

Research Article

Rapid invasion of Indo-Pacific lionfishes *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828) in Flower Garden Banks National Marine Sanctuary, Gulf of Mexico, documented in multiple data sets

Michelle A. Johnston*, Marissa F. Nuttall, Ryan J. Eckert, John A. Embesi, Travis K. Sterne, Emma L. Hickerson and George P. Schmahl

NOAA Office of National Marine Sanctuaries, Flower Garden Banks National Marine Sanctuary, 4700 Avenue U, Bldg. 216, Galveston TX 77551, USA

*Corresponding author

E-mail: Michelle.A.Johnston@noaa.gov

Received: 3 December 2015 / Accepted: 1 April 2016 / Published online: 14 April 2016

Handling editor: Charles Martin

Abstract

Non-native red lionfish *Pterois volitans* (Linnaeus, 1758) and devil firefish *Pterois miles* (Bennett, 1828) have become established on continental shelf areas throughout the western Atlantic Ocean, the Caribbean Sea, and the Gulf of Mexico. Lionfish were first observed in the Gulf of Mexico in 2009, and sighted at Flower Garden Banks National Marine Sanctuary (FGBNMS) in 2011. We document the first appearance of lionfish and sighting frequency in FGBNMS using fish surveys from long-term monitoring data, diver sighting and removal data, and observations from Remotely Operated Vehicle surveys. Our results quantify and identify trends in lionfish density, biomass, and sighting frequency within the national marine sanctuary. Lionfish populations demonstrated different patterns among the three banks of FGBNMS. While lionfish have shown a steadily increasing trend at East Flower Garden Bank and West Flower Garden Bank from 2011 to 2014, populations decreased at Stetson Bank following the initial invasion. Because lionfish populations are projected to increase throughout the Gulf of Mexico, the continuation of long-term monitoring and volunteer diver programs with the combined analyses from multiple data sets similar to those used in this study are vital in early warning, detection, and documentation of invasive species and time-sensitive management issues.

Key words: coral reefs, invasive species, lionfish, monitoring, National Marine Sanctuary

Introduction

The invasion of Indo-Pacific lionfishes *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828) (hereafter “lionfish” refers to both species) is a serious threat to fish communities and coral reefs in the western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Albins and Hixon 2008; Lesser and Slattery 2011; Green et al. 2012; Cerino et al. 2013). Lionfishes are well-known for their venomous spines to ward off predators and their generalist preferences for both habitat and prey (Morris and Whitfield 2009; Albins and Hixon 2011). Invasive lionfishes can have significant impacts on biodiversity and the health of coral reefs by reducing the abundance and recruitment of native reef fishes and causing shifts from coral to algae-dominated reef communities (Albins and Hixon 2008; Albins and Hixon 2011;

Lesser and Slattery 2011; Green et al. 2012). After their introduction off the Florida coast in the 1980s, lionfish entered the southern Gulf of Mexico off the northern Yucatan Peninsula in 2009 via larval transport, expanding throughout the Gulf of Mexico in both shallow and deep waters (Schofield 2010; Aguilar-Perera and Tuz-Sulub 2010; Switzer et al. 2015; Nuttall et al. 2014).

Located in the northwestern Gulf of Mexico about 190 km offshore, Flower Garden Banks National Marine Sanctuary (FGBNMS) includes three underwater features: East Flower Garden Bank (EFGB), West Flower Garden Bank (WFGB), and Stetson Bank (Figure 1). The banks include the northernmost coral reefs in the continental United States, support abundant fish assemblages over several distinct habitats, and range in depth from 16–150 m (Bright et al. 1985). Depths ranging from 16–40 m at EFGB and WFGB

