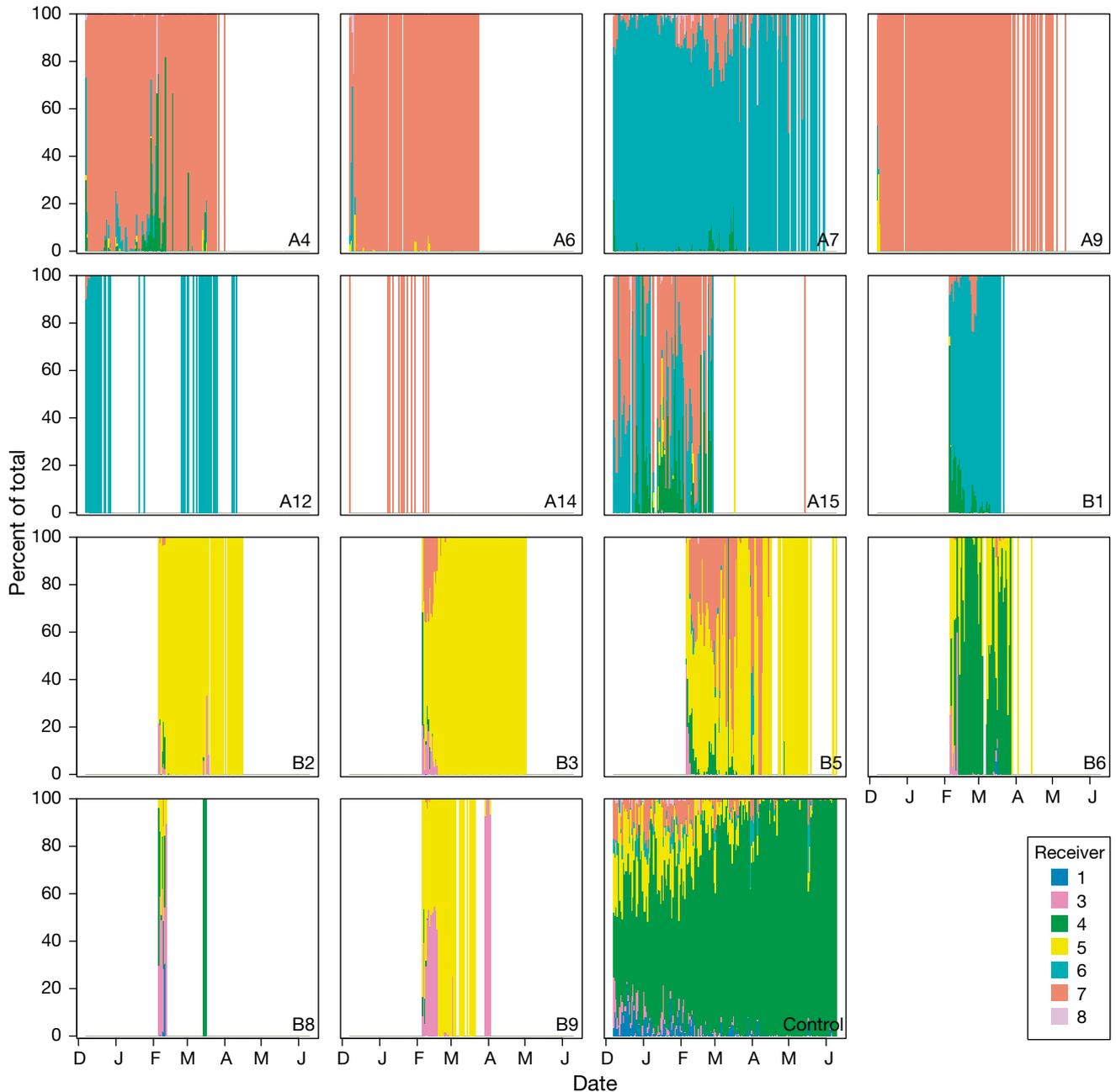


Fig. 7. Percent (of total) daily lionfish *Pterois volitans* or control transmitter detections recorded on each stationary receiver at 210 Rock, North Carolina, 2008–2009. Numbers for A and B fish (tagged on 4 December 2008 and 6 February 2009, respectively) are provided in the lower right corner of each panel, and receivers are color coded as shown in the key

lionfish appeared to move larger distances early in the study (through April 2009) and shorter distances thereafter, with the only exception being a few days of large distances moved by some A fish in April and May (Fig. 9). Also, both groups of telemetered lionfish displayed consistently higher than average movement rates in the week following their release (Fig. 9).

