

# Movement ecology of Indo-Pacific lionfish on Caribbean coral reefs and its implications for invasion dynamics

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**Abstract** The spread of marine invasive species at large geographic scales depends largely on current-driven larval dispersal. However, at smaller spatial scales, movements occurring after larval settlement can greatly influence the success of local control programs. We conducted the first dedicated tracking study of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) on Caribbean coral reefs. Using a mark-resighting approach, we estimated the scale and frequency of movements of 79 tagged lionfish on patchy and continuous reefs to study factors influencing movement. Many tagged lionfish moved relatively little, with ~60 % of fish resighted at least once and 10 % not moving from their initial tagging location. However, maximum movements (as far as 1.35 km in 15 days) far exceeded previous estimates. Lionfish movement was density dependent, declined at larger body sizes, and depended on seascape structure. Lionfish on continuous reefs moved faster and more often than those on patch reefs, and lionfish in patchy habitats moved farther when patches were closer together. Invasions taking place over heterogeneous

seascapes such as coral reefs are difficult to manage effectively with spatially uniform regional management plans, but understanding an invader's movement ecology can help to optimize the distribution of limited resources for invasive management.

**Keywords** Lionfish · Fish · Mark-recapture · Movement · Dispersal · Landscape

## Introduction

The growing ecological and economic impacts of marine invasive species provide an urgent impetus to understand invasion dynamics to inform effective mitigation strategies (Bax et al. 2003; Wilson et al. 2008). Because most marine animals have a planktonic early life stage, studies of invasive spread in the sea have largely been limited to modelling current-driven larval dispersal at large geographic scales (e.g., Freiwald 2012; Kinlan et al. 2005; Wonham and Lewis 2009). The role of post-settlement (i.e., juvenile and adult) movement in contributing to the spread of marine invasive species has received comparatively little attention, perhaps because a large proportion of marine invasive species are sessile plants or invertebrates (Molnar et al. 2008). However, the movement of post-settlement individuals is now recognized as an important process influencing the distribution, demography, and persistence of many marine populations

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(Freiwald 2012; Pittman and McAlpine 2003). Consequently, for mobile invaders such as predatory sea stars, crabs, and fishes, adult movement could contribute significantly to population connectivity and range expansion (Hastings et al. 2005; Kinlan et al. 2005; Palmer et al. 2011).

The invasion by Indo-Pacific lionfish (*Pterois volitans* and *P. miles*, hereafter referred to as lionfish) of the western Atlantic represents a recent and dramatic example of a mobile marine invader. Since their introduction off the coast of Florida in the 1980s, these generalist predators have spread rapidly throughout the western Atlantic and Caribbean Sea to the detriment of invaded ecosystems (Côté et al. 2013). Although larval transport is responsible for the bulk of lionfish dispersal occurring at broad geographic scales (Johnston and Purkis 2011), there are discrepancies between rates of spread predicted by models of current-driven larval dispersal and those observed in the field (Côté et al. 2013; Freshwater et al. 2009). Moreover, studies of larval dispersal are of limited practical value to managers tasked with mitigating the impacts of lionfish through the targeted removal of adults (Akins 2012). The frequency of culling required to meet management goals will depend largely on rates of recolonization (Frazer et al. 2013; Green et al. 2014), which are determined partly by larval recruitment but also by the immigration of fish from neighbouring reefs (Lewis 1997). However, virtually no information on lionfish movement is currently available to inform culling programs.

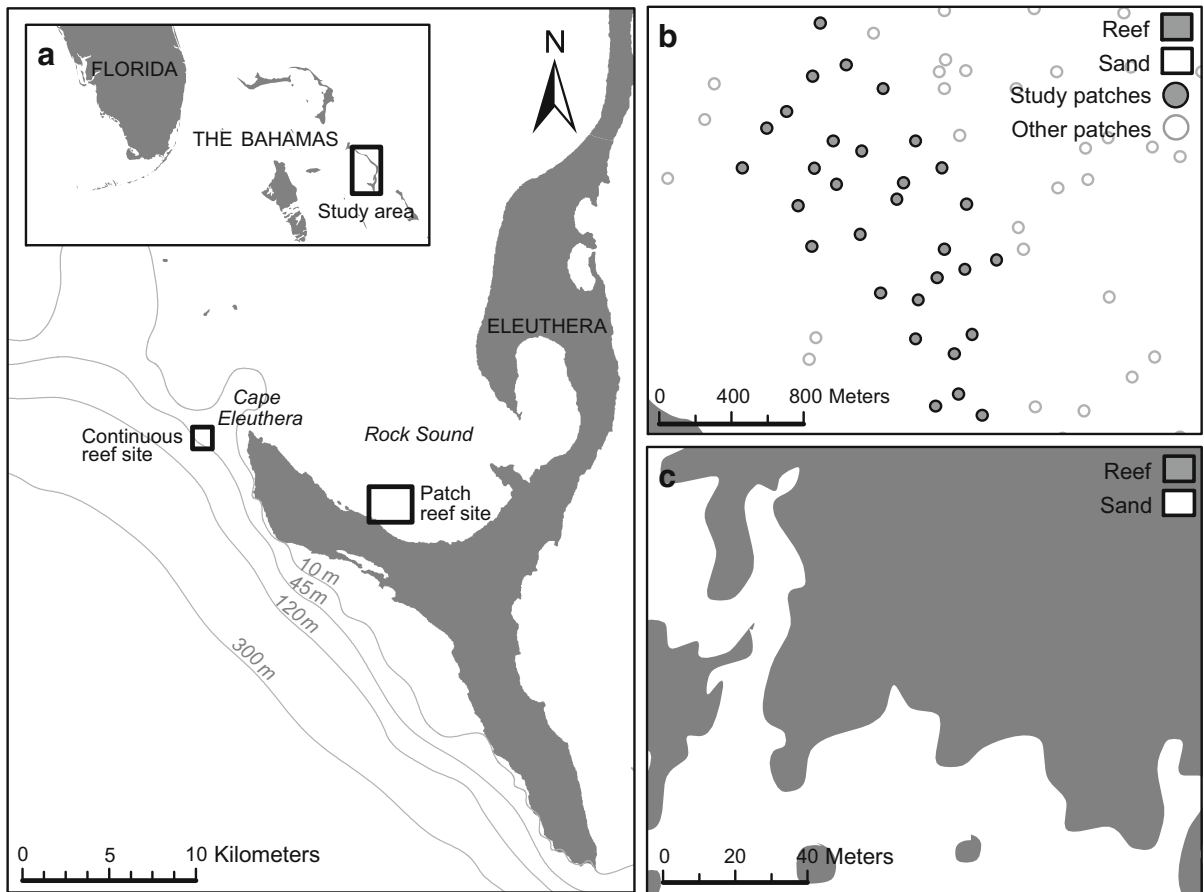
The only study of lionfish movement to date suggests highly restricted movements and small home ranges. In a Florida estuary, three-quarters of tagged lionfish moved less than 10 m from their tagging location over ~30 days at liberty, with a maximum observed movement of 420 m in 67 days (Jud and Layman 2012). However, this study focused on small lionfish ( $\leq 25$  cm total length) inhabiting a linear estuarine environment that is very different from the coral reef habitats most often invaded and most severely impacted by this invasive predator. Furthermore, adult lionfish exhibit many traits of good long-distance dispersers. As relatively large-bodied, intermittently active swimmers, they have the ability to cover great distances (Jenkins et al. 2007), while their venomous spines and capacity for prolonged fasting without detriment to health or survival (Morris et al. 2008) should minimize the risk of mortality by predation or starvation during movement through unfavorable habitats.