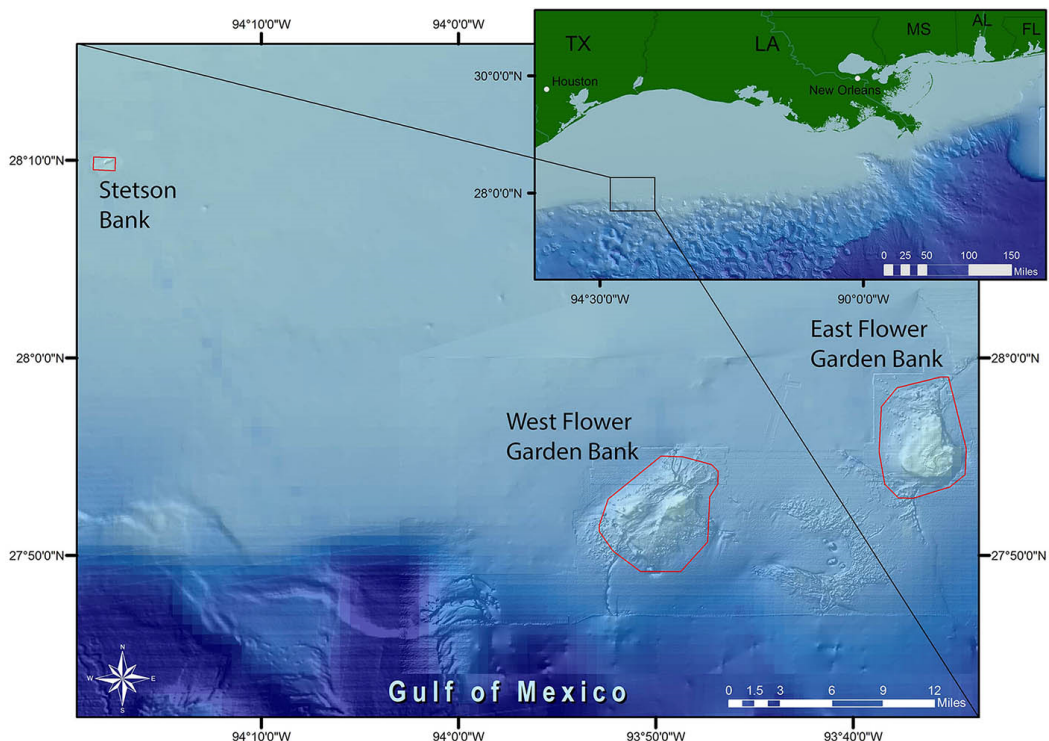


Figure 1. Bathymetry of Flower Garden Banks National Marine Sanctuary with boundaries outlined in red, consisting of Stetson Bank (2.18 km²), East Flower Garden Bank (65.86 km²), and West Flower Garden Bank (77.54 km²), located on the outer Texas-Louisiana continental shelf (inset).

consist of natural reef habitat averaging above 50% coral cover, dominated by *Orbicella franksi* (Gregory, 1895) and *Pseudodiploria strigosa* (Dana, 1846) (Clark et al. 2014; Johnston et al. 2015a). The lesser studied mesophotic habitat from 60–90 m includes algal-sponge zones, mesophotic coral reefs, and mud flats (Schmahl et al. 2008). Benthic cover at Stetson Bank consists primarily of sponges and algae (thick turfs and fleshy macroalgal species) (Debose et al. 2012). In the northern Gulf of Mexico, lionfish were observed in 2010 at Sonnier Bank (Schofield et al. 2011); one of the numerous interconnected bank features located 120 km northeast of FGBNMS. In July of 2011, lionfish were observed by FGBNMS divers on all three banks in the marine sanctuary (Schofield et al. 2011) (Figure 2).

Long-term monitoring programs at FGBNMS and regional research programs have helped document the appearance and rapid spread of lionfish in the national marine sanctuary, as well as surrounding banks in the northwestern Gulf of Mexico (Clark et al. 2014; Nuttall et al. 2014). A long-term coral-reef monitoring program began at EFGB and WFGB in 1989 and continues annually in partnership between the Bureau of Offshore Energy Management (BOEM) and



Figure 2. Lionfish hovering above the coral reef at East Flower Garden Bank. Photograph by Amanda Sterne.

FGBNMS. Monitoring at Stetson Bank began in 1993 by the volunteer group Gulf Reef Environmental Action Team (GREAT), and was conducted by FGBNMS from 1999 to 2014. The long-term monitoring programs evaluate changes in benthic communities, reef fish population dynamics, water

quality, and other indices of reef vitality at designated study sites at EFGB, WFGB, and Stetson Bank.

