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INVASION NOTE

Occurrence of invasive lionfish (*Pterois volitans*) larvae in the northern Gulf of Mexico: characterization of dispersal pathways and spawning areas

L. L. Kitchens · C. B. Paris · A. C. Vaz · J. G. Ditty · M. Cornic · J. H. Cowan Jr. · J. R. Rooker

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Abstract Here we document for the first time the presence of invasive lionfish larvae (*Pterois volitans*) in the Gulf of Mexico. Three lionfish larvae (standard length: 3.9–5.9 mm) were collected during summer ichthyoplankton surveys in the northern Gulf of Mexico in 2011, with species identification confirmed through the genetic analysis of mitochondrial DNA. Pigmentation patterns of these larvae are described and compared with published lionfish descriptions. Otolith microstructure analysis revealed that larvae were 14–17 days old and that spawning occurred in June and July. A biophysical dispersal model was used to backtrack larvae to their potential spawning locations and results indicated that spawning occurred in the southern Gulf of Mexico near the Yucatán Peninsula, suggesting that these larvae may have been transported into the northern Gulf of Mexico by the Loop Current. Here we provide useful information for identifying lionfish larvae and offer insight into lionfish spawning and larval dispersal pathways.

Keywords Lionfish · *Pterois volitans* · Fish larvae · Gulf of Mexico · Larval dispersal · Morphology

Introduction

Populations of the invasive red lionfish (*Pterois volitans,* hereafter lionfish) have expanded at an unprecedented rate across the western Atlantic Ocean

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L. L. Kitchens (✉) · M. Cornic · J. R. Rooker
Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Road, Galveston, TX 77553, USA
e-mail: l.kitchens@tamu.edu

L. L. Kitchens · J. R. Rooker
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA

C. B. Paris · A. C. Vaz
Division of Applied Marine Physics, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

J. G. Ditty
National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, 4700 Avenue U, Galveston, TX 77551, USA

J. H. Cowan Jr.
Department of Oceanography and Coastal Sciences, Louisiana State University, 2247 Energy, Coast and Environment Building, Baton Rouge, LA 70803, USA

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within the past two decades (González et al. 2009; Morris et al. 2009; Ruttenberg et al. 2012). Native to the Indo-Pacific Ocean, this predatory reef fish was first introduced into Florida waters as a result of aquarium releases in the 1980's (Morris and Whitfield 2009) and has since become rapidly established in tropical and subtropical waters throughout the Atlantic coast of the U.S., Caribbean Sea, and Gulf of Mexico. Lionfish first invaded the Gulf of Mexico in 2009, potentially due to larval transport from spawning populations in the Caribbean Sea via the Loop Current (Aguilar-Perera and Tuz-Sulub 2010). Populations quickly became widespread in the Gulf of Mexico, colonizing the coastline of every Gulf state as well as natural and artificial reefs in offshore waters within a 5-year period (Dahl and Patterson 2014; USGS-NAS 2015).

Lionfish possess a suite of life history attributes that facilitate successful and rapid colonization of non-native habitats, including defensive venomous spines, efficient predatory skills, fast growth, and high reproductive rates (Morris et al. 2009; Green et al. 2011; Albins and Hixon 2013). As generalists, lionfish use a variety of marine habitats such as seagrass beds, mangroves, and coral reefs (Kulbicki et al. 2012; Valdez-Moreno et al. 2012; McTee and Grubich 2014) within their invaded range, which extends from Venezuela to North Carolina (Schofield 2009; Lasso-Alcalá and Posada 2010). They are known to feed on a variety of fishes and invertebrates (Morris and Akins 2009; Valdez-Moreno et al. 2012), and experience little to no predation in their new territory (Cure et al. 2012; Kulbicki et al. 2012). As a result, their presence can reduce biodiversity and influence the trophic structure in certain marine ecosystems (Albins and Hixon 2008; Green et al. 2012). In fact, invasion of western Atlantic and eastern Pacific waters by Indo-Pacific lionfishes (genus *Pterois*) has become one of the top issues of concern to global conservation (Sutherland et al. 2010).

Lionfish have extensive dispersal capabilities as a result of their reproductive strategy. They are known to spawn during the first quarter of the year (Ruiz-Carus et al. 2006; Vásquez-Yeomans et al. 2011), but evidence suggests that lionfish may spawn year round at a frequency of every 4 days (Morris and Whitfield 2009), resulting in an annual fecundity of over 2 million eggs (Morris 2009). Reproductive studies of lionfish from the Red Sea suggest that spawning occurs near the surface, where females release a buoyant pair of mucous-encapsulated egg clusters. Over time, the mucous clusters deteriorate and the eggs are released into the water column (Fishelson 1975) where ocean currents can disperse the eggs and larvae across large distances during the 20–35 day planktonic larval period prior to settlement (Ahrenholz and Morris 2010; Vásquez-Yeomans et al. 2011; Kulbicki et al. 2012). As a result, the reproductive traits of lionfish have likely played a significant role in the rapid and widespread expansion of their populations across the western Atlantic Ocean.