A better understanding of the post-settlement movements of invasive lionfish across invaded habitats is a crucial step in determining how best to distribute culling effort in space and time to optimize the use of limited management resources (Côté et al. 2013). Given our growing understanding of the influence of landscape connectivity in helping or hindering dispersal in terrestrial and marine environments (Hastings et al. 2005; Pittman et al. 2011; Pittman and McAlpine 2003; Turgeon et al. 2010), a complete picture of lionfish spatial ecology should include assessments of habitat-dependent movement (Côté et al. 2013). The goal of our study was therefore to quantify movements of adult lionfish in contrasting coral reef habitats. Using a mark-resighting method, we assessed the scale and frequency of lionfish movements on patchy and continuous reefs to explore general and habitat-dependent movement. Given that movement might occur readily across continuous areas of favourable habitats but be restricted by habitat fragmentation and the presence of sand barriers (Chapman and Kramer 2000; Fahrig 2007; Hastings et al. 2005; Turgeon et al. 2010), we anticipated a greater frequency of movement and a lower degree of long-term residence in high-connectivity, continuous reef habitats compared to less connected patch reef habitats. We also examined how finer-scale landscape characteristics, such as patch size, inter-patch distance, and rugosity, affected the probability of movement between reef patches (Bowler and Benton 2005). In addition, we asked how biotic factors such as body size, sex, and conspecific density might influence movement behaviour in each habitat (Bowler and Benton 2005). We conclude by exploring the implications of our results for lionfish invasion dynamics and management strategies.

## Materials and methods

### Study sites

We carried out tracking studies in July and August 2011 on two types of coral reef habitats off the island of Eleuthera, The Bahamas (Fig. 1a). The patch reef habitat comprised of 31 natural coral reef patches (Fig. 1b) occurring in a matrix of sand, with occasional seagrass and sparse gorgonians and sponges. Reef patches were at an average depth of 3 m, ranged in area



**Fig. 1** Study locations in South Eleuthera, The Bahamas (a). The patchy habitat area comprised 31 patch reefs (not drawn to scale) in Rock Sound (b), while the continuous habitat area encompassed reefs spurs and sandy grooves (c)

from  $\sim 17$  to  $570 \text{ m}^2$ , and were distributed over a  $2 \text{ km}^2$  area in Rock Sound ( $76^\circ 49.000\text{W}$ ,  $22^\circ 22.500\text{N}$ ), east of Cape Eleuthera. The minimum distance between two adjacent patches was approximately 80 m. The continuous reef habitat was represented by a  $100 \times 100 \text{ m}$  expanse of wide coral reef spurs and narrow sandy grooves at an average depth of 15 m, west of Cape Eleuthera ( $76^\circ 22.280\text{W}$ ,  $24^\circ 51.160\text{N}$ ; Fig. 1c). Both sites experienced similar water temperatures, ranging between  $29.4$  and  $32.2 \text{ }^\circ\text{C}$ . Although the two study areas differ in overall size, they held similar areas of coral reef and numbers of lionfish.

#### Data collection

We tracked lionfish movements using a mark-resighting design with external visual tags. This method was preferred over telemetry due to the challenges of signal loss and interference associated with tracking

crevice-dwelling species occurring at high densities (Jorgensen et al. 2006; Topping and Szedlmayer 2011). We tagged all lionfish  $>100 \text{ mm}$  in total length (TL) encountered on the study sites during the first 2 weeks of July 2011. Lionfish were tagged in situ by a team of two SCUBA divers using a method developed for this species that reduces the physiological stress, physical injury, and mortality associated with conventional surface-based tagging (Akins et al. 2014). Briefly, lionfish were captured using large transparent vinyl nets, measured (total length TL, to nearest cm) and photographed through the net, and then gently held against the substratum with only the tail protruding from the net. An 18-gauge syringe tip was inserted through the upper portion of the caudal peduncle and a 10-cm streamer tag with a unique 3-digit number (FTSL-73, Floy Tag & Mfg., Seattle, WA, USA) was threaded through the tip. The syringe tip was withdrawn to leave the tag in place. Two to three rays were

clipped from one pelvic fin to allow visual recognition of tagged fish and estimate tag loss. After a brief recovery period, fish were released near the point of capture. The total handling time was generally less than 1 min and fish behaved normally following release, typically retreating to a previous shelter.

Tagged lionfish were relocated through thorough lionfish-specific searches of each study area following the method of Green et al. (2013), carried out every 3–4 days for approximately 7 weeks. Surveys were conducted between 08.00 and 17.00, and proceeded across the same sequence of study sites between surveys. Survey times were well outside crepuscular periods when lionfish are expected to be most active (Cure et al. 2012), and thus minimized the possibility of failing to detect lionfish in transit between reefs. Tag numbers were read and recorded from a distance, using dive lights as needed, to minimize disturbance to tagged fish. We also recorded size (TL, estimated visually to nearest cm) and position of all untagged lionfish encountered during site surveys. Lionfish position was recorded upon first capture and at each subsequent resighting by recording the time on a dive watch synchronized to a portable GPS receiver (Garmin GPSMAP 76CSx, Garmin International Inc., Olathe, KS, USA; accuracy:  $\pm 3$  m) towed in a surface dive buoy, ensuring that the buoy was positioned directly over the target fish before recording data.