## DISCUSSION

We described the movements of invasive lionfish on the continental shelf in North Carolina, USA, while simultaneously examining various environmental influences on detection rate of a control transmitter. We found that environmental conditions were correlated with the likelihood of detecting

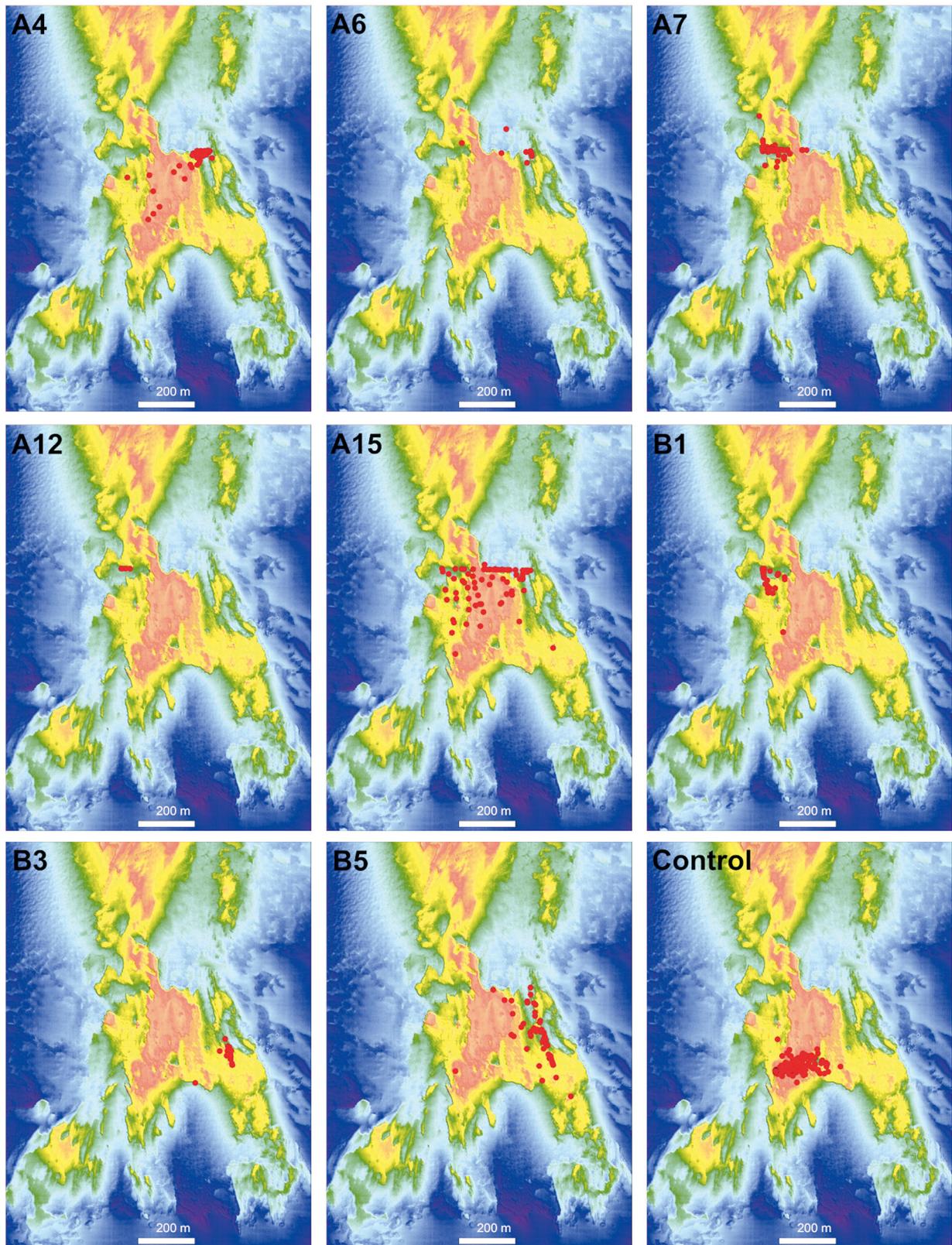


Fig. 8. Daily center-of-activity locations (●) for selected telemetered lionfish *Pterois volitans* and the control transmitter at 210 Rock, North Carolina, 2008–2009. Numbers for A and B fish (tagged on 4 December 2008 and 6 February 2009, respectively) and the control transmitter are provided in the upper left corner of each panel

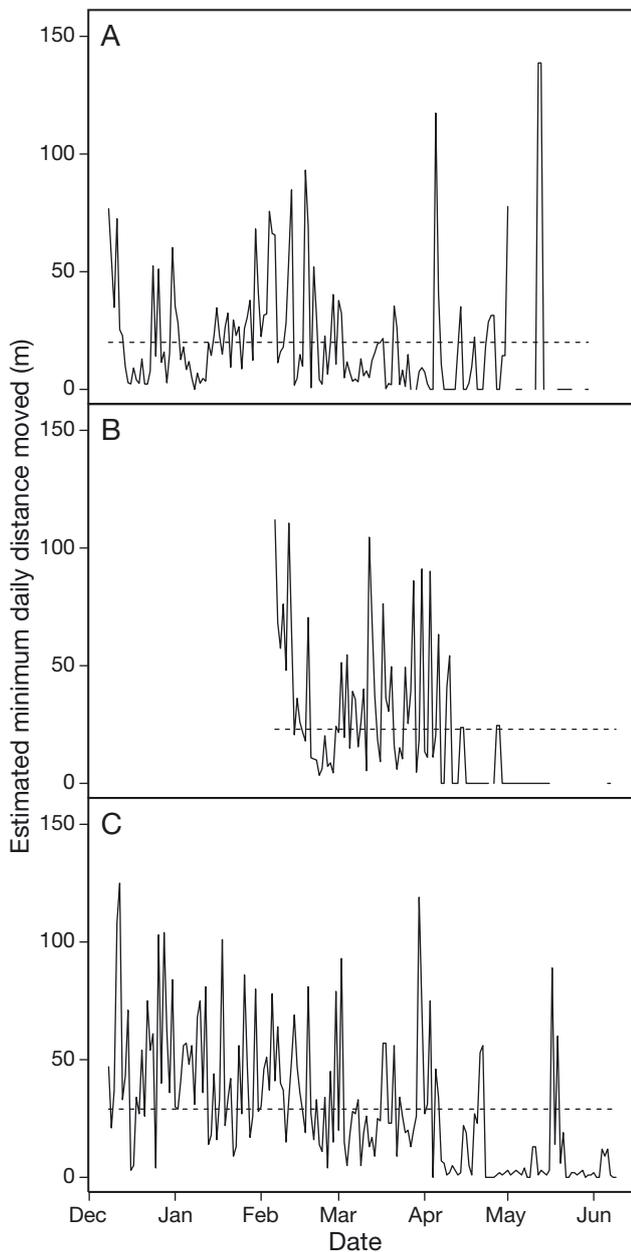


Fig. 9. Estimated minimum daily distance moved (m) for (A) A lionfish *Pterois volitans* tagged on 4 December 2008, (B) B lionfish tagged on 6 February 2009, and (C) the control transmitter at 210 Rock, North Carolina, 2008–2009. Dashed lines are mean daily distance moved

telemetered lionfish, but additional diel differences in detection rate suggest that non-environmental sources of noise may be important as well. Regarding lionfish movements, all telemetered individuals included in the analyses moved entirely within small areas ranging between 50 and 400 m in diameter for up to 6 mo. These results provide general guidance for researchers designing acoustic teleme-

try studies in coral and temperate reef systems, and can also assist scientists and managers working to develop management or control strategies for invasive lionfish.