Basic information on the early life stage of lionfish is needed in order to better assess their distribution and understand the population dynamics of this invasive species (Côté et al. 2013). While there have been thousands of documented sightings of lionfish in the Gulf of Mexico over the past 5 years (USGS-NAS 2015), only juvenile and adult stages have been reported thus far. Here, we examine the important early life period (larval stage) of lionfish collected in the Gulf of Mexico. The primary objectives of this study were to provide an early life description (diagnostic characters and pigmentation) of lionfish larvae captured during ichthyoplankton cruises in the Gulf of Mexico and characterize environmental conditions in which larvae were found. In addition, a biophysical connectivity modeling system was used in conjunction with otolith-based age estimates to predict the spawning locations of these lionfish larvae.

Methods

Two ichthyoplankton cruises were conducted during the summer (June and July) of 2011 in the northern Gulf of Mexico between 27° and 28°N and 88° and 91°W (Fig. 1). Samples were collected using a bongo net (dual 61-cm diameter frames) fitted with paired 333 μm and 500 μm mesh nets. Following Rooker et al. (2013), bongo nets were obliquely towed to a depth of approximately 100 m at 48 sites on each cruise with a distance of approximately 15 km between sites. Boat speed during all tows was maintained at ~2.5 knots and sampling was only conducted during the day (ca. 0700 to 1900 h). At each site, in situ hydrographic data were collected using a handheld YSI sonde and a Seabird conductivity-temperature-depth (CTD) sonde attached to the bongo

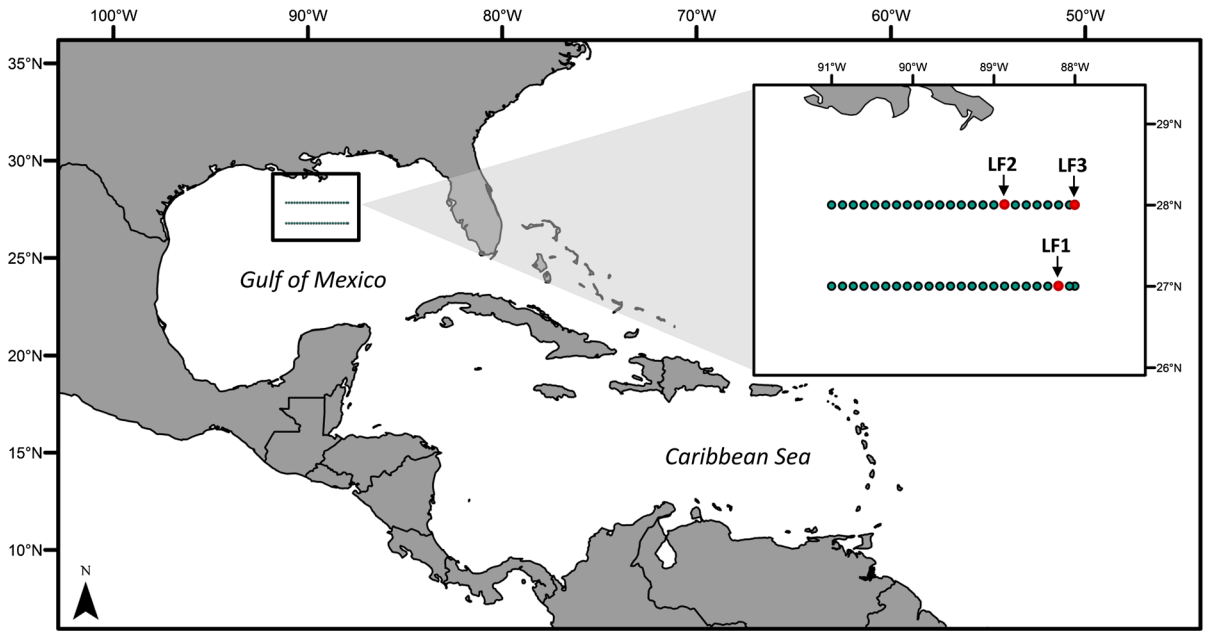

Fig. 1 Location of transects sampled in the northern Gulf of Mexico during June and July 2011. *Green circles* indicate sites sampled during each cruise and *red circles* indicate collection sites of lionfish larvae

frame. Plankton samples were immediately fixed in 95% ethanol and later transferred to 70% ethanol for storage.