Here we examined stationary visual fish surveys from long-term monitoring data, lionfish sighting and removal data, and Remotely Operated Vehicle (ROV) data in depths below recreational SCUBA limits to evaluate the occurrence and colonization of lionfish. The data allowed us to document and track the invasion progress following initial sightings at EFGB, WFGB, and Stetson Bank from 2011 to 2014.

Methods

We used three different sets of data from 2011 to 2014 to examine the lionfish invasion across all three banks that comprise the FGBNMS. EFGB (65.86 km²) and WFGB (77.54 km²), located roughly 190 km south of the Texas–Louisiana border, support coral reef and associated reef communities colonizing uplifted underwater salt diapirs at depths ranging from 17–140 m. Stetson Bank (2.18 km²), located approximately 130 km southeast of Galveston, Texas, is an uplifted claystone feature that supports a benthic community of tropical marine sponges, coral, and other invertebrates (Figure 1).

The first data set was based on long-term monitoring data (LTM data) from EFGB, WFGB, and Stetson Bank. Annual fish census LTM data surveys from EFGB and WFGB were collected within two 100 m × 100 m (1 ha) study sites. The study sites, located on the reef crests of both banks, consisted of survey depths ranging from 17–27 m. For each survey, fishes were visually assessed by SCUBA divers using a modified Bohnsack and Bannerot (1986) stationary visual fish survey technique that consisted of an imaginary cylinder with a radius 7.5 m extending from the seafloor to the surface. All fish species observed within five minutes were recorded. For smaller fish, size was classified to the nearest 5 cm, and total lengths for all fish >35 cm were individually estimated and recorded. A minimum of 24 randomly located surveys were conducted within both study sites at EFGB and WFGB annually. Fish survey dives began at 0700 CDT and were repeated throughout the day until dusk. Long-term monitoring field work occurred annually during summer months (June–August). The same survey methods were used at Stetson Bank. With the exception of 2011, when fish surveys were limited due to time constraints, a minimum of twelve surveys were conducted annually at Stetson Bank near permanent mooring buoy locations. Beginning in 2013, annual fish census surveys were conducted at random locations throughout Stetson Bank within

depth ranges of 19–30 m. From LTM data at all three banks, lionfish sighting frequency and biomass (g 100 m⁻²) were calculated. Biomass estimates were calculated using species-specific length-weight conversion formulas from FishBase (Bohnsack and Harper 1988; Froese and Pauly 2009). Lionfish density was calculated for individuals (ind) ha⁻¹.

The second data set was derived from lionfish sightings recorded by FGBNMS and scientific divers (Diver data) who were conducting general field work using SCUBA from 2011 to 2014. The majority of dives (< 40 m depths) for each year occurred near permanent mooring buoys during summer and fall months (May–October) when weather in the region was optimal for field work offshore. Recorded lionfish sightings on dives included the date, time, location, depth, and estimated total length. Each dive was treated as a sample. FGBNMS divers and trained volunteers also removed lionfish using pole spears when possible (FGBNMS permits FGBNMS-2009-001, FGBNMS-2011-002, and FGBNMS-2014-001). Morphometric/meristic data recorded for each lionfish removed included weight, total length, standard length, and sex. Significant monotonic trends over time were measured using the Mann-Kendall test and significant differences between years were detected using a one-way ANOVA on log (n+1) transformed data in R version 3.2.0 (Hipel and McLeod 1994).

The third source of information, lionfish observations in habitats below recreational diving limits at EFGB and WFGB, were obtained through Remotely Operated Underwater Vehicle video footage (ROV data). ROV surveys were conducted between 60–90 m where the habitat consists primarily of natural coralline algae reef. In 2011 and 2012, ROV data were collected in partnership with Clark et al. (2014) at multiple predetermined drop sites, distributed evenly between habitat and area. In 2013, limited ROV surveys were conducted at predetermined sites of interest at EFGB. No surveys were conducted at Stetson Bank or in 2014. Once the ROV was on bottom, video was recorded and notes were captured in five minute intervals, recording benthic invertebrate and fish observations, depth, and location for the duration of the dive. These notes were used to calculate the average depth of each drop site and document the quantity, approximate location, and approximate depth of all lionfish encountered. Each dive was treated as a sample.

