

Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

**This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.**

**Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.**

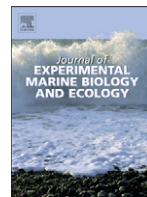
**In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:**

**<http://www.elsevier.com/copyright>**



Contents lists available at SciVerse ScienceDirect

## Journal of Experimental Marine Biology and Ecology

journal homepage: [www.elsevier.com/locate/jembe](http://www.elsevier.com/locate/jembe)

## Site fidelity and movement patterns of invasive lionfish, *Pterois* spp., in a Florida estuary

Zachary R. Jud <sup>\*</sup>, Craig A. Layman

Marine Sciences Program, Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA

### ARTICLE INFO

#### Article history:

Received 6 October 2011

Received in revised form 18 January 2012

Accepted 27 January 2012

Available online xxxx

#### Keywords:

Fish

Growth

Home range

Invasive species

Movement

Tagging

### ABSTRACT

Understanding how individuals within a population of invasive organisms disperse during various life history stages has obvious implications for long term population dynamics in the invaded range. With the rapid expansion of the invasive Indo-Pacific lionfish (*Pterois volitans* and *Pterois miles*) in the western Atlantic and Caribbean, it has become increasingly important to understand how individuals move following initial recruitment, as this may have critical implications for population control and management. We conducted a 10-month mark–recapture study in the lower Loxahatchee River estuary (Florida, USA) to identify movement patterns and site fidelity in juvenile and young adult lionfish. We tagged 55 lionfish, ranging in size from 45 to 185 mm standard length (66–256 mm total length). Eighty percent of the tagged fish were recaptured at least one time during the course of the study. Lionfish in this system exhibited extremely high site fidelity over extended periods of time and across multiple size classes. Maximum range occupied by individuals along the shoreline of the estuary was small (mean = 28 m, asymmetrical 95% CI: 10 to 51 m), and did not vary with lionfish size. The majority of lionfish recaptures (74%) occurred at or near (0–10 m) the previous capture site, even after weeks or months at liberty. In systems where lionfish exhibit extremely high site fidelity and small maximum ranges, localized population control may be feasible, since lionfish removed from a given habitat would be replaced largely through larval recruitment rather than migration of older individuals. However, since lionfish grow extremely rapidly (averaging 0.46 mm/day, but reaching as high as 0.78 mm/day in one individual), localized control efforts would need to be carried out frequently in order to maintain a younger, smaller population. Localized control may be less effective if lionfish exhibit greater movement and lower site fidelity in other invaded systems.

© 2012 Elsevier B.V. All rights reserved.

### 1. Introduction

Patterns of dispersal through ontogeny play an important role in the establishment and spread of invasive organisms (Carlton, 1989; Kolar and Lodge, 2001; Wilson et al., 2009). In marine systems, factors associated with reproduction and early life history (e.g., spawning frequency, egg and larval dispersal, larval survival, and settlement behavior), combined with some type of anthropogenic dispersal vector, are typically believed to drive the initial distribution of invasive organisms (Carlton, 1996; Carlton and Geller, 1993; Ruiz et al., 1997). However, movements that occur during later life history stages can also influence the distribution and population structure of invasive species over time. Understanding how individuals within a population of invasive organisms move following initial recruitment has a number of implications related to long term dispersal, as well as control and eradication (Brown et al., 2006; Cookingham and Ruetz, 2008; Lapointe et al., 2010; Vrieze et al., 2011).

The Indo-Pacific lionfish *Pterois volitans* and *Pterois miles* (morphologically indistinguishable species, hereafter referred to as lionfish) have spread rapidly throughout the western Atlantic and Caribbean (Freshwater et al., 2009; Hamner et al., 2007; Schofield, 2009; Whitfield et al., 2002). Several parameters associated with lionfish dispersal during early life history have been documented, including spawning frequency, gamete production, and pelagic larval duration (Ahrenholz and Morris, 2010; Morris et al., 2011). High fecundity, combined with an approximately 26-day pelagic larval phase, likely led to the rapid and widespread dispersal of the species throughout their invaded range. However, little is known about post-recruitment movement patterns in lionfish, despite the fact that these movements may affect population dynamics. While existing lionfish population models include parameters related to recruitment and early life history processes, they do not account for movement of individuals following recruitment (Barbour et al., 2010a; Morris et al., 2010). Several short-term foraging studies (Albins and Hixon, 2008; Côté and Maljković, 2010; Green et al., 2011) have inferred that lionfish do not typically undertake large movements during or between foraging bouts. However, these studies were not designed to track lionfish movement over extended periods of time (weeks to months).

<sup>\*</sup> Corresponding author at: Tel.: +1 305 919 5602; fax: +1 305 919 4030.  
E-mail address: [zackjud@gmail.com](mailto:zackjud@gmail.com) (Z.R. Jud).