Preserved samples were sorted in the lab to remove all ichthyoplankton, and lionfish larvae were visually identified based on morphometric and meristic characters (Imamura and Yabe 1996). Species identification of lionfish larvae was verified using genetic techniques. First, genomic DNA was extracted from ethanol-fixed larvae using a Kapa2G Express Extract kit (Kapa Biosystems) and stored at −20 °C. DNA isolated from adult lionfish in Puerto Rico was used as a positive control. Polymerase chain reactions were then prepared using a Kapa2G Fast Genotyping Mix with LionA-H (5′-CCA TCT TAA CAT CTT CAG TG-3′) and LionB-H (5′-CAT ATC AAT ATG ATC TCA GTAC-3′) primers (Freshwater et al., 2009) to target a ca. 750 bp portion of the mitochondrial control region (d-loop). Amplifications were performed using a Mastercycler (Eppendorf) following the protocol outlined in Freshwater et al. (2000). The PCR amplicons were submitted for purification and sequencing at the Genomics Core Lab at Texas A&M University at Corpus Christi. We combined our sequence dataset with reference lionfish sequences published in GenBank by Freshwater et al. (2009) and aligned the nucleotide sequences using the ClustalW algorithm in Molecular Evolutionary Genetic Analysis 6.0 (MEGA6) software. A neighbor-joining phylogenetic tree was then generated using Tamura-Nei's model with a bootstrap analysis of 1000 replicates in MEGA6.

Information on early development of lionfish larvae is limited to brief descriptions of five larvae [3.8–11.0 mm standard length (SL)] from the eastern Indian Ocean off Australia (Imamura and Yabe 1996) and an 8.0 mm larva collected in the Yucatán Current off Cancun, Mexico (Vásquez-Yeomans et al. 2011). To supplement information on early development, we examined the three larvae molecularly verified as lionfish from our northern Gulf of Mexico ichthyoplankton collections and compared pigmentation patterns with published descriptions. Due to caudal body damage, we had to estimate SL for our two largest specimens, and did so by multiplying the distance between the snout and termination of the dorsal fin base by 1.15, a factor obtained from images and illustrations of *Pterois* larvae in the literature. Images of the early flexion larva (3.9 mm SL) were captured with a Nikon AZ100 M microscope/camera package and NIS Elements BR software.

Saggital otoliths were extracted from each larva and cleaned of adhering tissue using dissecting probes. Otoliths were cleared in immersion oil for 24–48 h

and embedded in epoxy resin (Flo-Texx) on a glass slide. The age of each specimen was determined by counting growth increments (assumed to be daily) along the longest axis of each otolith by two independent readers using an image analysis system (Image-Pro Plus software). The spawning location of each lionfish larva was then predicted using the Connectivity Modeling System (CMS, Paris et al. 2013) backtracking module. CMS integrates a given velocity field backwards in time by using a fourth order Runga-Kutta scheme and is based on flow turbulence using simple diffusion ($k = 10\ m^2/s$ from Okubo 1971). The flow fields used here are daily hindcasts from the Gulf of Mexico Hybrid Coordinate Ocean Model (GoM-HYCOM, http://hycom.org/dataserver/goml0pt04/expt-20pt1), which covers the Gulf of Mexico (77.36°W–98.0°W, 18.09°N–30.71°N) with a horizontal resolution of 1/25 degrees and presents 20 vertical hybrid layers. The GoM-HYCOM assimilates remotely sensed and in situ ocean observations using the U.S. Navy Coupled Ocean Data Assimilation (NCODA) system. The model is forced by winds and surface fluxes from the Navy Operational Global Atmospheric Prediction System (NOGAPS, http://www.nrlmry.navy.mil/metoc/nogaps/nogaps_char.html) at a resolution of 0.5° and is nested within the basin scale Atlantic HYCOM.

Releases in the CMS were based on both the position and estimated age (in days) of each lionfish larva collected in the Gulf of Mexico. For each larva, 500 virtual stochastic backwards trajectories were simulated, with a dispersal time equal to the estimated age (days) of each individual. In one set of simulations, larvae were released in equal numbers from 0 to 100 m and behaved as passive particles. In another simulation, the ontogenetic vertical distribution of lionfish eggs and larvae was reproduced in the model, following patterns observed by in situ observations (Table 1). Lionfish eggs form bundles that are low density and tend to float in layers close to the surface; this characteristic can influence the distribution of eggs and larvae and was therefore incorporated in the model. In this scenario, 500 larvae were released every 20 m from 10 to 90 m.

Table 1 Ontogenetic vertical migration scheme used on simulations

Depth (m)	Age (days)		
	2	7	28
1	99	0	0
10	1	27	17
30	0	38	23
50	0	29	22
70	0	5	20
90	0	1	18

The value on each cell corresponds to the probability of a larva to be found at a specific depth at a certain age. This matrix considers age as forward in time, so the matrix was inverted, with the time spent on each vertical distribution corrected for each lionfish (*Pterois volitans*) larva according to its age

Results and discussion

Three lionfish larvae (LF1 = 3.9, LF2 = 4.6, and LF3 = 5.9 mm SL) ranging from early flexion to postflexion developmental stages were collected during the summer of 2011, with one collected during June (LF1) and two during July (LF2, LF3) (Table 2). The mitochondrial D-loop region of each larva was sequenced and all larvae aligned closely with published lionfish sequences (Freshwater et al. 2009) and sequences from our adult control sample. GenBank BLASTs for each sample yielded highest matches with lionfish (*P. volitans*, accession numbers FJ516409-FJ516454) with pairwise identity scores ranging from 99 to 100%. Further, a neighbor-joining phylogenetic tree was constructed using larval sequences, adult control sequences, and sequences from closely related species from GenBank BLASTs. Results show that larval sequences were contained in the same clade as our control sample sequence and published lionfish sequences, confirming our visual identification of these larvae as lionfish (Fig. 2).