Sighting frequency on each bank was calculated for all three data sets from 2011 to 2014 to determine how often lionfish were observed. We define sighting frequency as the percentage of all surveys or samples with lionfish present.

Table 1. Percent sighting frequency (with sample size in parentheses) for LTM data and Diver data for East Flower Garden Bank (EFGB), West Flower Garden Bank (WFGB), and Stetson Bank from 2011 to 2014.

Location	Bank Coordinates (DDM)		LTM Data				Diver Data			
	Latitude	Longitude	2011	2012	2013	2014	2011	2012	2013	2014
EFGB	27° 54.547 N	-93° 35.918 W	0% (24)	0% (24)	25.0% (24)	50.0% (30)	0% (145)	11.8% (153)	50.0% (94)	58.6% (116)
WFGB	27° 52.519 N	-93° 48.889 W	0% (24)	0% (24)	33.3% (24)	40.0% (30)	1.5% (69)	11.5% (183)	76.7% (73)	80.5% (82)
Stetson Bank	28° 09.986 N	-94° 17.766 W	0% (4)	0% (17)	4.7% (42)	2.9% (35)	0% (48)	18.4% (38)	33.9% (59)	12.7% (79)

Table 2. Lionfish observation records from ROV surveys by location and depth at East Flower Garden Bank (EFGB) and West Flower Garden Bank (WFGB).

Location	Bank Coordinates (DDM)		Year	Month	Lionfish Observed	Depth (m)
	Latitude, N	Longitude, W				
EFGB	27°57.32700	-93°35.76200	2012	July	4	75.3
WFGB	27°53.76019	-93°48.90397	2012	July	1	71.3
WFGB	27°51.48081	-93°49.73575	2012	August	1	79.2
WFGB	27°51.31200	-93°49.58546	2012	August	1	81.7
EFGB	27°57.23496	-93°35.96331	2013	October	5	65.8
EFGB	27°57.25735	-93°35.99196	2013	October	2	61.3
EFGB	27°57.25496	-93°35.99694	2013	October	2	61.0
EFGB	27°57.27086	-93°36.05074	2013	October	2	67.4
EFGB	27°57.25247	-93°35.99507	2013	October	6	61.0
EFGB	27°57.26922	-93°35.99935	2013	October	6	65.0
EFGB	27°57.24132	-93°35.01911	2013	October	4	62.0

Results

From 2011 to 2014, lionfish sightings varied among the three banks (Table 1). In the LTM data, lionfish were documented for the first time in 2013 at EFGB (25% sighting frequency), WFGB (33.3% sighting frequency), and Stetson Bank (4.7% sighting frequency). Sighting frequency continued to increase in the 2014 LTM data at EFGB (50%) and WFGB (40%), but decreased at Stetson Bank (2.9%).

In the Diver data, one lionfish was observed at WFGB in 2011 (Table 1). In 2012, lionfish sighting frequency increased at EFGB (11.8%), WFGB (11.5%), and Stetson Bank (18.4%). In the 2013 Diver data, lionfish sightings increased noticeably at EFGB (50%), WFGB (76.7%), and Stetson Bank (33.9%). Similar to the LTM data in 2014, sighting frequency from the Diver data continued to increase at EFGB (58.6%) and WFGB (80.5%), but decreased at Stetson Bank (12.7%).

No lionfish sightings occurred on the 31 ROV surveys conducted at EFGB and WFGB in 2011 (Table 2). For ROV surveys in 2012, lionfish sighting frequency increased to 6.3% at EFGB and 16.7% at WFGB. In 2013, no ROV surveys occurred at WFGB, but surveys at EFGB documented an increase in sighting frequency (50%).

From 2011 to 2014, a total of 735 lionfish were observed at WFGB, followed by 448 at EFGB and 162 at Stetson Bank (Figure 3). Of the 1,345 observations, 56% of those lionfish were removed from sanctuary waters by permitted FGBNMS scientific and volunteer divers. Weights of removed lionfish ranged from 0.9–1015.9 g (mean 273.4 g), significantly increasing as the invasion progressed ($\tau = 0.1$; $P < 0.001$) (Figure 4). Total length of lionfish ranged from 4.0–42.0 cm (mean 25.6 cm), also significantly increasing from 2011 to 2014 ($\tau = 0.1$; $P < 0.001$) (Figure 4). Of all the lionfish that have been removed from FGBNMS, 44% were females, 51% were males, and 5% were juveniles of undetermined sex.