The goal of this study was to examine movement patterns of post-recruitment lionfish at a temporal scale of weeks to months. Our specific objectives were to (1) identify level of site fidelity among lionfish, and (2) determine whether maximum range occupied was a function of body size. Additionally, we used recapture data to identify daily growth rates across a range of lionfish sizes. Such data may play a significant role in the design and implementation of future management and eradication plans, as lionfish site fidelity and movement patterns may ultimately drive the success of localized control efforts. Although lionfish movements may differ among invaded systems, our findings provide a starting point for similar studies in other habitats.

## 2. Materials and methods

To identify lionfish movement patterns, we conducted a mark-recapture study in the lower Loxahatchee River estuary (26°57' N, 80°06' W), near Jupiter, Florida (VanArman et al., 2005). The lower portion of this estuary is heavily marine influenced, with semidiurnal tides pushing ocean water into the system through Jupiter Inlet. Substrate in the lower Loxahatchee estuary is primarily sand, with structurally complex habitats (e.g., seagrass, mangroves, and human-made structures) restricted to shoreline areas (Jud et al., 2011). Along the section of shoreline that we utilized for this study, structurally complex habitats (mostly small artificial reefs and docks) were discrete and patchy, rather than continuous, and were separated by an average of 30 m (range: 6–97 m) of largely bare sand bottom. Because of the linear nature of the system, habitats could be classified along an estuarine (i.e., further upstream) to marine (i.e., further downstream) gradient. Compared to other frequently invaded habitats (e.g., coral reefs), the patchy nature and linear arrangement of habitats, shallow water depth, and proximity to shore made a tagging study in the

Loxahatchee estuary logistically easier to conduct. Although lionfish are typically considered reef fish, their presence in an estuary is not surprising given that they are commonly found in nonreef habitats (e.g., turbid bays and estuaries) in their native range (A. Anton, Unpublished results; Kulbicki et al. 2012).

We tagged lionfish along a section of the south shoreline of the Loxahatchee estuary located between 2.0 and 3.7 km from the ocean (Fig. 1). Although lionfish have been found further upriver in the Loxahatchee estuary, we chose this section because it was similar to some other habitats (e.g., mangroves, coastal rock jetties, shallow artificial reefs, and canals) that have been invaded by lionfish (Barbour et al., 2010b; Biggs and Olden, 2011; Morris and Akins, 2009). We sampled this section of shoreline at least one time per month from September 2010 to July 2011 (except February and March 2011). During each daytime sampling event, we visually surveyed an ~30 m wide belt along the entire section of shoreline while snorkeling. We attempted to capture and tag all untagged lionfish that were observed during the visual surveys.

Lionfish were captured using hand nets and anesthetized using tricaine methanesulfonate (MS-222) mixed with aerated seawater (100 mg/l). Standard length (SL) and total length (TL) were measured. Fish were then tagged using Floy fingerling tags (FTF-69, Floy Tag & Mfg.). These 6.4 × 3.2 mm plastic tags were sutured into the dorsal musculature between the spinous and soft dorsal fins and secured with a single overhand knot (Fig. 2). Slack was left in the loop of suture to allow for growth. Each tag contained a unique three digit number. Additionally, to facilitate underwater visual identification of individual tagged fish, color-coded glass beads (~3 mm diameter) were added to the loop of suture material. Depending on body size, each fish received between zero and three glass beads. The arrangement of bead colors was unique to each fish and could be readily identified while snorkeling.