### Detection rate

A variety of factors, e.g. water flow, biological (animal) noise, signal collision, loss of transmitter power over time, vessel noise, wind, waves, biofouling, and rainfall, can influence the ability of underwater receivers to detect pinging transmitters (Heupel et al. 2008, Claisse et al. 2011, Topping & Szedlmayer 2011, How & de Lestang 2012, Gjelland & Hedger 2013, Mathies et al. 2014, Stocks et al. 2014). We found that environmental conditions were correlated with the daily detection rate of the control transmitter in our system, and the GAM that included environmental predictor variables explained a large amount of the deviance in detection rate. It is important to identify and account for factors that influence detection rate because true patterns in animal behaviors can be confounded with patterns in those factors (Payne et al. 2010). For instance, without the proper use of controls, it is impossible to disentangle a far-away fish detected a few times during good conditions from a nearby fish detected a few times during poor conditions (Gjelland & Hedger 2013).

Daily detection rate was most strongly related to water temperature, being highest when water temperature was low and lowest when water temperature was high. This contrasts with acoustic theory where higher water temperatures are typically associated with an increase in signal strength and transmission (Winter 1996). Thermoclines may be more likely to develop when water temperature is high, and thermoclines bend, refract, and depress sound signals (Voegeli & Pincock 1996, Singh et al. 2009). Increased temperatures may also increase the activity of noise-making fauna such as snapping shrimp *Alpheus* spp. and *Synalpheus* spp., which produce noise at the same frequency as the transmitters in our study (Johnson et al. 1947, Knowlton & Moulton 1963). Ambient biological noise is also often significantly higher during the summer and lower in winter (Radford et al. 2008).

We also found that detection rate was higher when wave period was shorter and barometric pressure was higher, suggesting that low pressure systems or fronts (whether approaching, nearby, or recently passed through) may have periodically reduced the detection rate (Gjelland & Hedger 2013, Mathies et

al. 2014). There are 3 potential mechanisms by which fronts or other weather events may influence detection rate. First, weather events may cause higher movements of water masses, which explained up to 92% of the short-term variability in detection rates on a similar hard bottom reef in Georgia (Mathies et al. 2014). Second, weather systems may re-suspend sediments, which can increase scatter and reduce sound signal transmission (How & de Lestang 2012). Longer period waves are more likely to re-suspend sediments because they influence water much more deeply than short period waves. Third, air bubbles from rain or waves during weather events could be mixed into the surface layer of water, and can strongly attenuate sound signals (Medwin & Clay 1998). One or a combination of these factors might have reduced telemetered lionfish detection probabilities in our study.

Reefs tend to be acoustically noisy environments (Lammers et al. 2008) due to choruses from fish schools (McCauley & Cato 2000, Tricas & Boyle 2014) and invertebrates (Johnson et al. 1947, Knowlton & Moulton 1963), and there is often a diel periodicity in noise production in aquatic environments (Radford et al. 2008). Diel periodicity could not be specifically tested for in the GAM that used daily detection rate as the response variable, but detection rate clearly varied over the course of the day, being lowest at sunrise, highest during the day, and in between during the night. These results are consistent with previous studies from Florida (Breder 1968), the Indian and Pacific Oceans (Cato 1978, Welsh et al. 2012), as well as New Zealand reefs, where biological noise was more intense at dawn and dusk than during the day or night (Radford et al. 2008). Myriad marine species capable of producing sound inhabit 210 Rock, including snapping shrimp, toadfishes *Opsanus* spp., white grunt *Haemulon plumierii*, tomtate *Haemulon aurolineatum*, and red grouper *Epinephelus morio*.

It is unlikely that signal collision strongly influenced transmitter detection rates in our study. Signal collision occurs when 2 (or more) transmitters emit their signals simultaneously, resulting in a lack of detection of either transmitter by receivers, and is a concern when many transmitters with short delays occur in the same area at the same time (Topping & Szedlmayer 2011). In our study, we used transmitters with a long (and variable) time between pings, and never had >25 telemetered lionfish at the 210 rock at the same time. Moreover, the highest detection probabilities in our study occurred during the winter when the highest number of transmitters were in the

system, and the lowest detection probabilities occurred when the fewest transmitters were present (i.e. in late spring), suggesting that signal collision was not the main cause of variable detection rates.