All tagged individuals that were resighted at the end of the study were captured and euthanized humanely at the surface in a clove oil and seawater solution (Green et al. 2012). Fish were then dissected and sex, body mass, visceral fat mass, and stomach contents were recorded. For fish that were not recaptured, we converted total length (cm) to weight (g) using the allometric scaling equation  $a_l L^{b_l}$ . For lionfish on patch reefs, we used  $a_l = 0.008$  and  $b_l = 3.1246$ , as calculated from specimens collected at this site during a previous study ( $R^2 = 0.91$ ,  $N = 1,242$  specimens ranging from 1.1 to 39.5 cm TL, S. Green unpublished data). For lionfish on deeper continuous reefs, we used  $a_l = 0.00497$ ,  $b_l = 3.291$ , as calculated for lionfish from reefs of a similar type and depth in New Providence, The Bahamas (Green et al. 2014).

Habitat characteristics, including rugosity, relief, substrate cover, and prey density, were measured along one to three 10 m transects on patch reefs, depending on patch size, and along six 10 m transects

on continuous reef. Rugosity was estimated by fitting a fine-link 5-m-long chain to the contours of the substrate, perpendicular to the transect line at 2-m intervals, and measuring the straight-line distance between the start and end of the chain (Wilson et al. 2007). Rugosity was calculated as the ratio of the total chain length to the straight-line length, with larger numbers indicating greater rugosity. Relief was measured as the height (cm) from the sea floor to the highest point on the reef. Reef area and inter-patch distance were measured from satellite imagery using ImageJ (Schneider et al. 2012). We were unable to complete surveys of prey fish density and substrate cover in each study area due to hurricane activity at the end of the study period and thus did not include these data in subsequent analyses.

#### Data analysis

All statistical analyses were carried out using the statistical software R, v2.14.1 (R Development Core Team 2008).

#### *Tracking and measuring movement and activity range*

Positional data from tagged lionfish were visualized using Garmin MapSource (v6.13.6, Garmin International Inc., Olathe, KS, USA) and ArcGIS ArcMap v10.0 (ESRI, Redlands, CA). For each tagged individual, we created a resighting history and recorded the number of resightings, duration between resightings, and movement between resightings, as well as the total movement over the entire study period. Here, movement is defined as the straight-line distance between two sighting locations, and total movement is defined as the sum of these distances across all resightings. We also assigned each tagged individual to one of three size classes (small, intermediate, or large), defined by dividing into thirds the range of total lionfish lengths for each habitat. For individuals resighted more than twice, we calculated activity range estimates using the minimum convex polygon (MCP) method in ArcGIS ArcMap v10.0 (ESRI, Redlands, CA) (Mireles et al. 2012; Vincent et al. 2005). Because our surveys took place exclusively during the day, these activity range estimates represent a minimum diurnal activity range, which is a subset of the overall home range that would include both diurnal

and nocturnal position fixes. We used generalized linear modelling to examine correlates of diurnal activity ranges.

### *Residency and population turnover*

We used a Kaplan–Meier survival analysis to assess differences in median residency and population turnover between the two habitat types. Residency was defined as the number of days tagged lionfish remained in the study areas. We used the rate of disappearance of tagged fish from each study area after the first week following tagging as a proxy for population turnover rates. We tested the significance of differences using a log-rank test (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011). Given the low expected natural mortality of adult lionfish (Morris 2009) and the near-absence of potential lionfish predators (e.g., very large grouper, barracuda, nurse sharks, or spearfishers) in the study areas, tagged fish that were not resighted were assumed to have emigrated out of the study areas, although a few of these individuals may have remained undetected within the study areas.

### *Factors influencing movement*

We explored factors influencing the scale and rate of movement using a series of hurdle models, which consider the binary and continuous components of ecological processes separately (Zuur et al. 2009). In our case, the decision to move or not is modelled as a binomial process, while the scale and rate of movement are modelled linearly. Our hurdle models used a negative binomial distribution to account for overdispersion in our data, with identical covariates applied to both portions of the model unless stated otherwise (Zuur et al. 2009).

We first modelled movement over the entire time at liberty by considering the effects of habitat type (patch or continuous), time at liberty, and intrinsic characteristics (body mass, sex, gonadosomatic index (GSI), and body condition estimated from the percentage of body mass composed of visceral fat as measured in euthanized lionfish) on the decision to move, and for those lionfish that did move, daily rate of movement ( $\text{m/day}^{-1}$ ) and total number of movements  $>10$  m. In this analysis, the number of movements was defined as an inter-patch displacement in patchy habitat and as

transition between several distinct shelter sites in continuous reef habitat. Because very few fish were recaptured for dissection, few data points were available for modelling the effects of sex, GSI, and body condition or for imputing missing values. For this reason, we used an ‘available-case’ analysis and modelled the effects of these variables separately to minimize bias due to missing data (Gelman and Hill 2006).

We next used hurdle models to examine the correlates of movement between resightings on patch reefs alone as differences in area and lionfish densities could not be easily calculated between locations on a continuous reef. We considered the effects of residence time in the initial patch and distance to the closest neighbouring patch as well as differences in patch area, rugosity, relief, and the density ( $\text{individuals/m}^2$ ) and median size (TL, cm) of lionfish between initial and destination patches on total distance moved (m) and, separately, on the rate of movement per day ( $\text{m/day}^{-1}$ ). Differences in these metrics between patches were calculated as the value on the destination patch minus the value on the initial patch. Although rugosity and relief information was included in early versions of the hurdle models, it did not add explanatory power in any model and both variables were dropped from the analysis. Although we included multiple movements per individual fish, these data were considered independent, as spatio-temporal autocorrelation is expected to be negligible when position fixes are obtained several days apart (Vincent et al. 2005) or at sites that are far apart relative to the movement ability of the study species (Rhodes et al. 2009).

## **Results**

### *Tagging summary*

We tagged and released a total of 38 fish at the patch reefs and 41 fish on the continuous reef (Table S1). Tagged fish ranged in size from 10.0 to 38.0 cm TL. Lionfish on patch reefs (mean  $\pm$  1 SD: 22.8 cm  $\pm$  5.9 cm, range 10–34.5 cm) were on average 5 cm smaller than those on continuous reefs (27.5  $\pm$  4.2 cm, range 20.0–38.0 cm, Welch’s *t* test;  $t_{66.66} = 4.18$ ,  $P < 0.0001$ ). Only one individual showed scarring indicative of tag loss at 32 days after tagging, but this specimen was subsequently identified based on comparison with photographs taken at first capture.