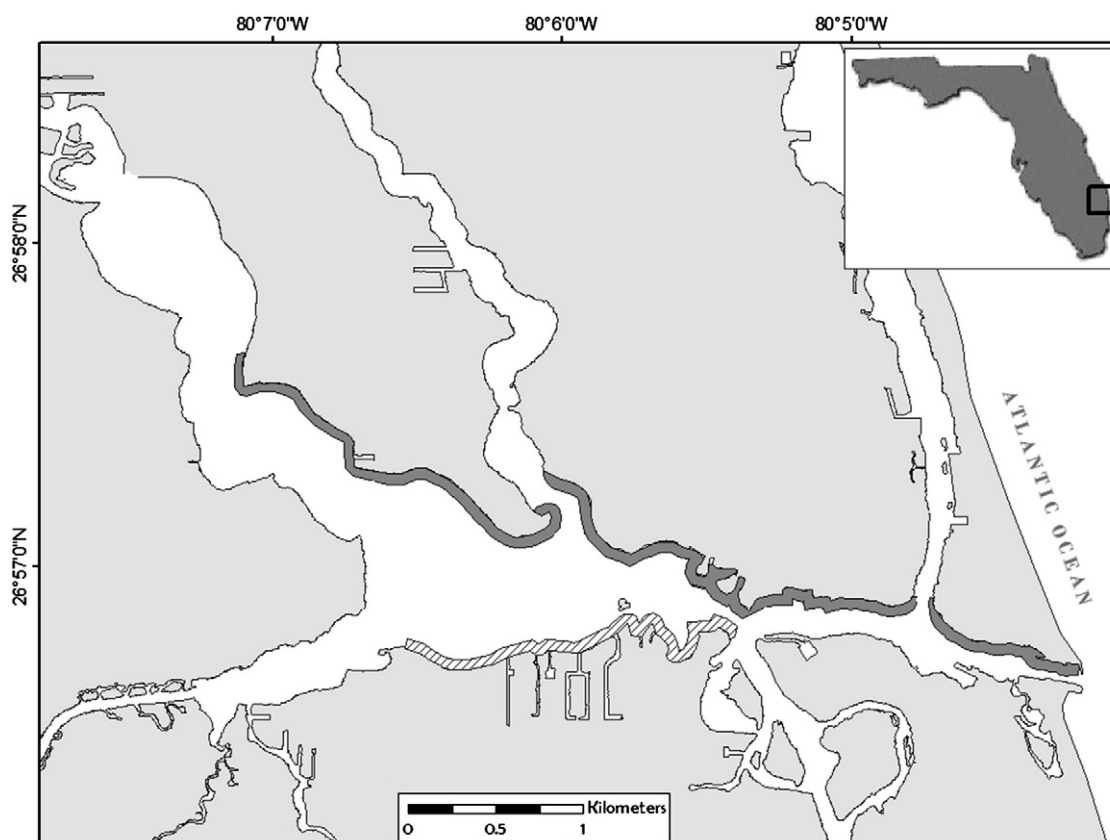


Fig. 1. Map of the Loxahatchee estuary, Jupiter, Florida (center of black box in inset map). The lionfish mark-recapture study was conducted along the south shoreline of the estuary, in the area indicated by hatching. Additional surveys were conducted along the north shoreline (dark gray shading) as part of a concurrent study (Jud et al., 2011). Both survey areas extended ~30 m from shore (not to scale).



**Fig. 2.** Tagged lionfish (*Pterois* spp.), showing the oval Floy fingerling tag (FTF-69, Floy Tag & Mfg.) and two color-coded glass beads, sutured into the dorsal musculature between the spinous and soft dorsal fins. A three digit number is printed on the reverse of the Floy tag.

Tag retention rates using this method were not directly tested, but no tag shed was observed in two caged individuals over a period of ~3 months, and only two untagged individuals captured in the field had scars that were suggestive of tag loss. Following tagging, fish were placed into aerated seawater until fully recovered, and then returned to their exact capture location. GPS was used to record the location of each tagging site. To document the exact position of a fish within the tagging site, we precisely described various habitat characteristics (e.g., specific rocks, sponges, human-made items) that were immediately adjacent to the individual at the time of capture.

Recaptures of tagged lionfish during visual surveys were divided into two categories; (1) visual sightings and (2) physical recaptures. Visual sightings occurred when the identity and exact location of a previously tagged lionfish could be determined while snorkeling, without physically handling or removing the fish from the water. Physical recapture of lionfish with hand nets was necessary to acquire positive identification when tags became obscured by the growth of fouling organisms. These individuals were briefly removed from the water to verify identity, and then returned to their exact capture site. We used this opportunity to clean the tags and measure individuals to calculate growth rates. For the remainder of the paper, these two categories will be referred to jointly as “recaptures” (i.e., including both visual sightings and physical recaptures). By lumping visual sightings and physical recaptures for analysis purposes, we provide more fine-scale spatial and temporal detail regarding movement patterns.

In addition to surveying the study area along the south shoreline, we concurrently conducted extensive visual surveys for lionfish in other sections of the estuary (Fig. 1) as part of a separate study (Jud et al., 2011). These surveys were conducted every 11–12 weeks and would have allowed us to identify tagged lionfish that had migrated out of the core study area and into other parts of the estuary. At the conclusion of the tagging study in July 2011, all remaining tagged lionfish were collected.