The lionfish larvae in this study exhibited short, deep pectoral fin bases with precocious, elongate rays that extend posteriorly to about the notochord tip. Extent and location of pectoral fin pigmentation is difficult to assess reliably in our specimens due to broken fin rays and tattered inter-ray membranes. Our smallest larva, however, has small melanophores in irregular patches scattered over the outer half of existing pectoral fin rays, as noted for early lionfish larvae from the Indian Ocean (Imamura and Yabe 1996).

Body pigmentation of these larvae is restricted primarily to the lobes of the mid- and hindbrain, and to the midlines of the posterior half of the body (Fig. 3).

Table 2 Data associated with lionfish (*Pterois volitans*) larvae collected during ichthyoplankton cruises in the northern Gulf of Mexico in 2011

Sample	Standard length (mm)	Age (days)	Collection date	Latitude (°N)	Longitude (°W)	Sea surface temperature (°C)	Salinity
LF1	3.9	14	6/16/2011	27.00	88.20	29.27	38.21
LF2	4.6	15	7/19/2011	28.00	88.87	29.66	37.86
LF3	5.9	17	7/19/2011	28.00	88.00	29.20	37.87

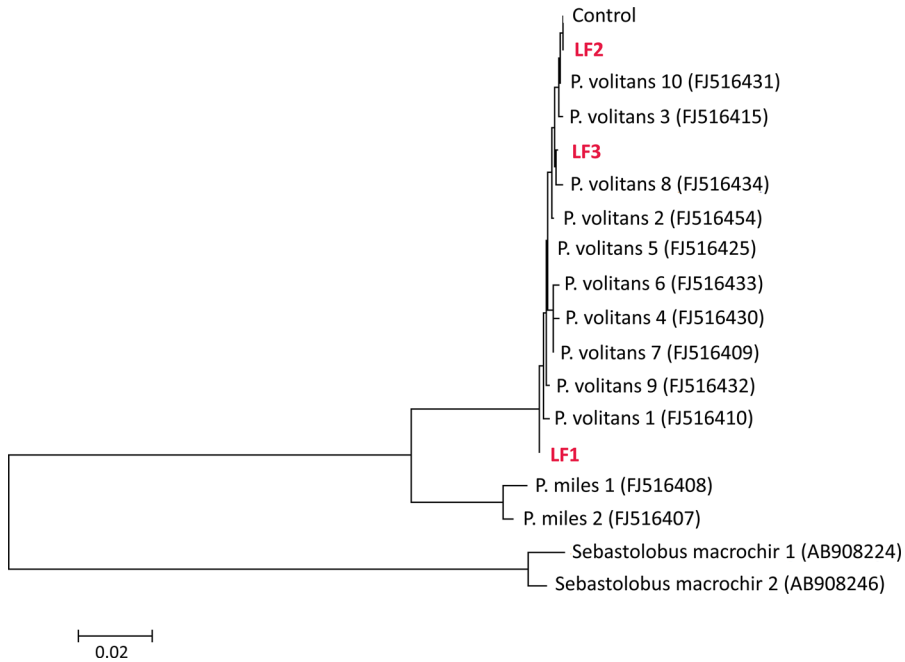

Fig. 2 Neighbor-joining phylogenetic tree of mtDNA D-loop sequences constructed using larvae (LF 1–3), an adult control, and GenBank sequences of lionfish (*Pterois volitans* 1–10) and closely related taxa (*Pterois miles* 1–2 and *Sebastolobus macrochir* 1–2). Scale bar indicates sequence divergence

Our early flexion larva (LF1) has pigment embedded on the dorsoposterior surface of the midbrain between lobes, and single more deeply embedded pigments in the otic region near the ventrolateral margin of each hindbrain lobe. Together, these three pigments form a 'triangular' pattern on the head (Fig. 3) as was previously noted for an 8.0 mm larva from the southern Gulf of Mexico (Vásquez-Yeomans et al. 2011). By comparison, lionfish larvae from the Indian Ocean lack head pigment (Imamura and Yabe 1996). LF1 also has a single pigment embedded in nape musculature along each side of the brainstem, while LF2 and LF3 have a short series of embedded pigments obscured by musculature along the first few developing precaudal vertebrae. Previous descriptions of lionfish larvae do not report pigment in the nape area (Imamura and Yabe 1996; Vásquez-Yeomans et al. 2011).