## Residency and population turnover

Across both habitats, 49 individuals (62 % of tagged fish) were recaptured at least once. Initial recapture rates were similar in both habitat types (patch: 58 %; continuous: 66 %; Welch's  $t$  test:  $t_{75,16} = 0.86$ ,  $P = 0.38$ ), and fish in both habitats had a similar mean time at liberty of approximately 2 weeks (patch: 11 days, range 1–36 days; continuous: 15 days, range 1–39 days; Welch's  $t$  test:  $t_{75,44} = -1.18$ ,  $P = 0.23$ ).

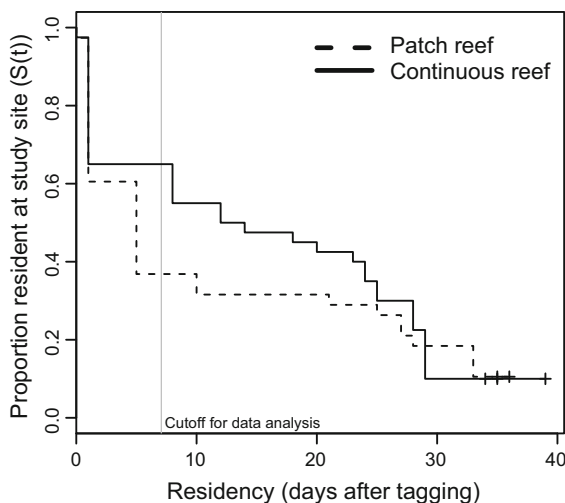
The number of tagged lionfish remaining within each habitat declined sharply in the first few days following tagging, potentially as the result of a tagging effect, and then declined steadily over time (Fig. 2). A survival analysis on the number of resightings per fish that remained within the study area for at least 7 days showed that resightings declined significantly more rapidly on the patch reefs than the continuous reef site (Log-rank;  $P = 0.02$ ), and the average number of resightings per individual was significantly greater on the continuous reef (continuous:  $4.6 \pm 2.1$ , patch:  $3.4 \pm 1.3$ , Welch's  $t$  test;  $t_{44,25} = 2.43$ ,  $P = 0.02$ ). A survival analysis on the residency of tagged fish showed that roughly 65 % of lionfish tagged on patch reefs were not resighted within 5 days after tagging,

while the remainder stayed within the tagging area for roughly 20 days before additional disappearances were observed. In contrast, less than 40 % of lionfish tagged on the continuous reef were not resighted within 5 days post-tagging, while the remainder disappeared at a steady rate over time. The median residency, defined as the duration after which 50 % of all original tagged fish remained, was 5 days on the patch reefs and 13 days on the continuous reef. The proportion of tagged fish remaining in each habitat converged towards the end of the study period (Log-rank;  $P = 0.17$ ), with roughly 10 % of tagged fish remaining.

We considered the possibility that differences in resightings between habitats might arise from differences in habitat complexity, which influences detectability. Mean relief and rugosity across 78 transects at each site were significantly greater on the continuous reef than on patch reefs (rugosity: patch  $0.78 \pm 0.17$  SD, continuous  $0.85 \pm 0.11$  SD, Welch's  $t$  test,  $t_{99,64} = -4.82$ ,  $P = 0.002$ ; relief: patch  $1.21 \pm 1.16$  SD, continuous  $2.94 \pm 2.96$  SD, Welch's  $t$  test,  $t_{129,36} = -3.16$ ,  $P < 0.001$ ). Lower detectability owing to higher structural complexity is therefore unlikely to account for the more rapid loss of tagged fish on patch reefs.

The end of the field study period coincided with the passage of category 3 hurricane Irene almost directly over the study sites. We took this opportunity to determine whether hurricane activity displaced lionfish from their habitual shelter areas. A survey on the continuous reef 3 days following peak hurricane activity revealed that of 21 tagged lionfish present 5 days before the storm, only 7 remained.

At the end of the study, 10 tagged fish (6 females, 4 males) were recovered from the patch reefs and 8 tagged fish (6 females, 2 males), from the continuous reef. The mean total time at liberty for individuals with at least one resighting was 21 days from initial tagging (range 5–39 days). During an opportunistic survey conducted on the continuous reef in February 2012, after completion of the study, two tagged individuals remained 170 and 174 days after tagging.



**Fig. 2** Proportion of tagged lionfish that were resighted in two contrasting reef habitats in Eleuthera, The Bahamas, in relation to residency, measured as the numbers of days after tagging. The vertical ticks indicate fish still present in each study area at the end of the observation period and are treated as censored data. The vertical grey line indicates the 7-day cut-off point prior to which data were excluded from statistical comparisons of the rate of loss of tagged fish

## Activity range size estimates

Minimum diurnal activity range estimates were determined for 18 lionfish on the continuous reef. Diurnal activity range areas were highly overlapping



among individuals and ranged in size from 20 to 1,340.5 m<sup>2</sup>, with a mean ( $\pm$ SD) of 552 m<sup>2</sup> ( $\pm$ 436.5 m<sup>2</sup>). Diurnal activity range did not vary with sex (GLM,  $P = 0.24$ ), total length ( $P = 0.32$ ), days at liberty ( $P = 0.28$ ), or number of resightings ( $P = 0.45$ ). The relative rarity of movements between patch reefs led to us to treat these movements as range shifts, and we did not calculate home range areas for lionfish on patch reefs.