For each lionfish recapture, we calculated the number of days that had passed since the previous capture. Since some fish were recaptured multiple times, we examined (1) movements that occurred during each discrete at-large period, and (2) total observed maximum range occupied between initial tagging and final recapture. We used digitalized aerial imagery to measure the straight-line distance moved between each recapture. All movements were categorized as upstream or downstream. Maximum range occupied was calculated by measuring the straight-line distance between the most upstream and the most downstream capture locations for each fish. While range measurements (like home range) are typically reported as two-dimensional area values (Burt, 1943; Hammerschlag-Peyer and Layman, 2010), we report

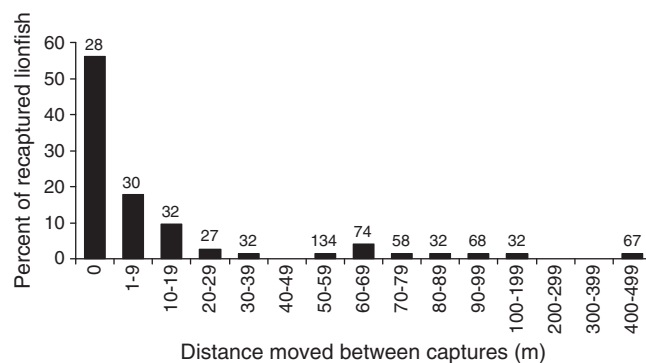
one-dimensional values (i.e., distance) for maximum range occupied because structurally complex habitats are arrayed in a relatively narrow band along the shoreline in the Loxahatchee estuary. Since all of our documented lionfish movements were along this linear shoreline, a one-dimensional interpretation of maximum range occupied simplifies comparison of habitat use among tagged individuals.

We calculated daily growth rates for all individuals that were physically recaptured and measured (change in SL/days at liberty). Regression analysis was used to quantify the relationship between lionfish size and daily growth rate. For this analysis, we chose to use estimated length at the midpoint of each at-large period (initial SL + final SL \* 0.5) rather than using initial or final length. This allowed us to account for variability in time at liberty among individuals. Mean daily growth rate (calculated from all physical recaptures) was used to estimate SL at the time of each visual sighting, where exact measurements were lacking. Actual and estimated lengths at the time of each discrete recapture were used to compare direction of movement among 25 mm size classes. To relate body size to overall maximum range occupied, we first calculated SL at the midpoint of each individual's total at-large period (from initial tagging to final recapture). We then used these midpoint SL values to compare maximum range occupied across 25 mm size classes.

### 3. Results

Between September and November 2010, and April and May 2011, we tagged 55 lionfish in the Loxahatchee estuary (see Table 1, Supplementary material). Tagged fish ranged in size from 45 to 185 mm SL (66 to 256 mm TL), with a mean  $\pm$  standard deviation of  $102 \pm 26$  mm SL ( $144 \pm 35$  mm TL). Forty-four individuals were recaptured at least one time, representing an 80% recapture rate. Of the 44 recaptured individuals, 27 (61%) were recaptured once and 10 (23%) were captured twice. The remaining seven individuals (16%) were recaptured 3–5 times each. In total, 73 discrete recapture events were recorded during the course of the study. Thirty-eight of these were visual sightings, and 35 were physical recaptures. The mean total time at liberty ( $\pm$  standard deviation) for the 44 recaptured individuals was  $56 \pm 44$  days (from initial tagging to final recapture). Two individuals were recaptured 197 days after they were tagged, the longest period at liberty.

The majority of lionfish did not move between captures. Out of 73 discrete recapture events, 41 (56%) represented fish that had remained in the exact location ( $\pm 0.5$  m) since their previous capture, and an additional 13 (18%) were fish that had moved less than 10 m (Fig. 3). Only two recaptures (3%) represented movements of more than 100 m. The greatest distance moved during any single at-liberty period was 420 m in 67 days by a 126 mm SL individual. All recaptured lionfish were located along the south shoreline of the estuary, where tagging



**Fig. 3.** Distance moved between captures for 73 discrete recapture events. Mean time at liberty (number of days between discrete recaptures) is presented above each distance category.

had been carried out, and all were found in structurally complex habitats. Concurrent with this study, we thoroughly surveyed a 5.5 km section of the north shoreline of the estuary on multiple occasions, killing > 200 lionfish (Jud et al., 2011). We did not detect any tagged lionfish during these surveys.

Regression analysis was conducted to establish the relationship between lionfish length (SL) in mm, and daily growth rate (G) in mm/day, for all lionfish that were physically recaptured and measured, resulting in the equation:

$$G = -0.0019SL + 0.6587 (n = 35, R^2 = 0.14, P < 0.05 : \text{Fig. 4})$$

The mean daily growth rate ( $\pm$  standard deviation) based on 35 physical recaptures (representing 28 individuals) was  $0.46 \pm 0.13$  mm/day. The most rapid growth rate was 0.78 mm/day in an individual that grew from 68 to 86 mm SL in 23 days (Fig. 4).