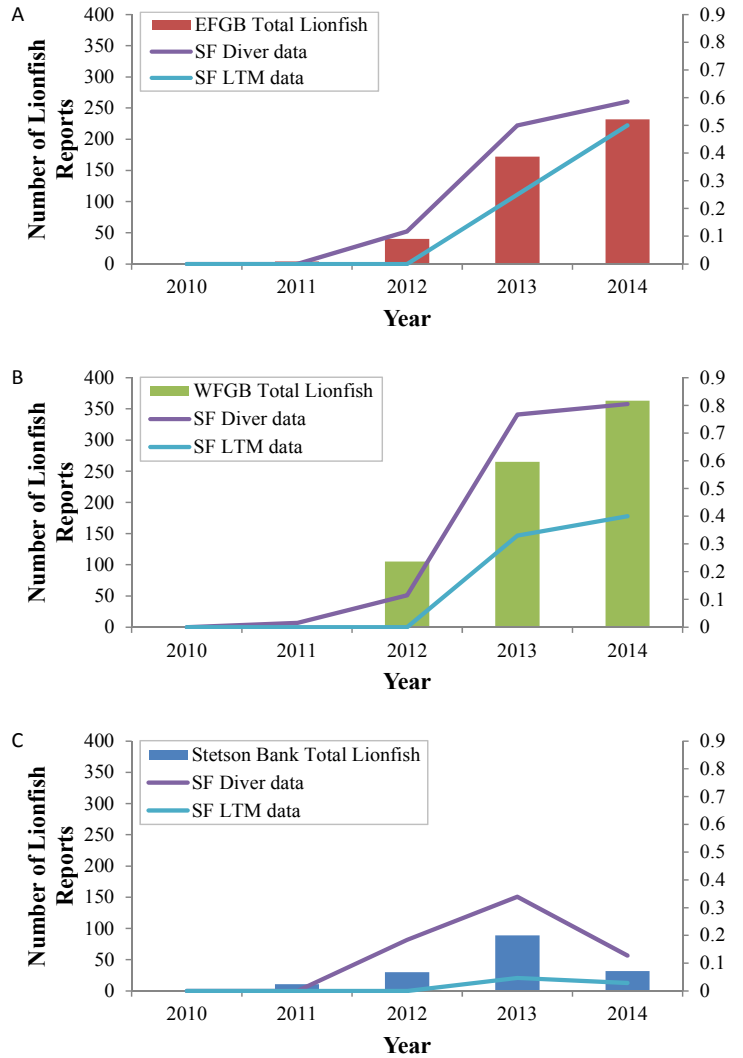


Figure 3. Total number of reported lionfish sightings (left axis) and mean sighting frequency (right axis) for (A) East Flower Garden Bank (EFGB), (B) West Flower Garden Bank (WFGB), and (C) Stetson Bank from 2011 to 2014 (See Table 1 for localities). Lionfish from LTM data and Diver data are shown as sighting frequency (SF).