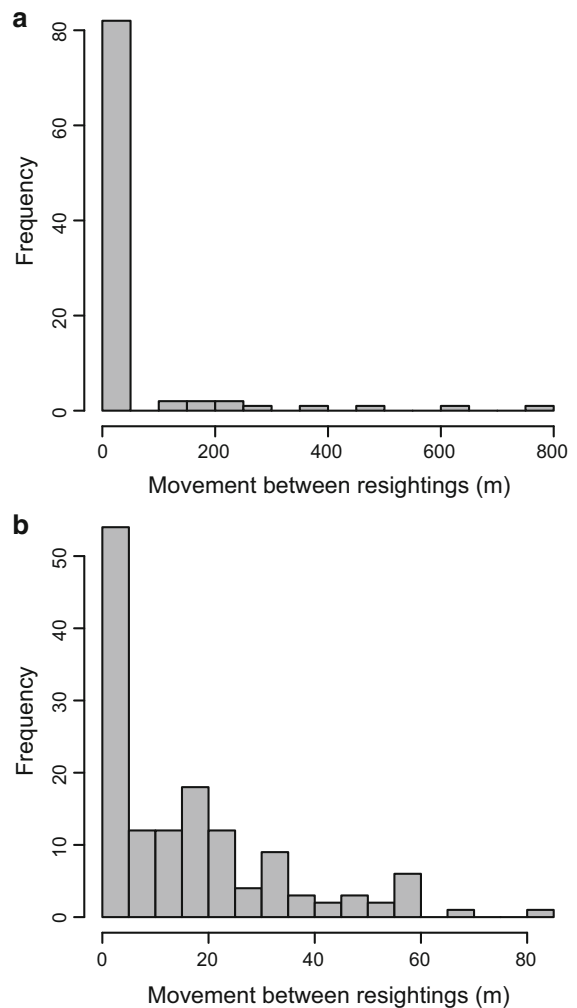
### Scale and frequency of movements

On patch reefs, most tagged fish remained on the patch of first capture. Of the 22 fish tagged on patch reefs that were resighted at least once, only 10 undertook at least one movement between patches, traveling 300–800 m across open habitat to immediately neighbouring patches. Six of these fish subsequently moved between patches a second time.

The mean total distance moved by lionfish across patch reefs over the course of the study was  $166 \pm 338$  m, with a maximum total movement of 1.38 km over 15 days for a fish at liberty for 28 days (fish 035; Table S1). Even the shortest movements in the patch reef habitat represented movements between patches rather than movements within reefs. The mean rate of movement over the entire time at liberty on the patch reefs was  $6.7 \pm 12.0$  m day<sup>-1</sup> (range 0–49.3 m day<sup>-1</sup>; 22 individuals).

The distribution of distances moved between resightings on patch reefs was strongly positively skewed, with no movement or short-distance movements being common, and longer movements rarer (Fig. 3a). The mean maximum rate of movement between resightings that were at least 1 day apart on patch reefs was  $13.03 \pm 33.4$  m day<sup>-1</sup> (range 0–146.3 m day<sup>-1</sup>; 22 individuals).

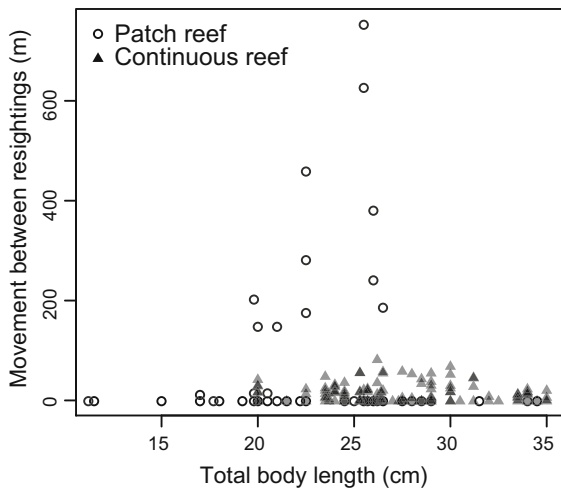
On the continuous reef, only 6 fish (14 %) remained at the shelter sites where they were first captured, while the remainder frequently moved short distances between shelter sites (i.e., overhangs or holes in the reef structure). The mean total movement by lionfish on the continuous reef over the course of the study period was  $80 \pm 48$  m, with a maximum total movement of 158 m over 35 days (fish 035; Table S1). The mean rate of movement over the entire time at liberty on the continuous reef site was  $3.9 \pm 2.8$  m day<sup>-1</sup> (range 0.2–12.2 m day<sup>-1</sup>; 27 individuals).



**Fig. 3** Frequency distribution of distances (m) travelled between resightings by tagged lionfish in patchy coral reef habitat (a) and continuous coral reef habitat (b)

As on patch reefs, the distribution of distances moved between resightings on the continuous reef was strongly positively skewed (Fig. 3b). Longer-range movements comparable to those on patch reefs likely occurred to locations outside the study area and so were not detected during our surveys. The maximum rate of movement between resightings that were at least 1 day apart on the continuous reef was  $6.1 \pm 9.5$  m day<sup>-1</sup> (range 0–49.2 m day<sup>-1</sup>; 27 individuals).

Although all fish undertook short movements in each habitat, the longest movements in both habitats were undertaken by fish of intermediate body lengths (Fig. 4). On patch reefs, 8 of 21 (38 %) intermediately-sized individuals (20–28 cm TL) accounted for 75 % of



**Fig. 4** Frequency distribution of individual movement events across lionfish body sizes in patch and continuous reef habitats showing a trend towards greater maximum movements between resightings at intermediate body sizes

movements longer than the median movement (187 m). On the continuous reef, 11 of 29 individuals (37 %) of intermediate size (23–32 cm TL) accounted for 71 % of longer-than-median movements (37 m). The maximum movement between resightings was significantly greater for lionfish in intermediate size classes than for either smaller or larger fish across both habitat types (Kruskal–Wallis;  $\chi^2 = 9.28$ ,  $P = 0.01$ ). The possibility that this pattern was caused by the disproportionate emigration of the largest fish out of the study area was ruled out by the lack of correlation between body length and number of resightings ( $R^2 = 0.02$ ,  $n = 47$ ,  $P = 0.5$ ) or residency ( $R^2 = 0.008$ ,  $n = 47$ ,  $P = 0.2$ ).

#### Factors influencing movement over the time at liberty

The likelihood of movement increased significantly with time at liberty, but did not vary between habitat types or with any of the lionfish characteristics considered (Table 1a).

The total distance moved increased significantly with time at liberty (odds ratio (OR) = 1.09, Table 1b), and the rate of movement was significantly greater on patch reefs than on continuous reef (Table 1b) by a factor of roughly 50 %. There were significantly fewer movements per individual on patch reef habitat than continuous reef habitat (Table 1d). There was no significant effect of body mass, sex, GSI,

or body condition on the rate of movement or the number of movements per individual (Table 1), but this lack of significance could be due to the small sample sizes.