### Lionfish movements

Movement is a critical but poorly understood aspect of a species' population dynamics. Movement influences population abundance, species interactions, and genetic variability across a landscape, and ties together nearly all aspects of the ecology of a species. For invasive lionfish, the extent of movement can determine how quickly the species can invade new habitats, the spatial scale of potential lionfish impacts, or the success of control (i.e. removal) strategies (Morris & Whitfield 2009, Akins 2012). Fish movement has been studied using a variety of approaches, but the rapid evolution of telemetry techniques over the last few decades has proved to be a powerful tool in understanding movements (Heupel et al. 2006). Recent advances using remote hydrophone arrays to passively monitor fish movements have generally provided more accurate information on fish movements than active tracking (Meyer et al. 2010), and often at a lower cost (Espinoza et al. 2011).

Using a telemetry approach with a remote receiver array, we showed that invasive adult lionfish moved very little around a natural North Carolina hard bottom reef, spending up to 6 mo in small (i.e. <400 m) patches. These results are consistent with the few studies that have examined lionfish movements. For instance, Jud & Layman (2012) used conventional tagging to determine that 74% of juvenile lionfish moved <10 m between tagging and recapture in a Florida estuary over the course of 10 mo, although movements of up to 420 m were observed. Lionfish also moved little during focal studies of foraging behavior (Albins & Hixon 2008, Côté & Maljkovi 2010, Green et al. 2011), although movement was only monitored for hours to days in these cases. Overall, however, it appears that juvenile and adult lionfish move little, suggesting that invasive lionfish may colonize new areas during larval settlement and less so as juveniles or adults. Nevertheless, we have observed an adult lionfish (~30–40 cm TL) crossing a large (i.e. 45 m) expanse of sand near 210 Rock (R. Muñoz, pers. obs.). This observation suggests that, although relatively sedentary, lionfish have the capacity to undertake occasional forays, sometimes crossing habitats of low structural complexity (Green et al. 2011, Jud & Layman 2012).

A number of telemetered lionfish disappeared from the study area. Five fish (20%) were never detected on any receiver and may have emigrated from the study area as a flight response to the surgery, which is a relatively common occurrence (White & Garrott 1990, Winter 1996), and is consistent with their observed greater movement during the first week after surgery. Only 3 lionfish were detected by the receiver array in late May, suggesting that the remaining 17 telemetered lionfish 'disappeared' from the array at some point during the study. There are 5 plausible explanations for the disappearance of telemetered lionfish during the study: (1) emigration from the study area, (2) predation upon telemetered lionfish, followed by movement of the predator out of the study area, (3) death of the lionfish, followed by the transmitter settling into a crevice where it remained undetected, (4) movement of telemetered lionfish into certain areas or habitats within the study area where the detection rate was very low or zero, or (5) the drastic decline in detection rate by March 2009 such that telemetered lionfish were not detected in places where they had been previously detected. We know detection rate declined drastically after March 2009 (based on detections of the control transmitter), so it is impossible to know whether fish emigrated or were consumed during a time of very low detection probabilities. If lionfish did emigrate from the study area as part of their normal behavior, the movement rates we presented would be underestimated because we would only have summarized movements of the individuals with the highest site fidelity. We also observed higher movement rates ~1 wk post-surgery, suggesting a small positive bias in movement rates shortly after surgery, but this bias did not persist beyond a couple of weeks.

It is unlikely that a large number of telemetered lionfish died over the duration of our study. First, we conducted a laboratory study where 4 lionfish were implanted with transmitters and held for 9 mo. All of these fish healed quickly, and all fish survived the 9 mo study and many additional years at a local aquarium. There is no discernible reason why fish in the laboratory would survive while fish in the field would not. Second, surgeries were conducted by a Doctor of Veterinary Medicine who has extensive experience performing surgeries on fish, which is different from most telemetry studies where biologists perform the surgeries. Third, fish were held on board the vessel until normal swimming behavior had resumed, and then returned to the bottom by SCUBA divers, who did not notice any unusual behavior upon release; telemetered lionfish swam away and

behaved normally. Fourth, most lionfish were picked up by different receivers over the course of the study, suggesting that lionfish were moving among receivers throughout the study.