LF1 has pigment located along the posterior half of the developing soft dorsal fin base and posterior third of the anal fin base, and an irregularly spaced series of melanophores located along the lateral midline between the dorsal and ventral series (Fig. 3). LF1 has a small, obscure pair of embedded melanophores ventrally along the posterior margin of the caudal peduncle as stated by Imamura and Yabe (1996), and several diffuse external melanophores over the musculature of the lower hypural plate not previously

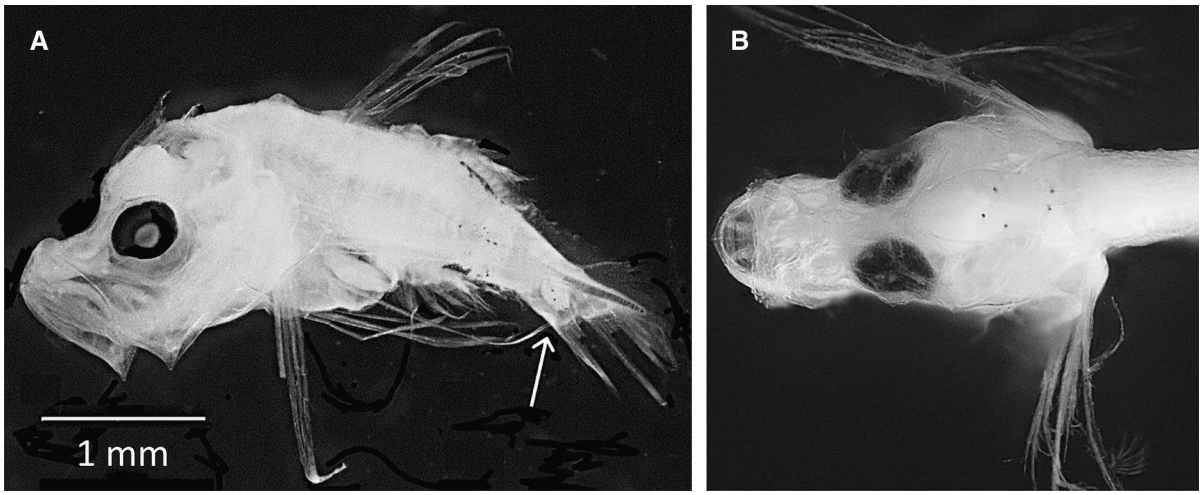

Fig. 3 An early flexion lionfish larva (LF1, 3.9 mm SL) captured during June 2011 in the northern Gulf of Mexico (**a** lateral view, **b** dorsal view of head). *Arrow* indicates location of diffuse external melanophores scattered over musculature of lower hypural plate and pair of small melanophores embedded ventrally along posterior margin of caudal peduncle (**a**). Note embedded pigment on dorsoposterior surface of midbrain between lobes: single, small, deeply embedded pigments near ventrolateral margin of each lobe of the hindbrain and single pigments in nape musculature on each side of brainstem (**b**)

reported (Fig. 3). Due to caudal peduncle damage in LF2 and LF3, we cannot reliably assess presence/absence and extent of lateral midline pigmentation, or confirm whether these two larvae retain the embedded pair ventrally along the peduncle or have pigment on the tail. The 8.0 mm larva from the southern Gulf of Mexico, however, lacks pigment ventrally along the peduncle and externally on the tail with lateral midline pigmentation reduced to a single melanophore below the last dorsal fin ray (Vásquez-Yeomans et al. 2011). Larvae from the Indian Ocean lack pigment along the body midlines anterior to the caudal peduncle until >4.5 mm (Imamura and Yabe 1996). Overall, pigmentation in early lionfish larvae from the Gulf of Mexico differs from the pattern reported for lionfish from the Indian Ocean (Imamura and Yabe 1996). For instance, our early flexion 3.9 mm larva has several diffuse external melanophores scattered over the developing lower hypural plate and pigment embedded in nape musculature (Fig. 3) not reported in earlier descriptions. Pigment also appears along the body midlines earlier (i.e., at smaller SL) in larvae from the Gulf of Mexico than Indian Ocean (Imamura and Yabe 1996).

Although neuston nets were also deployed at each sampling site during our ichthyoplankton cruises, lionfish larvae were caught exclusively in oblique bongo net tows. Thus, our findings suggest that small larvae may reside in the water column rather than near the surface; however, a larger larva ($\sim$8 mm SL) was previously collected in surface waters with a neuston net (Vásquez-Yeomans et al. 2011), possibly signifying that vertical position in the water column changes during ontogeny. Lionfish were found at sites with relatively low sea surface temperatures (mean $\pm$ SD: 29.38 $\pm$ 0.25 °C) and high salinities (37.98 $\pm$ 0.20) compared to other sites sampled in the transects (mean sea surface temperature: 30.3 $\pm$ 0.92 °C, salinity: 36.1 $\pm$ 4.64). Sea surface height anomaly maps (AVISO, www.aviso.oceanobs.com) indicated that these samples were found along the northern edge of the Loop Current, which is a frontal zone often characterized by enhanced productivity and higher abundances of pelagic fish larvae (Lamkin 1997; Rooker et al. 2012; Kitchens and Rooker 2014).