#### Factors influencing movement between resightings in patchy habitat

The likelihood of moving to a new patch was not significantly influenced by prior residence time (days), differences in patch area ( $m^2$ ), or differences in the median size (TL, cm) of lionfish between patches. However, the likelihood of moving to a new patch was significantly greater when the destination patch was closer (OR = 0.97), and, more importantly, supported a lower lionfish density than the initial patch (OR < 0.0001; Table 2a). Thus, lionfish became many orders of magnitude more likely to move to another patch as the difference in lionfish density between the initial and chosen patches increased. There was also a near-significant interaction between lionfish density and median size (OR < 0.0001; Table 2a), indicating that the increased likelihood of movement when moving down a density gradient became many orders of magnitude more pronounced when also moving down a mean size gradient.

For fish that did move, the only determinant of distance moved between resightings was the small but significant influence of distance to the nearest patch. Counter-intuitively, lionfish moved longer distances when patches were closer together (Table 2b), such that a lionfish moving between patches 500 m apart would make trips that were roughly 3 m shorter than lionfish moving between patches 100 m apart. The rate of movement between resightings showed a small but significant increase with shorter residency times on the initial patch, larger destination patches, shorter distances to the nearest patch, and when the destination patch supported lionfish of a lower median size (Table 2c). As with the probability of movement, differences in lionfish density emerged as the most important predictor of the rate of lionfish movement. The rate of movement between resightings increased significantly when the destination patch supported a lower density of lionfish than the initial patch (Table 2c). There was again a near-significant interaction between lionfish density and median size (Table 2c).



**Table 1** Factors influencing movement over time at liberty

Response	Factor	$b \pm SE$	$P$
(a) Probability of moving during time at liberty (zero hurdle model)	Habitat (patch)	$-20.07 \pm 5,273.00$	0.99
	Time at liberty (days)	$0.09 \pm 0.040$	0.02*
	Body mass (g)	$<0.001 \pm <0.001$	0.95
	<i>Body condition (% fat)</i>	$30.64 \pm 206.83$	0.88
	<i>Sex (male)</i>	$0.80 \pm 2.61$	0.86
	<i>Gonadosomatic index</i>	$216.46 \pm 562.78$	0.68
(b) Distance moved over time at liberty (count model)	Time at liberty (days)	$0.03 \pm 0.01$	0.04*
	Body mass (g)	$<0.001 \pm <0.001$	0.80
	<i>Body condition</i>	$104.47 \pm 92.44$	0.26
	<i>Sex (male)</i>	$-0.21 \pm 1.10$	0.49
	<i>Gonadosomatic index</i>	$-50.64 \pm 74.12$	0.84
(c) Movement rate over time at liberty (count model)	Habitat (patch)	$1.54 \pm 0.38$	<0.0001*
	Time at liberty (days)	$-0.03 \pm 0.01$	0.10
	Body mass (g)	$<0.001 \pm <0.001$	0.72
	<i>Body condition</i>	$11.68 \pm 91.31$	0.89
	<i>Sex (male)</i>	$-0.39 \pm 0.98$	0.69
	<i>Gonadosomatic index</i>	$-70.68 \pm 85.29$	0.41
(d) Number of movements over time at liberty (count model)	Habitat (patch)	$-1.50 \pm 0.51$	0.003*
	Time at liberty (days)	$0.02 \pm 0.01$	0.09
	Body mass (g)	$4.13 \pm 7.42$	0.57
	<i>Body condition</i>	$-65.53 \pm 101.48$	0.52
	<i>Sex (male)</i>	$-0.39 \pm 0.99$	0.69
	<i>Gonadosomatic index</i>	$-20.85 \pm 57.52$	0.72

Factors influencing movement over the entire time at liberty of tagged lionfish in Eleuthera, The Bahamas. The results were derived from hurdle General Linear Models. (a) The probability of moving is the zero hurdle shared by all models. The results of subsequent separate count models are given for (b) distance moved, (c) rate of movement, and (d) number of movements over time at liberty. For categorical factors, the baseline level for comparison is given in parentheses. For continuous factors, the unit of measurement is given in parentheses. Major variables are shown in normal case ( $N = 78$ ) while minor variables ( $N = 18$ ) are shown in italics. Minor variables were modelled separately from the main factors due to a low sample size given the low recapture rate at the end of the study (see “Methods”)

\* Significant variable

## Discussion

Understanding the extent and drivers of movement is critical for predicting the distribution of mobile invasive species and designing effective control programs. Our study provides the first systematic description of the fine-scale spatial ecology of invasive lionfish in coral reef habitats. We show that lionfish are much more mobile than previously thought and exhibit habitat- and size-dependent movement. Our findings have significant implications for invasion dynamics and for the management of lionfish and mobile marine invaders in general.

Some lionfish stay: residency and activity range size estimates

Our study demonstrates a high frequency of residency when compared to previous studies, at least for a subset of individuals. Our initial recapture rate of 58–66 %, observed across two contrasting coral reef habitats, is high compared to typical returns of less than 10 % in mark-recapture studies of most fishes (Freiwald 2012). It is also higher than the 24 % recapture rate seen in an earlier tagging study of lionfish with opportunistic rather than systematic surveys (Akins et al. 2014), but our results are comparable to typical returns of

**Table 2** Factors influencing movement between resightings in patchy habitat

Response	Factor	$b \pm SE$	$P$
(a) Probability of movement between resightings (zero hurdle model)	Residence time on initial patch	$-0.079 \pm 0.079$	0.31
	Distance to nearest patch (m)	$-0.023 \pm 0.011$	0.03*
	$\Delta$ area (m <sup>2</sup> )	$-0.011 \pm 0.007$	0.12
	$\Delta$ lionfish density (fish/m <sup>2</sup> )	$-427.6 \pm 201.7$	0.03*
	$\Delta$ median total length (cm)	$0.297 \pm 0.194$	0.13
	Density: median TL interaction	$53.8 \pm 28.7$	0.06~
(b) Distance moved between resightings (count model)	Residence time on initial patch	$-0.018 \pm 0.039$	0.63
	Distance to nearest patch (m)	$-0.007 \pm 0.002$	<0.001*
	$\Delta$ area (m <sup>2</sup> )	$<0.001 \pm <0.001$	0.42
	$\Delta$ lionfish density (fish/m <sup>2</sup> )	$2.508 \pm 2.253$	0.26
	$\Delta$ median total length (cm)	$-0.005 \pm 0.019$	0.75
	Density: median TL interaction	$1.123 \pm 0.625$	0.07~
(c) Movement rate between resightings (count model)	Residence time on initial patch	$-0.246 \pm 0.020$	<0.001*
	Distance to nearest patch (m)	$-0.006 \pm 0.001$	<0.001*
	$\Delta$ area (m <sup>2</sup> )	$0.002 \pm <0.001$	<0.001*
	$\Delta$ lionfish density (fish/m <sup>2</sup> )	$-3.304 \pm 1.172$	0.004*
	$\Delta$ median total length (cm)	$0.024 \pm 0.009$	0.01*
	Density: median TL interaction	$2.250 \pm 0.423$	<0.001*