The movements of lionfish in our study describe the winter and perhaps spring time periods only, since most telemetered fish were detected from December through April. Lionfish are rarely found in water <14°C in North Carolina (Whitfield et al. 2014). Since the bottom temperature was 14–16°C for at least 2 mo in our study, it is possible that lionfish were moving less than normal due to ambient water temperatures being close to their thermal tolerance. Lionfish may have larger home ranges and display less site fidelity in the summer months when the water is warmer. Future adult lionfish telemetry studies conducted during the summer may also require that receivers be moved closer together, given the lower detection probabilities we found during summer months.

## CONCLUSIONS

The introduction of non-native species into marine ecosystems around the world is a threat to ecological communities because non-native species can displace native species and alter patterns in biodiversity and community structure (Grosholz et al. 2000). The introduction of lionfish into the western Atlantic Ocean could be one of the biggest threats to reef fish communities in the region (Albins & Hixon 2008). Lionfish exhibit many characteristics of a successful invader: a broadly distributed pelagic egg and larval stage, high fecundity, broad diet, and few habitat preferences (Morris & Whitfield 2009). Our work is the first long-term study on the movements of adult lionfish, and we found that individuals moved very little at a natural hard bottom reef in North Carolina in winter and spring, their movement being much less than similar-sized predatory reef fish elsewhere (e.g. Farmer & Ault 2011, Topping & Szedlmayer 2011, Fabrizio et al. 2014). Our movement analyses for lionfish were somewhat complicated by highly variable detection probabilities, but we were able to quantify variable detection probabilities by using a control transmitter in the study area. We also showed that the detection rate of the control transmitter was likely influenced by both environmental conditions and biological noise, which must be properly accounted for in future telemetry studies in similar systems, e.g. by using more powerful transmitters.

**Acknowledgements.** We thank E. Anderson, C. Butler, J. Cudney, B. Degan, G. Fisher, J. Hackney, N. Hawthorne, B. Stringer, B. Teer, and J. Vander Pluym for assistance with various aspects of this study. We also thank A. Hohn, T. Kellison, N. Klibansky, P. Marraro, and K. Purcell for reviewing previous versions of this manuscript. The use of trade, product, industry, or firm names, products software, or models, whether commercially available or not, is for informative purposes only and does not constitute an endorsement by the US government or NOAA.