Otolith-based age estimates indicated that the lionfish larvae were 14 (LF1), 15 (LF2), and 17 (LF3) days old (Table 2). Hatch dates, calculated by subtracting age from collection date, ranged from June 2 to July 4, 2011. Little is known regarding the spawning of lionfish in the Gulf of Mexico and Caribbean Sea, but results from Vásquez-Yeomans et al. (2011) and the present study confirm that lionfish at least spawn from March to July in this region. However, spawning may occur year-round in the Gulf of Mexico, as this has been observed in lionfish

populations near North Carolina and the Bahamas (Morris 2009).

CMS results using otolith-based ages indicated that all larvae were transported northward from their spawning locations via the Loop Current (Fig. 4, see Supplementary Material for backtracking animations), which is a high speed current that brings water into the Gulf of Mexico through the Yucatán Channel at speeds reaching 1 m sec^{-1} (Vukovich and Maul 1985). In fact, results show that these larvae were transported approximately 200 to 880 km from their spawning areas within 14–17 days. Most of the back-tracked spawning locations for lionfish occurred in the southern Gulf of Mexico, although one lionfish (LF3) may have hatched in the Caribbean Sea. "High probability" spawning areas (i.e., areas with the greatest number of backward-projected simulation particles) in the vertical migration model were clustered in deep waters of the southern Gulf of Mexico (LF1 and LF3), along the northern edge of the Yucatán Shelf (LF2), and near Cozumel in the Caribbean Sea (LF3). The model gave similar results when larvae behaved as passive particles, with only slight shifts in the location of high probability spawning areas. The geographic range of predicted spawning locations for all three lionfish larvae included regions along the shelf of the Yucatán Peninsula where deepwater corals are known to be present (Schroeder et al. 2005).