We used the mean daily growth rate value to estimate SL for each of the 38 visual sightings, allowing us to examine movement patterns based on size for all 73 discrete recaptures. For most size classes, the greatest proportion of individuals remained stationary between captures (Fig. 5). When movements did occur, downstream movements were more frequent than upstream; however, the magnitude of most movements was small. Of the ten longest discrete movements that we observed ( $\geq 30$  m), nine were in an upstream-to-downstream direction. The individuals that made these longer movements ranged in size from 80 to 146 mm (mean  $\pm$  SD:  $116 \pm 24$  mm), and were tagged throughout the study area. Direction of movement appeared to vary between seasons. While the frequency of downstream movements (including the small number of longer movements) was similar between fall/early winter and spring/early summer, there were fewer upstream movements during the spring/early summer period.

The mean observed maximum range occupied for the 44 individuals that were recaptured was 28 m (asymmetrical 95% confidence interval: 10 to 51 m). Twenty-one individuals (48%) had maximum ranges of  $\leq 0.5$  m (i.e.,  $-0$  m) during their entire at-large period. Another nine fish (20%) had maximum ranges of  $\leq 6$  m. Only one individual had a maximum range of  $> 150$  m. Maximum range occupied did not vary among 25 mm size classes (Kruskal–Wallis;  $H = 1.54$ ,  $P = 0.67$ ). For six (35%) of the 17 individuals that were recaptured more than once, total observed maximum range occupied was a product of multiple downstream movements. Four individuals (24%) made a combination of upstream and downstream movements while at liberty, four (24%) remained stationary, and three (17%) made multiple upstream movements.

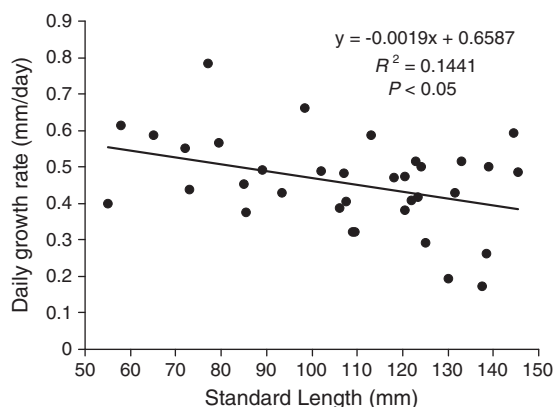


Fig. 4. Regression of lionfish standard length (SL; mm) versus daily growth rate (mm/day) based on 35 physical recaptures. Linear regression fit is shown. Standard lengths were estimated at the midpoint of each at-large period (initial SL + final SL  $\times 0.5$ ).

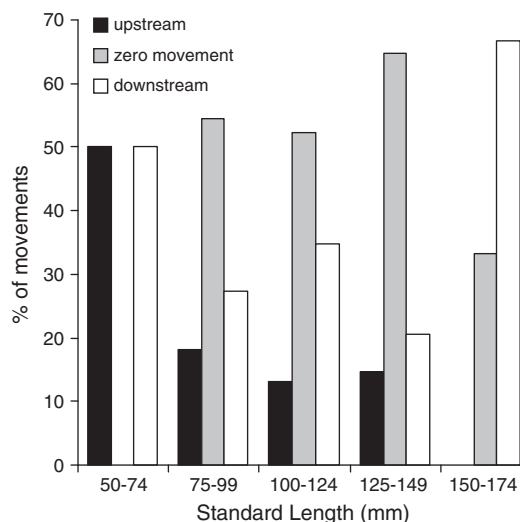


Fig. 5. Direction of movement versus lionfish standard length (at time of recapture) based on 73 unique recapture events. Standard length was directly measured for physical recaptures, and estimated for visual sightings using a calculated daily growth rate of 0.46 mm/day.

#### 4. Discussion

Lionfish in the Loxahatchee estuary appear to exhibit extremely high site fidelity over extended periods of time and across multiple size classes. We found that a large percentage of tagged individuals were recaptured at the same location (often within a few cm) as their previous capture, even after weeks or months at liberty. Based on our exceptionally high recapture rate (80%), these movement patterns are likely representative of the local estuarine lionfish population. While tagged lionfish were observed moving from one patch of suitable habitat to another along the south shoreline of the estuary, we did not document any individuals moving across the estuary to the north shoreline. To do so would require crossing 300–700 m of largely featureless sand bottom.

A number of factors may contribute to the high site fidelity that we observed in lionfish. Extreme prey naïveté and enemy release, which often occur following the introduction of a novel predator (Sih et al., 2010), could influence lionfish movement patterns. Native prey species may not recognize lionfish as predators, allowing the invaders to successfully hunt from a fixed location without having to actively forage for elusive prey. Furthermore, lionfish may not be recognized as prey by native predators, reducing the frequency of movements associated with predator avoidance. Alternatively, lionfish may forage at night, returning to a fixed resting spot during daylight hours, when all of our observations were made. While lionfish on invaded coral reefs are most active around sunrise and sunset, they do not appear to travel far during most foraging bouts (Côté and Maljković, 2010; Green et al., 2011), suggesting that our daytime observations provide an accurate estimate of long-term habitat use.