#### LITERATURE CITED

- Akins L (2012) Control strategies: tools and techniques for local control. In: Morris JA Jr (ed) Invasive lionfish: a guide to control and management. Gulf Carib Fish Inst Spec Publ Ser 1, Marathon, FL, p 24–50
- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238
- Arias-González JE, González-Gándara C, Cabrera JL, Christensen V (2011) Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ Res* 111:917–925
- Bacheler NM, Bailey KM, Ciannelli L, Bartolino V, Chan KS (2009a) Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma*. *Mar Ecol Prog Ser* 391:1–12
- Bacheler NM, Buckel JA, Hightower JE, Paramore LM, Pollock KP (2009b) A combined telemetry – tag return approach to estimate fishing and natural mortality rates of an estuarine fish. *Can J Fish Aquat Sci* 66:1230–1244
- Bacheler NM, Paramore LM, Burdick SM, Buckel JA, Hightower JE (2009c) Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. *Fish Bull* 107:405–419
- Betancur-R R, Hines A, Acero AP, Orti G, Wilbur AE, Freshwater DW (2011) Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. *J Biogeogr* 38:1281–1293
- Breder CM (1968) Seasonal and diurnal occurrences of fish sounds in a small Florida bay. *Bull Am Mus Nat Hist* 138:329–378
- Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information–theoretic approach, 2nd edn. Springer, New York, NY
- Carpenter JW, Marion CJ (2013) Exotic animal formulary, 4th edn. Saunders, St. Louis, MO
- Cato DH (1978) Marine biological choruses observed in tropical waters near Australia. *J Acoust Soc Am* 64:736–743
- Claisse JT, Clark TB, Schumacher BD, McTee SA and others (2011) Conventional tagging and acoustic telemetry of a small surgeonfish, *Zebrasoma flavescens*, in a structurally complex coral reef environment. *Environ Biol Fishes* 91:185–201
- Côté IM, Maljković A (2010) Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 404:219–225
- Domeier ML (2005) Methods for the deployment and maintenance of an acoustic tag tracking array: an example from California's Channel Islands. *Mar Technol Soc J* 39:74–80
- Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fish Res* 108:364–371
- Fabrizio MC, Manderson JP, Pessutti JP (2014) Home range and seasonal movements of black sea bass (*Centropristis striata*) during their inshore residency at a reef in the mid-Atlantic Bight. *Fish Bull* 112:82–97
- Farmer NA, Ault JS (2011) Grouper and snapper movements and habitat use in Dry Tortugas, Florida. *Mar Ecol Prog Ser* 433:169–184
- Farmer NA, Ault JS, Smith SG, Franklin EC (2013) Methods for assessment of short-term coral reef fish movements within an acoustic array. *Movement Ecol* 1:7
- Giacalone VM, D'Anna G, Garofalo G, Collins K, Badalamenti F (2005) Estimation of positioning error from an array of automated omni-directional receivers in an artificial reef area. In: Spedicato MT, Lembo G, Marmulla G (eds) Aquatic telemetry: advances and applications. Proc 5th Conf Fish Telemetry. FAO/COISPA, Rome, p 245–253
- Gjelland KØ, Hedger RD (2013) Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Meth Ecol Evol* 4:665–674
- Green SJ, Akins JL, Côté IM (2011) Foraging behavior and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 433:159–167
- Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* 7:e32596
- Grosholz ED, Gregory MR, Dean CA, Shirley KA, Maron JL, Conners PG (2000) The impacts of a nonindigenous marine predator in a California bay. *Ecology* 81:1206–1224
- Harms CA (2005) Surgery in fish research: common procedures and postoperative care. *Lab Anim (NY)* 34:28–34
- Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman & Hall/CRC, London
- Heupel MR, Semmens JM, Hobday AJ (2006) Automated tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar Freshw Res* 57:1–13
- Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA (2008) Effects of biofouling on performance of moored data logging acoustic receivers. *Limnol Oceanogr Methods* 6:327–335
- How JR, de Lestang S (2012) Acoustic tracking: issues affecting design, analysis and interpretation of data from movement studies. *Mar Freshw Res* 63:312–324
- Johnson MW, Everest FA, Young RW (1947) The role of snapping shrimp (*Crangon* and *Synalpheus*) in the production of underwater noise in the sea. *Biol Bull* 93:122–138
- Jud ZR, Layman CA (2012) Site fidelity and movement patterns of invasive lionfish, *Pterois* spp., in a Florida estuary. *J Exp Mar Biol Ecol* 414-415:69–74
- Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the East Coast of the United States. *Mar Ecol Prog Ser* 283:269–278
- Knowlton RE, Moulton JM (1963) Sound production in the snapping shrimps *Alpheus* (*Crangon*) and *Synalpheus*. *Biol Bull* 125:311–331
- Lammers MO, Brainard RE, Au WWL, Mooney TA, Wong KB (2008) An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other habitats. *J Acoust Soc Am* 123:1720–1728