Factors influencing movement between resightings of tagged lionfish in Eleuthera, The Bahamas. The results were derived from hurdle General Linear Models of individual movement events between patches ( $N = 232$ ). (a) The probability of moving between resightings is the zero hurdle shared by all models. The results of subsequent separate count models are given for (b) distance moved and (c) rate of movement, between resightings. The distance to the nearest patch was not included in the zero hurdle analysis as it was not expected to be a factor in deciding to leave a patch

\* Significant variable

~ Near-significant variable

50–75 % in systematic mark-recapture studies of other, mostly site-attached, coral reef fishes (Chapman and Kramer 2000). The high recapture rate (80 %) observed in tagged juvenile lionfish in a Florida estuary (Jud and Layman 2012) was probably due to the linear nature of the suitable habitat, which limited the possible directions of movement and increased the likelihood of recapture. Based on the residency curves (Fig. 2), there are some low-mobility individuals (~10 % of tagged fish) that remained within a restricted area until the end of the study and up to 170 days after tagging. This result contrasts with the findings of other tagging studies in tropical and temperate reef fish, which generally find a much larger proportion of resident (~80 %) than of mobile individuals within a population (Freiwald 2012).

As with all mark-resighting studies, there are several reasons other than emigration to explain why tagged lionfish might not have been resighted. One possibility is a decline in detectability due to a shift

towards more cryptic behaviour, which has been observed in areas where lionfish are regularly culled (Côté et al. 2014). Our study areas have never been subjected to regular culling and any behavioural changes in response to a brief in situ tagging procedure are expected to be minimal compared to repeated culling attempts or more invasive implantation of a telemetry transmitter. At any rate, any increase in cryptic behaviour should have a more pronounced effect on detectability in habitats of greater complexity, at least with conventional underwater visual census methods (e.g., Green et al. 2013). However, the lionfish-focused searches adopted for our study are meant to minimize the effects of habitat complexity, and observed differences in complexity across habitats were small. Thus, although a post-tagging change in lionfish behaviour and detectability might account for some early lionfish losses, we do not believe that this explains overall differences in resighting frequencies between habitats. Additional possibilities for failure to

resight tagged lionfish include tag loss and/or tagging-related mortality. However, previous tank trials of streamer tags in lionfish have reported 100 % recovery and tag retention (Akins et al. 2014). An increase in tag-induced predation also seems unlikely because there are few records of predation on lionfish in the Caribbean and we observed very few predators large enough to consume adult lionfish on our study sites. Given that alternative reasons for the loss of tagged fish are unlikely, we believe that the majority of fish lost to follow-up surveys emigrated out of the study areas.

Multiple recaptures of the same individuals at a given site provide evidence for the existence of home ranges (Attwood and Cowley 2005). In patchy habitat, repeated individual captures tended to occur with the same patch, and we did not observe lionfish repeatedly moving among the same patches, which might have suggested that these multiple patches were part of a home range. Home range size of lionfish on reef patches is probably simply equal to patch size, although it may also include some of the surrounding sand or seagrass habitat. Activity range size was more easily estimated in continuous habitat. The diurnal activity range size of lionfish on the continuous reef at Eleuthera ( $552 \pm 436.5 \text{ m}^2$ ) was greater than the mean linear home range of 28 m previously reported in estuarine environments (Jud and Layman 2012). Moreover, an opportunistic nocturnal survey on the continuous reef suggests that lionfish leave their daytime shelters to either forage or spawn in a different area of the reef (NT, personal observations), a pattern observed in other reef fish (Holland et al. 1993), including other species of lionfish (Moyer and Zaiser 1981). Given that lionfish are known to be most active at dawn and dusk (Cure et al. 2012), the diurnal activity range we report is likely much smaller than home range estimates incorporating nocturnal movements (e.g., Verweij and Nagelkerken 2007). A longer study of externally tagged fish or acoustic tagging might ultimately reveal even larger activity ranges than documented here and allow for a more robust analysis of predicted determinants of true home range size.

#### Some lionfish move: Scale and frequency

The overall scale and frequency of lionfish movements observed here are greater than previously recorded. In a Florida estuary, three-quarters of tagged lionfish did not move more than 10 m from their initial tagging location

and movements were generally short, with only 3 % moving more than 100 m, and a maximum movement of 420 m over 67 days at liberty (Jud and Layman 2012). In contrast, our study documented frequent movements of up to 50 m in continuous reef habitat and infrequent movements of up to 800 m among coral reef patches. The maximum movement we recorded was 1.38 km over 15 days at liberty in patch reef habitat.

Reported differences in the maximum distances travelled in patchy and continuous reefs may be an artefact of differences in the sizes of the study areas. We readily acknowledge that the maximum distances moved in continuous reef habitat might be as large or larger than those recorded in the much larger patch reef study area. However, because the maximum distance moved between resightings in each habitat was much smaller than the longest axis of the corresponding study area, differences in study area sizes are not expected to have biased other metrics of movement, such as mean movement distance or rate of movement between resightings. Notwithstanding this caveat, lionfish clearly have the potential to move long distances.

Invasive lionfish on coral reefs are not only more mobile than previously thought, but they also appear to be more mobile than many other reef fishes. Similar-sized predators in the Caribbean show a similar distribution of local movements (Chapman and Kramer 2000) but invasive lionfish demonstrated a greater scale and frequency of long-distance movements, including those crossing large expanses of sand often considered to be barriers to the movement of most reef fishes. Post-settlement dispersal is mainly limited by risk of mortality, associated with increased risks of predation or starvation while travelling through unfavourable habitat (Bartoń et al. 2012; Fahrig 2007). However, as previously stated, lionfish have venomous spines and can fast for long periods (Morris et al. 2008), which probably reduces the risks of movement compared to other fishes. Given that the rate of invasive range expansion is largely determined by the distances moved by the most mobile individuals in a population (Bartoń et al. 2012), traits that reduce the risk of long-distance movements have undoubtedly contributed to the highly successful range expansion of invasive lionfish.