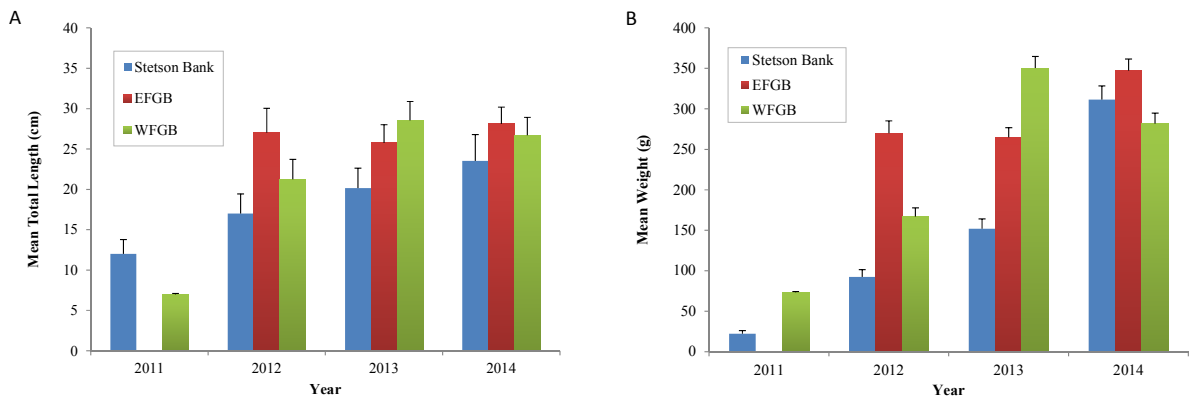


Figure 4. (A) Mean total length (cm) and (B) mean weight (g) of lionfish removed from East Flower Garden Bank (EFGB), West Flower Garden Bank (WFGB), and Stetson Bank from 2011 to 2014 with standard error bars.

Estimates of mean lionfish density from LTM data increased more than three-fold from 12 ind ha⁻¹ in 2013 to 38 ind ha⁻¹ in 2014 at the EFGB study site, and doubled from 14 ind ha⁻¹ in 2013 to 28 ind ha⁻¹ in 2014 at the WFGB study site. In contrast, lionfish density at Stetson Bank decreased from 4 ind ha⁻¹ in 2013 to 2 ind ha⁻¹ in 2014. Lionfish density differed significantly between 2013 and 2014 (ANOVA, $F_{1,148} = 13.7$; $P < 0.003$) for the banks combined.

Estimates of mean lionfish biomass from LTM data showed similar increases between 2013 and 2014 at EFGB and WFGB study sites. Mean (\pm SE) biomass was estimated to be 42.94 \pm 30.04 g 100 m⁻² at EFGB in 2013, more than doubling to 89.75 \pm 27.41 g 100 m⁻² in 2014. At WFGB, mean lionfish biomass was 50.38 \pm 22.75 g 100 m⁻² in 2013 and increased to 119.19 \pm 40.85 g 100 m⁻² in 2014. At Stetson Bank, biomass decreased from 5.51 \pm 4.07 g 100 m⁻² in 2013 to 2.21 \pm 2.21 g 100 m⁻² in 2014. Lionfish biomass differed significantly between 2013 and 2014 (ANOVA, $F_{1,148} = 13.6$; $P < 0.003$) for the banks combined.

Discussion

We documented the rapid invasion of lionfish at FGBNMS using LTM data from EFGB, WFGB, and Stetson Bank, sighting and removal data from FGBNMS scientific and volunteer divers, and ROV data taken at depths ranging from 60–90 m. Diver data revealed a rapid increase in lionfish sighting frequency from 2011 to 2014 at EFGB and WFGB, and an initial increase followed by a decrease at Stetson Bank. LTM data showed a similar trend for each of the banks, but sightings lagged behind observations from Diver data.

While lionfish were first observed by divers on all three banks in 2011, they were not recorded in the LTM data until 2013. This is most likely due to limited numbers of lionfish present during the first two years of the invasion and the survey method used. The Bohnsack and Bannerot (1986) stationary survey technique is noted for its ability to detect visibly active reef fishes as the observer remains in place throughout the duration of the survey (Ruttenberg et al. 2012). While lionfish at FGBNMS are more visible above the reef during crepuscular periods, some may remain undetected by tightly tucking themselves under coral overhangs or in deep reef crevices during the day (Kulbicki et al. 2012). All LTM data surveys taken at EFGB and WFGB study sites and Stetson Bank were located on the shallow portions of the reef, restricting surveys to areas < 30 m deep.

In Diver data recorded from 2012 to 2013, EFGB showed a four-fold increase in lionfish sighting frequency, WFGB showed a > six-fold increase, and sighting frequency at Stetson Bank nearly doubled, resulting in higher sighting frequencies than those captured in the long-term monitoring datasets. Because Diver data were collected opportunistically in non-random sites, there is the possibility that these locations were sampled multiple times, leading to overestimation and inflated sighting frequencies in comparison to the random long-term monitoring surveys. Although sighting frequency from FGBNMS Diver data was consistently higher than in the LTM data, both data sets showed similar increasing trends.