Invasive lionfish have been shown to occupy a very wide variety of habitats, including the sea floor at depths of 300 m, offshore and near-shore coral reefs, inshore seagrass, mangrove, and human-made habitats, and even estuarine habitats up to 5.5 km from the ocean (Albins and Hixon, 2011; Barbour et al., 2010b; Biggs and Olden, 2011; Jud et al., 2011). While ontogenetic shifts in habitat use have been documented in many species of reef fishes, with the most common shifts occurring between inshore nursery habitats (e.g., estuaries, mangrove forests, sea grass beds) and offshore adult habitats (e.g., coral reefs) (Adams et al., 2006; de la Moriniere et al., 2002; Gillanders et al., 2003; Grol et al., 2011; Mumby et al., 2004; Verweij et al., 2007), it is not presently known how lionfish use different habitats through ontogeny. Although the spatial and temporal scale of this study prevented any definitive conclusions from being drawn regarding ontogenetic habitat

shifts in lionfish, we were able to provide some initial observations about habitat use in the Loxahatchee estuary across the range of sizes that we tagged. Because we did not observe a positive relationship between maximum range occupied and lionfish body size, nor did we see strong evidence of incremental downstream movements with increasing size, it seems likely that juvenile and young adult lionfish that initially settle in estuaries do not necessarily experience an inshore-to-offshore migration like many other marine fishes. However, since most of the larger movements we observed were in a downstream direction (regardless of fish size), it is possible that some individuals do eventually leave the estuary and enter the ocean.

As with any passive tagging study, we were only able to positively confirm the presence of individuals that were recaptured; the ultimate fate of tagged fish that were not recaptured was unknown (e.g., mortality, tag shed, and long-distance migration). Tagging studies often underestimate (or completely fail to detect) long-distance movements of fishes, since recapture efforts usually occur at or near the initial tagging location (Gillanders et al., 2003). Since we did not search for tagged lionfish in the myriad offshore habitats adjacent to the Loxahatchee estuary, we are unable to reject the possibility that some individuals did move out of the system.

It is possible that lionfish larger than those tagged in this study may exhibit a different set of movement behaviors. The size range we tagged was a product of the relatively recent nature of the invasion in the Loxahatchee estuary (Jud et al., 2011). We tagged the largest lionfish that we observed in the newly invaded system (185 mm SL, 256 mm TL), but this was smaller than the maximum size obtained by lionfish in the western Atlantic and Caribbean (483 mm TL; R. Straney, Unpublished results). However, since lionfish begin to reach sexual maturity at approximately 100 mm TL (~70 mm SL), our sample included both juveniles and young adults (Morris, 2009). This suggests that sexual maturity alone does not trigger a shift towards offshore (i.e., coral reef) habitats for lionfish that initially recruit to inshore habitats.

The smallest lionfish we observed were almost always solitary. However, larger individuals were frequently found in groups of 2–10. Lionfish that were tagged as small solitary juveniles were often later recaptured at another location in the presence of several other individuals. It is not clear whether some specific habitat characteristic is causing these aggregations, or whether they are of a social origin. During the course of this study, we observed that lionfish are capable of making an audible noise when disturbed. Although sound production has not previously been documented in lionfish, other members of Scorpaenidae are known to be soniferous (Kasumyan, 2008). It is possible that vocalization plays a role in the social behavior of lionfish (including aggregating behaviors), as is the case with other soniferous reef fishes (Mann et al., 2009; Nelson et al., 2011; Tricas et al., 2006).

The Loxahatchee estuary represents a simple linear system in which to develop an initial understanding of how lionfish move through their environment. We feel that the same tagging effort in a more complex three-dimensional habitat (e.g., a continuous tract of coral reef) would have resulted in much lower recapture rates due to the difficulties associated with thoroughly surveying such systems. Although habitats in the Loxahatchee estuary are similar to some other nearshore habitats that have been invaded by lionfish (mangroves, canals, small artificial reefs, etc.), the structural arrangement of these habitats is quite different from the continuous coral reefs where lionfish are frequently found. It is unclear how the movement patterns we documented in an estuarine system will compare to other invaded habitats, especially coral reefs. If the patterns we observed hold true in other systems, it seems likely that lionfish would readily move between closely situated habitat patches (or within continuous habitats), but would be less likely to move across large open expanses between habitats patches.