- Lapointe NWR, Thorson JT, Angermeier PL (2010) Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac River system. *Ecol Freshw Fish* 19:566–577
- Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biol Invasions* 13:1855–1868
- Lucas MC, Baras E (2000) Methods for studying spatial behavior of freshwater fishes in the natural environment. *Fish Fish* 1:283–316
- Mathies NH, Ogburn MB, McFall G, Fangman S (2014) Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Mar Ecol Prog Ser* 495:27–38
- McCaughey RD, Cato DH (2000) Patterns of fish calling in a nearshore environment in the Great Barrier Reef. *Philos Trans R Soc Lond B Biol Sci* 355:1289–1293
- Medwin H, Clay CS (1998) Fundamentals of acoustical oceanography, 1st edn. Academic Press, New York, NY
- Meyer CG, Papastamatiou YP, Clark YB (2010) Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. *Mar Biol* 157:1499–1511
- Morris JA Jr, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ Biol Fishes* 86:389–398
- Morris JA Jr, Whitfield PE (2009) Biology, ecology, control, and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Tech Memo NOS NCCOS 99
- Muñoz RC, Currin CA, Whitfield PE (2011) Diet of invasive lionfish on hard bottom reefs of the Southeast USA: insights from stomach contents and stable isotopes. *Mar Ecol Prog Ser* 432:181–193
- Neter J, Wasserman W, Kutner MH (1989) Applied linear regression models, 2nd edn. Irwin, Homewood, IL
- Parker RO, Dixon RL (1998) Changes in a North Carolina reef fish community after 15 years of intense fishing – global warming implications. *Trans Am Fish Soc* 127: 908–920
- Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Mar Ecol Prog Ser* 419: 295–301
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.r-project.org](http://www.r-project.org) (accessed on 23 October 2014)
- Radford CA, Jeffs AG, Tindle CT, Montgomery JC (2008) Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia* 156: 921–929
- Schofield PJ (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquat Invasions* 4: 473–479
- Schofield PJ (2010) Update on the geographic spread of invasive lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquat Invasions* 5(Suppl 1):S117–S122
- Simpfendorfer CA, Heupel MR, Heuter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Can J Fish Aquat Sci* 59:23–32
- Singh L, Downey NJ, Roberts MJ, Webber DM and others (2009) Design and calibration of an acoustic telemetry system subject to upwelling events. *Afr J Mar Sci* 31: 355–364
- Stocks JR, Gray CA, Taylor MD (2014) Testing the effects of near-shore environmental variables on acoustic detections: implications on telemetry array design and data interpretation. *Mar Technol Soc J* 48:28–35
- Sutherland WJ, Bardsley S, Bennun L, Clout M and others (2011) Horizon scan of global conservation issues for 2011. *Trends Ecol Evol* 26:10–16
- Topping DT, Szedlmayer ST (2011) Site fidelity, residence time and movements of red snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring. *Mar Ecol Prog Ser* 437:183–200
- Topping DT, Szedlmayer ST (2013) Use of ultrasonic telemetry to estimate natural and fishing mortality of red snapper. *Trans Am Fish Soc* 142:1090–1100
- Tricas TC, Boyle KS (2014) Acoustic behaviors in Hawaiian coral reef fish communities. *Mar Ecol Prog Ser* 511:1–16
- Turchin P (1998) Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, MA
- Voegeli FA, Pincock DG (1996) Overview of underwater acoustics as it applies to telemetry. In: Baras E, Philippart JC (eds.) Underwater biotelemetry. University of Liege, Liege, Belgium, p 23–30
- Vrieze L, Bergstedt R, Sorensen P (2011) Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*). *Can J Fish Aquat Sci* 68:523–533
- Welsh JQ, Fox RJ, Webber DM, Bellwood DR (2012) Performance of remote acoustic receivers within a coral reef habitat: implications for array design. *Coral Reefs* 31: 693–702
- White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA
- Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay WR Jr, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Mar Ecol Prog Ser* 235:289–297
- Whitfield PE, Hare JA, David AW, Harter SL, Muñoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the western North Atlantic. *Biol Invasions* 9:53–64
- Whitfield PE, Muñoz RC, Buckel CA, Degan BP, Freshwater DW, Hare JA (2014) Native fish community structure and Indo-Pacific lionfish *Pterois volitans* densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. *Mar Ecol Prog Ser* 509:241–254
- Winter J (1996) Advances in underwater biotelemetry. In: Murphy BR, Willis DW (eds.) Fisheries techniques. American Fisheries Society, Bethesda, MD, p 555–590
- Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J Am Stat Assoc* 99:673–686
- Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL
- Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