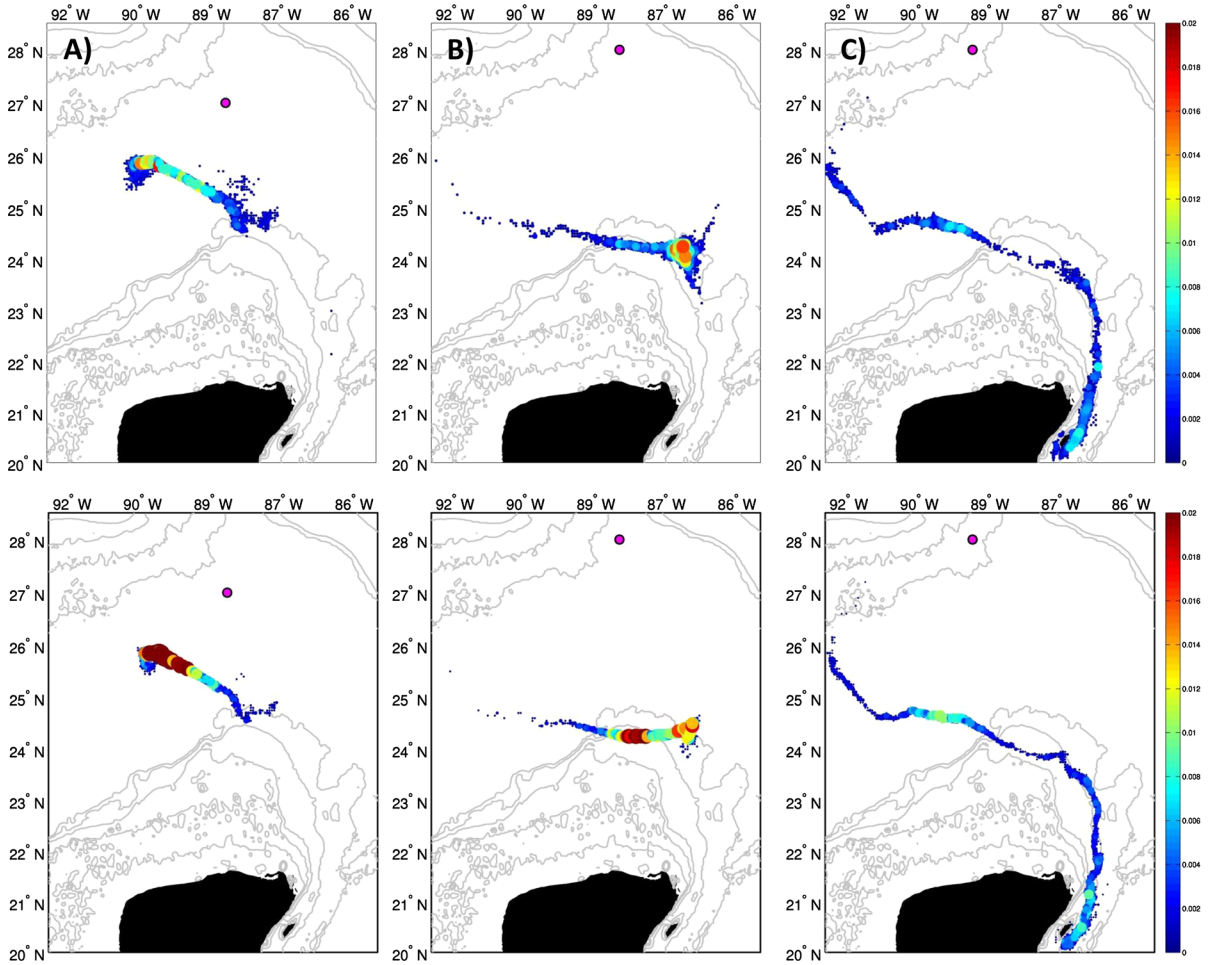

Fig. 4 Distribution of probable spawning sites for lionfish larvae with and without vertical migration (*top* and *bottom*, respectively); **a** LF1 (14 days old), **b** LF2 (15 days old), and **c** LF3 (17 days old). Each backtrack simulation released 1000 larvae with the HYCOM GoM velocity fields on the site of the larva sampling. Scales represent the spawning site probability density function, calculated by binning the final larvae positions from the CMS backward trajectories into a 0.05° by 0.05° grid

Additionally, Cozumel is another potential spawning site of LF3, and this region is characterized by abundant coastal reef habitat. Regardless, adult lionfish are not limited to residing in natural reef habitat, as they have also been observed in artificial reefs, mangroves, seagrasses, mud bottoms, and even estuaries (Claydon et al. 2012; Jud and Layman 2012; Kulbicki et al. 2012; Dahl and Patterson 2014). Further, lionfish do not appear to be restricted to a certain depth range, as adults have been reported from surface waters down to 152 m and possibly deeper (USGS-NAS 2015). While little is known regarding spawning habitat preferences of lionfish, results of the CMS models suggest that some spawning may occur in deep waters, as most of the potential spawning sites were at depths >200 m (Fig. 4).

In summary, we provide evidence for the occurrence of lionfish larvae in the Gulf of Mexico and the potential for spawning in this region. Results from our larval backtracking model indicate that it is plausible that lionfish colonized the northern Gulf of Mexico through the transport of early life stages by the Loop Current, as predicted spawning locations of all three larvae occurred in the southern Gulf of Mexico near the Yucatán Peninsula. Thus, it is possible that populations in the Caribbean Sea and southern Gulf of Mexico may supply recruits to the northern Gulf of Mexico and downstream regions such as west Florida or the Florida Keys. However, given that only three samples of a limited size range were examined in this study, it is difficult to make any conclusions regarding the distribution and dispersal patterns of lionfish larvae in the Gulf of Mexico. Therefore, additional sampling is required to develop a better understanding of the early life ecology of lionfish and improve our ability to characterize dispersal pathways in this region.

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References

Aguilar-Perera A, Tuz-Sulub A (2010) Non-native, invasive red lionfish (*Pterois volitans* [Linnaeus, 1758]: Scorpaenidae), is first recorded in the southern Gulf of Mexico, off the northern Yucatán Peninsula, Mexico. Aquat Invasions 5:S9–S12

Ahrenholz DW, Morris JA (2010) Larval duration of the lionfish, *Pterois volitans,* along the Bahamian Archipelago. Environ Biol Fish 88:305–309

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

Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. Environ Biol Fish 96:1151–1157

Claydon JAB, Calosso MC, Traiger SB (2012) Progression of invasive lionfish in seagrass, mangrove and reef habitats. Mar Ecol Prog Ser 448:119–129

Côté IM, Green SJ, Morris JA, Akins JL, Steinke D (2013) Diet richness of invasive Indo-Pacific lionfish revealed by DNA barcoding. Mar Ecol Prog Ser 472:249–256

Cure K, Benkwitt CE, Kindinger TL, Pickering EA, Pusack TJ, McIlwain JL, Hixon MA (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. Mar Ecol Prog Ser 467:19–181

Dahl KA, Patterson WF III (2014) Habitat-specific density and diet of rapidly expanding invasive red lionfish, *Pterois volitans*, populations in the northern Gulf of Mexico. PLoS ONE 9(8):e105852

Fishelson L (1975) Ethology and reproduction of pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier), (Pteroidae, Teleostei). Pubbl Staz Zool Napoli 39(Suppl.):635–656

Freshwater DW, Khyn-Hansen C, Sarver SK, Walsh PJ (2000) Phylogeny of *Opsanus* spp. (Batrachoididae) inferred from multiple mitochondrial-DNA sequences. Mar Biol 136:961–968

Freshwater D, Hines A, Parham S, Wilbur A, Sabaoun M, Woodhead J, Akins L, Purdy B, Whitfield PE, Paris CB (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

González J, Grijalba-Bendeck M, Acero PA, Betancur RR (2009) The invasive red lionfish, *Pterois volitans*, in the southwestern Caribbean Sea. Aquat Invasions 4:507–510

Green SJ, Akins JL, Côté IM (2011) Daily patterns of foraging behaviour and prey consumption in the Indo-Pacific lionfish *Pterois volitans* on Bahamian coral reefs. Mar Ecol Prog Ser 433:156–167