Salinity variation is one factor that differentiates estuarine lionfish habitats from most other invaded systems. Although the upper portion of the Loxahatchee estuary does experience fluctuating salinity due to freshwater inflow, we do not believe that this influenced lionfish

movement patterns in the lower portion of the estuary where tagging was carried out. A strong salt wedge was consistently present at our study site (Jud et al., 2011), and salinity in the lower portion of the water column was almost always the same as seawater (~35‰). Since we observed some upstream movements during the wettest part of the year (late summer to fall), as well as a reduction in upstream movements during the driest part of the year (spring to early summer), it seems unlikely that freshwater inflow alone was responsible for the downstream movements we documented.

While complete eradication of lionfish in the western Atlantic and Caribbean is unlikely (Barbour et al., 2010a; Morris et al., 2010), the post-recruitment movement patterns we identified may play an important role in the effectiveness of future lionfish management and control efforts in certain habitats. If the high site fidelity and small maximum ranges that we observed in the Loxahatchee estuary also occur in other invaded systems, these behavioral traits would likely increase the effectiveness of localized control measures, since lionfish removed from a given habitat would largely be replaced through larval recruitment alone, rather than a combination of recruitment and direct migration of older individuals. In systems where lionfish exhibit high site fidelity and small post-recruitment movements, intensive local removal over time could lead to populations of lionfish that are dominated by younger individuals, resulting in a smaller ecological impact through reduced prey consumption and diminished reproductive capacity. Based on our observations, successful localized control through continuous removal seems more likely for discrete or patchy habitats that are similar to those found in the Loxahatchee estuary (e.g., small and isolated natural or artificial reefs) as opposed to continuous and complex habitats like expansive fringing or barrier coral reefs. Because of the extremely rapid growth rate exhibited by lionfish, localized control efforts would need to be carried out frequently in order to maintain a younger, smaller population. For this reason, future management goals must maintain a realistic balance between the cost and effort needed to locally control lionfish populations and the actual benefit (ecological, economic, esthetic, etc.) associated with reduced lionfish abundance.

## Acknowledgments

We would like to thank J. Lee for assistance in the field and D. Sabin for creating maps of the study sites. Additionally, we appreciate the continued support and cooperation of numerous homeowners along the Loxahatchee estuary as well as the Loxahatchee River District. Lionfish were collected pursuant to Florida Fish and Wildlife Conservation Commission Permit # SAL-09-1118A-SR. Partial funding was provided by NSF OCE #0746164 and OCE #0940019.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at [doi:10.1016/j.jembe.2012.01.015](https://doi.org/10.1016/j.jembe.2012.01.015).

## References

- Adams, A.J., Dahlgren, C.P., Kellison, G.T., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I., Serafy, J.E., 2006. Nursery function of tropical back-reef systems. *Mar. Ecol. Prog. Ser.* 318, 287–301.
- Ahrenholz, D.W., Morris Jr., J.A., 2010. Larval duration of the lionfish *Pterois volitans* along the Bahamian Archipelago. *Environ. Biol. Fishes* 88, 305–309.
- Albins, M.A., Hixon, M.A., 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar. Ecol. Prog. Ser.* 367, 233–238.
- Albins, M., Hixon, M., 2011. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ. Biol. Fishes* 1–7.
- Barbour, A.B., Allen, M.S., Frazer, T.K., Sherman, K.D., 2010a. Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS One* 6, 1–7.
- Barbour, A.B., Montgomery, M.L., Adamson, A.A., Diaz-Ferguson, E., Silliman, B.R., 2010b. Mangrove use by the invasive lionfish *Pterois volitans*. *Mar. Ecol. Prog. Ser.* 401, 291–294.
- Biggs, C.R., Olden, J.D., 2011. Multi-scale habitat occupancy of invasive lionfish (*Pterois volitans*) in coral reef environments of Roatan, Honduras. *Aquat. Invasions* 6, 447–453.