#### Why move?

Individual decisions to move are influenced by the relative costs and benefits of moving, which in turn

depend on both extrinsic (context-dependent) and intrinsic (condition-dependent) factors (Clobert et al. 2009; Swingland 1984). Avoidance of intraspecific competition is a strong extrinsic driver of movement across taxa (Bowler and Benton 2005; Clobert et al. 2009). Competition is expected to be pronounced among lionfish given their high densities in their invaded range (Green and Côté 2009), density-dependent growth on patch reefs (Benkwitt 2013), and the scaling of prey consumption rates with lionfish body mass (Côté and Green 2012). Lionfish most likely experience exploitation rather than interference competition, given the absence of overt territoriality or aggression among foraging individuals (personal observations). Our results suggest that lionfish move between reef patches in part to avoid competition: the probability of moving to another reef was significantly higher when the initial reef supported a higher density of lionfish than the destination reef. On its own, such density-dependent movement would even out differences among patches in lionfish density, but density variation persists. Another factor, prey availability, is known to vary among patches and to influence lionfish density (Green et al. 2014). The combination of lionfish number, sizes and prey availability undoubtedly determine patch suitability for a traveling lionfish, but we could not determine prey abundance during this study. Once lionfish leave a patch, the distance they travel before re-settling depends on patch spacing. Lionfish move exclusively to adjacent patches when the distance to the nearest neighbouring patch exceeds roughly 150 m, but may move several patches away when patches are closer together. The counter-intuitive result is that lionfish end up moving further when patches are closer. This suggests that when patches are closely spaced and the risks of movement are low, lionfish may sample more than one reef before deciding where to settle.

Age- and size-related differences in dispersal behaviour are common intrinsic drivers of movement (Bowler and Benton 2005). The longest movements between resightings observed in this study were consistently undertaken by lionfish of intermediate size, regardless of habitat type. This pattern is best understood by considering size-specific costs and benefits of moving. The costs of moving might be high for the smallest individuals because they might not yet be physically capable of undertaking long movements and may face some risk of predation away from

familiar shelters (Attwood and Cowley 2005; Jenkins et al. 2007; Maljković et al. 2008). Indeed, a study of density-dependent growth of juvenile lionfish on artificial reefs reported very little movement of juveniles between reefs at all densities, despite evidence of intra-specific competition (Benkwitt 2013). While lionfish of similar size will compete for similarly-sized prey, the benefits to small lionfish of moving in terms of reducing intraspecific competition might be limited because their diet does not overlap greatly with that of larger, more competitive lionfish (Morris and Akins 2009). Conversely, the costs of moving for the largest individuals might be low, but the benefits are also low since they can outcompete smaller fish in their neighbourhood (Bowler and Benton 2005; Swingland 1984). Other coral reef predators, such as the Indo-Pacific grouper (*Epinephelus tauvina*), also show an increased tendency towards a sedentary lifestyle at large body sizes (Kaunda-Arara and George 2004). Fish of intermediate sizes, on the other hand, incur a relatively low cost of movement to realize the benefit of reduced intraspecific competition gained by moving to a less densely populated habitat patch.

#### Implications of habitat-dependent movement for invasion dynamics and management

We have shown that seascape structure influences the movements of a mobile marine invasive predator. Lionfish movements tend to be shorter and more frequent in continuous habitat, as individuals are more likely to find suitable habitat nearby, and rarer but longer in patchy habitats, where movements must at least match inter-patch distances. Moreover, the shorter median residency of tagged lionfish and the concave shape of the residency curve in patchy compared to continuous reef habitats suggest greater net population turnover in patchy habitats. Together, these differences should result in different patterns of spread across each of these two habitats. In newly invaded, continuous habitat, the spread of mobile adults may occur through slow and steady leading-edge dispersal. In patchy habitat, where individuals are forced to move farther to find suitable habitat, invaders will spread through sporadic and potentially more rapid jump dispersal using patches as stepping stones (Wilson et al. 2008).

Although larval transport remains the principal driver of invasive range expansion in the sea, the

movement of mobile adults is expected to contribute in two ways. First, post-settlement movements will determine the ultimate distribution of individuals across areas of high habitat connectivity, which will in turn affect competition and thus population dynamics. Larval supply is highly variable in space and time (Sale 2004), and the density and distribution of adult fish often does not correlate with larval supply or recruitment (Steele et al. 2002). Thus, the movement of adults is expected to contribute to local spread and population growth, particularly in times or regions of low propagule pressure such as in the early stages of invasion. Second, post-settlement movements may play an important role in range expansion by bridging gaps in current-driven larval transport pathways (Freshwater et al. 2009). For example, the strong northwesterly surface currents and the freshwater outflow of the Amazon-Orinoco plume (AOP) are thought to represent a formidable barrier to surface transport of lionfish larvae (Luiz et al. 2013). However, this barrier could be overcome by adult lionfish, given their freshwater tolerance (Jud and Layman 2014) and capacity for long-distance movement (this study). Importantly, the increasing anthropogenic fragmentation of coastal habitats is likely to amplify the competitive advantage of highly vagile invaders, such as lionfish, over native species experiencing higher costs of dispersal (Fahrig 2007).

Invasions taking place over heterogeneous land- or seascapes, including coral reefs, are difficult to manage effectively with spatially uniform regional management plans (Albers et al. 2010). Our findings are a first step towards more informed lionfish management planning and can help managers to choose appropriate removal demographics, sites, and frequencies based on their budget and management objectives (Epanchin-Niell and Wilen 2012). For example, when management aims to limit ecological impact in areas where lionfish are well established, culling should target the largest individuals, which have the highest consumption and reproduction rates (Green et al. 2014). On the other hand, when management prioritizes limiting spread in newly invaded areas, our results suggest that culling should instead target intermediate-sized individuals, which are more likely to drive recolonization, and patchy habitats, where longer-range movements may accelerate spread.

Our study highlights how post-settlement movements can be important for the spread and persistence

of marine invasive species and how the propensity for movement of lionfish is influenced by numerous factors including body size, competition, and the surrounding seascape. The movement behaviour of marine invaders can have profound effects on management outcomes, and we argue that basic research on the movement ecology of marine invasive species is a crucial first step in optimizing the allocation of limited management resources to achieve conservation goals.

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