It should be noted that the staff of FGBNMS currently works to remove lionfish when possible in attempts to suppress potential impacts on the native fish community due to predation; however, divers are limited to the upper portion of the reef crest (< 40 m depths) (Green et al. 2014; Johnston et al. 2015b). There is also limited time and funding for removal efforts. Lionfish below 40 m, as documented in ROV footage at EFGB and WFGB and at other reefs and banks in the northwestern Gulf of Mexico (Nuttall et al. 2014), are currently out of reach of removal efforts. Within the long-term monitoring study sites, removals do not take place until all fish surveys are complete, ensuring sighting frequency, density, and biomass data are not affected. However, because lionfish are opportunistically removed by permitted divers throughout the year, data are likely to be the minimum estimates, as abundance would presumably be higher if lionfish were not removed from the system. It is currently unknown how differing FGBNMS habitats at varying depths are used by lionfish, the levels of movement between different depths, and how these may be affected by removals.

Lionfish densities at FGBNMS have yet to reach levels recorded elsewhere in the Atlantic Ocean and Caribbean Sea. In North Carolina waters, a mean density of 150 lionfish ha⁻¹ is recorded (Morris and Whitfield 2009) compared to about 100 lionfish ha⁻¹ in the Bahamas (Darling et al. 2011). In the Bahamas, peak densities of about 390 lionfish ha⁻¹ were recorded (Green and Cote 2009). Based on patterns observed in the Caribbean Sea region (Morris and Whitfield 2009; Schofield 2009; Albins and Hixon 2011; Ruttenberg et al. 2012; Green et al. 2012), we anticipate lionfish sightings will continue to increase in the Gulf of Mexico.

Our data showed increases in sighting frequency, mean density, and biomass at EFGB and WFGB while all three of these measures decreased at after the initial invasion. The reason for the decline at Stetson Bank is unknown. Possible investigation

could include differences in habitat complexity, fish community composition, and oceanographic conditions between Stetson Bank and the two other banks. Lionfish sightings also increased in deep water habitat at EFGB and WFGB, as observed through ROV surveys; however, more research is needed to determine how lionfish populations in deeper habitats contribute to the shallower populations because much of our understanding about the lionfish invasion at FGBNMS comes from diver surveys on shallower habitats resulting in a depth related bias. Work by Switzer et al. (2015) suggests lionfish in the eastern Gulf of Mexico first settled in deeper (> 30 m) habitats and then expanded to shallower waters.

The use of multiple data sets proved valuable in documenting invasive lionfish in FGBNMS. Diver data documented lionfish one year earlier and more frequently than the annual LTM data monitoring program. These results suggest that observations from trained divers and citizen scientists can be valuable when documenting and responding to time-sensitive management and conservation issues, thus augmenting expensive monitoring programs (Scyphers et al. 2015). While it is recognized that these programs may lack random sampling and defined parameters, these “eyes on the water” are valuable to FGBNMS in filling information gaps, as the cost of monitoring the reefs 100 miles offshore becomes unrealistic if done multiple times per year. Trained volunteer divers act as sentinels for early warning, detection, and establishment, while agency monitoring programs use detailed methods to track changes following colonization (Ruttenberg et al. 2012).

There are still many unanswered questions about what approaches may be most effective in managing the lionfish invasion. While native fish biomass at FGBNMS remains high compared to many areas in the Caribbean Sea (Jackson et al. 2014; Johnston et al. 2015a), the lionfish invasion is still in the early stages. Perhaps the most important question is whether natural biotic controls will develop over time, working together with human intervention to suppress the lionfish population (Mumby et al. 2011). Recent studies have not supported this concept (Hackerott et al. 2013; Valdivia et al. 2014), but it could be further tested in national marine sanctuaries and other marine protected areas, where long-term monitoring efforts provide a baseline for this research. The magnitude of the lionfish invasion is a concern for all areas affected in the western Atlantic and Caribbean region, and data collection from both trained volunteer divers and agency programs, such as those conducted in FGBNMS will be important for documenting changes as the invasion progresses.