- Brown, G.P., Phillips, B.L., Webb, J.K., Shine, R., 2006. Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biol. Conserv.* 133, 88–94.
- Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24, 346–352.
- Carlton, J.T., 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.* 3, 265–273.
- Carlton, J.T., 1996. Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.* 78, 97–106.
- Carlton, J.T., Geller, J.B., 1993. Ecological roulette — the global transport of nonindigenous marine organisms. *Science* 261, 78–82.
- Cookingham, M.N., Ruetz III, C.R., 2008. Evaluating passive integrated transponder tags for tracking movements of round gobies. *Ecol. Freshw. Fish* 17, 303–311.
- Côté, I.M., Maljković, A., 2010. Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar. Ecol. Prog. Ser.* 404, 219–225.
- de la Morinière, E.C., Pollux, B.J.A., Nagelkerken, I., van der Velde, G., 2002. Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuar. Coast. Shelf Sci.* 55, 309–321.
- Freshwater, D.W., Hines, A., Parham, S., Wilbur, A., Sabaoun, M., Woodhead, J., Akins, L., Purdy, B., Whitfield, P.E., Paris, C.B., 2009. Mitochondrial control region sequence analyses indicate dispersal from the US East Coast as the source of the invasive Indo-Pacific lionfish *Pterois volitans* in the Bahamas. *Mar. Biol.* 156, 1213–1221.
- Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Mar. Ecol. Prog. Ser.* 247, 281–295.
- Green, S., Akins, J., Côté, I., 2011. Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar. Ecol. Prog. Ser.* 433, 159–167.
- Grol, M., Nagelkerken, I., Rypel, A., Layman, C., 2011. Simple ecological trade-offs give rise to emergent cross-ecosystem distributions of a coral reef fish. *Oecologia* 165, 79–88.
- Hammerschlag-Peyer, C.M., Layman, C.A., 2010. Intrapopulation variation in habitat use by two abundant coastal fish species. *Mar. Ecol. Prog. Ser.* 415, 211–220.
- Hamner, R.M., Freshwater, D.W., Whitfield, P.E., 2007. Mitochondrial cytochrome b analysis reveals two invasive lionfish species with strong founder effects in the western Atlantic. *J. Fish Biol.* 71, 214–222.
- Jud, Z.R., Layman, C.A., Lee, J.A., Arrington, D.A., 2011. Recent invasion of a Florida (USA) estuarine system by lionfish *Pterois volitans* / *P. miles*. *Aquat. Biol.* 13, 21–26.
- Kasumyan, A., 2008. Sounds and sound production in fishes. *J. Ichthyol.* 48, 981–1030.
- Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16, 199–204.
- Kulbicki, M., Beets, J., Chabanet, P., Cure, K., Darling, E., Floeter, S.R., Galzin, R., Green, A., Harmelin-Vivien, M., Hixon, M., Letourneur, Y., de Loma, T.L., McClanahan, T., McIlwain, J., MouTham, G., Myers, R., O'Leary, J.K., Planes, S., Vigliola, L., Wantiez, L., 2012. Distribution of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. *Mar. Ecol. Prog. Ser.* 446, 189–205.
- Lapointe, N.W.R., Thorson, J.T., Angermeier, P.L., 2010. Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac River system. *Ecol. Freshw. Fish* 19, 566–577.
- Mann, D., Locascio, J., Coleman, F., Koenig, C., 2009. Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. *Endang. Species Res.* 7, 229–236.
- Morris, J.A., Jr., 2009. The biology and ecology of the invasive Indo-Pacific lionfish. Ph.D. dissertation, North Carolina State University. 168 pp.
- Morris Jr., J.A., Akins, J.L., 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ. Biol. Fishes* 86, 389–398.
- Morris Jr., J.A., Shertzer, K.W., Rice, J.A., 2010. A stage-based matrix population model of invasive lionfish with implications for control. *Biol. Invasions* 13, 7–12.
- Morris Jr., J.A., Sullivan, C.V., Govoni, J.J., 2011. Oogenesis and spawn formation in the invasive lionfish, *Pterois miles* and *Pterois volitans*. *Sci. Mar.* 75, 147–154.
- Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorchynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., et al., 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427, 533–536.
- Nelson, M.D., Koenig, C.C., Coleman, F.C., Mann, D.A., 2011. Sound production of red grouper *Epinephelus morio* on the West Florida Shelf. *Aquat. Biol.* 12, 97–108.
- Ruiz, G.M., Carlton, J.T., Grosholz, E.D., Hines, A.H., 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am. Zool.* 37, 621–632.
- Schofield, P.J., 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.
- Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S., Vonesh, J.R., 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119, 610–621.
- Tricas, T.C., Kajiura, S.M., Kosaki, R.K., 2006. Acoustic communication in territorial butterflyfish: test of the sound production hypothesis. *J. Exp. Biol.* 209, 4994–5004.
- VanArman, J., Graves, G.A., Fike, D., 2005. Loxahatchee watershed conceptual ecological model. *Wetlands* 25, 926–942.
- Verweij, M.C., Nagelkerken, I., Hol, K.E.M., van den Beld, A., van der Velde, G., 2007. Space use of *Lutjanus apodus* including movement between a putative nursery and a coral reef. *Bull. Mar. Sci.* 81, 127–138.
- 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.
- Whitfield, P.E., Gardner, T., Vives, S.P., Gilligan, M.R., Courtenay Jr., W.R., Ray, G.C., Hare, J.A., 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Mar. Ecol. Prog. Ser.* 235, 289–297.
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J., Richardson, D.M., 2009. Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol. Evol.* 24, 136–144.