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS ONE 7:e32596

Imamura H, Yabe M (1996) Larval record of a red firefish, *Pterois volitans*, from northwestern Australia (Pisces: Scorpaeniformes). Bull Fac Fish Hokkaido Univ 47:41–46

Jud ZR, Layman CA (2012) Site fidelity and movement patterns of invasive lionfish, *Pterois* spp., in a Florida estuary. J Exp Mar Biol Ecol 414:69–74

Kitchens LL, Rooker JR (2014) Habitat associations of dolphinfish in the Gulf of Mexico. Fish Oceanogr 23:460–471

Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter SR, Galzin R, Green A, Harmelin-Vivien M, Hixon M, Letourneur Y, Lison de Loma T, McClanahan T, McIlwain J, MouTham G, Myers R, O'Leary JK, Planes S, Vigliola L, Wantiez L (2012) Distributions of Indo-Pacific lionfishes

Pterois spp. in their native ranges: implications for the Atlantic invasion. Mar Ecol Prog Ser 446:189–205

Lamkin J (1997) The Loop Current and the abundance of larval *Cubiceps pauciradiatus* (Pisces: Nomeidae) in the Gulf of Mexico: evidence for physical and biological interaction. Fish Bull 95:250–266

Lasso-Alcalá OM, Posada JM (2010) Presence of the invasive red lionfish, *Pterois volitans* (Linnaeus 1758), on the coast of Venezuela, southeastern Caribbean Sea. Aquat Invasions 5(2):53–59

McTee SA, Grubich JR (2014) Native densities, distribution, and diurnal activity of Red Sea lionfishes (Scorpanidae). Mar Ecol Prog Ser 508:223–232

Morris JA Jr, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environ Biol Fish 86:389–398

Morris JA Jr (2009) Biology and ecology of the invasive Indo-Pacific lionfish. Dissertation, North Carolina State University

Morris JA Jr, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Technical Memorandum NOS NCCOS 99

Morris JA Jr, Akins JL, Barse A, Cerino D, Freshwater DW, Green SJ, Munoz RC, Paris C, Whitfield PE (2009) Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. In: Proceedings of the 61st Gulf and Caribbean Fisheries Institute, vol 61, pp 1–6

Okubo A (1971) Oceanic diffusion diagrams. Deep-Sea Res 18:789–802

Paris CB, Helgers J, van Sebille E, Srinivasan A (2013) Connectivity modeling system: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environ Model Softw 42:47–54

Rooker JR, Simms JR, Wells RJD, Holt SA, Holt GJ, Graves JE, Furey NB (2012) Distribution and habitat associations of billfish and swordfish larvae across mesoscale features in the Gulf of Mexico. PLoS ONE 7(4):e34180

Rooker JR, Kitchens LL, Dance MA, Wells RJD, Falterman B, Cornic M (2013) Spatial, temporal, and habitat-related variation in abundance of pelagic fishes in the Gulf of Mexico: potential implications of deepwater Horizon oil spill. PLoS ONE 8(10):E76080

Ruiz-Carus R, Matheson RE Jr, Roberts DE Jr, Whitfield PE (2006) The western Pacific red lionfish, *Pterois volitans* (Scorpaenidae), in Florida: evidence for reproduction and parasitism in the first exotic marine fish established in state waters. Biol Conserv 128:384–390

Ruttenberg BI, Schofield PJ, Akins LJ, Acosta A, Feeley MW, Blondeau J, Smith SG, Ault JS (2012) Rapid invasion of Indo-Pacific lionfishes (*Pterois volitans* and *Pterois miles*) in the Florida Keys, USA: evidence from multiple pre-and post-invasion data sets. Bull Mar Sci 88(4):1051–1059

Schofield P (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

Schroeder WW, Brooke SD, Olson JB, Phaneuf B, McDonough JJ, Etnoyer P (2005) Occurrence of deep-water *Lophelia pertusa* and *Madrepora oculata* in the Gulf of Mexico. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 297–307

Sutherland WJ, Clout M, Côté IM et al (2010) A horizon scan of global conservation issues for 2010. Trends Ecol Evol 25:1–7

USGS-NAS (2015) United States Geological Survey-Nonindigenous Aquatic Species database (USGS-NAS). http://nas.er.usgs.gov. Accessed 15 Dec 2015

Valdez-Moreno M, Quintal-Lizama C, Gómez-Lozano R, García-Rivas MDC (2012) Monitoring an alien invasion: DNA barcoding and the identification of Lionfish and their prey on coral reefs of the Mexican Caribbean. PLoS ONE 7(6):e36636

Vásquez-Yeomans L, Carrillo L, Morales S, Malca E, Morris JA Jr et al (2011) First larval record of *Pterois volitans* (Pisces: Scorpaenidae) collected from the ichthyoplankton in the Atlantic. Biol Invasions 13:2635–2640

Vukovich FM, Maul GA (1985) Cyclonic eddies in the eastern Gulf of Mexico. J Phys Oceanogr 15:105–117