Acknowledgements

We thank the Bureau of Ocean Energy Management for their support of the long-term monitoring program at EFGB and WFGB, and the National Marine Sanctuary Foundation for their support of the monitoring at EFGB, WFGB, and Stetson Bank. We thank NOAA’s Coral Reef Conservation Program and National Center for Coastal Ocean Science (NCCOS) for their diving and ROV observations. We also thank the numerous scientific divers from Texas A&M University Galveston who helped conduct fish surveys and remove lionfish, as well as the crew of the RV MANTA and MV FLING. We also thank the anonymous referees for their insightful comments. The long-term monitoring program at EFGB and WFGB is funded through an interagency agreement between the U.S. Department of Interior’s Bureau of Ocean Energy Management and the National Oceanic and Atmospheric Administration’s Flower Garden Banks National Marine Sanctuary under contract numbers M09PG00011 and M14PG00020. Lionfish removals and field work at FGBNMS was carried out under permits FGBNMS-2009-001, FGBNMS-2011-002, and FGBNMS-2014-001.

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 Yucatan Peninsula, Mexico. *Aquatic Invasions* 5 (Suppl. 1): S9–S12, <http://dx.doi.org/10.3391/ai.2010.5.S1.003>
- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* 367: 233–238, <http://dx.doi.org/10.3354/meps07620>
- Albins MA, Hixon MA (2011) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes*, <http://dx.doi.org/10.1007/s10641-011-9795-1>
- Bohnsack JA, Bannerot SP (1986) A stationary visual technique for quantitatively assessing community structure of coral reef fishes. National Oceanic and Atmospheric Administration Technical Report NMFS 41, 1–15 pp
- Bohnsack JA, Harper DE (1988) Length-weight relationships of selected marine reef fishes from southeastern United States and the Caribbean. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-SEFC-215, 31 pp
- Bright TJ, McGrail DW, Rezak R, Boland GS, Trippett AR (1985) The Flower Gardens: A compendium of information. U.S. Dept. of the Interior, Minerals Management Service (MMS), Gulf of Mexico Outer Continental Shelf (OCS) Region, New Orleans, Louisiana. OCS Study MMS 85-0024, 103 pp
- Cerino D, Overton AS, Rice JA, Morris JA Jr. (2013) Bioenergetics and trophic impacts of the invasive Indo-Pacific lionfish. *Transactions of the American Fisheries Society* 142: 1522–1534, <http://dx.doi.org/10.1080/00028487.2013.811098>
- Clark R, Taylor JC, Buckel CA, Kracker LM (eds) (2014) Fish and benthic communities of the Flower Garden Banks National Marine Sanctuary: Science to support sanctuary management. National Oceanic and Atmospheric Administration Technical Memorandum NOS NCCOS 179, 317 pp
- Darling ES, Green SJ, O’Leary JK, Cote IM (2011) Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison on Kenyan and Bahamian lionfish populations. *Biological Invasions* 13: 2045–2051, <http://dx.doi.org/10.1007/s10530-011-0020-0>
- Debose JL, Nuttall MF, Hickerson EL, Schmahl GP (2012) A high-latitude coral community with uncertain future: Stetson Bank, northwestern Gulf of Mexico. *Coral Reefs* 32: 255–267, <http://dx.doi.org/10.1007/s00338-012-0971-3>

- Froese R, Pauly D (eds) (2015) FishBase. World Wide Web electronic publication. www.fishbase.org (accessed 24 April 2014)
- Green SJ, Cote IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* 28: 107, <http://dx.doi.org/10.1007/s00338-008-0446-8>
- Green SJ, Akins JL, Maljkovic A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* 7: e32596, <http://dx.doi.org/10.1371/journal.pone.0032596>
- Green SJ, Dulvy NK, Brooks ALM, Akins JL, Cooper AB, Miller S, Côté IM (2014) Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications* 24: 1311–1322, <http://dx.doi.org/10.1890/13-0979.1>
- Hackerott S, Valdivia A, Green SJ, Côté IM, Cox CE, et al. (2013) Native predators do not influence invasion success of Pacific Lionfish on Caribbean Reefs. *PLoS ONE* 7: e68259, <http://dx.doi.org/10.1371/journal.pone.0068259>
- Hipel KW, McLeod AI (1994) Time series modelling of water resources and environmental systems. <http://www.stats.uwo.ca/faculty/aim/RPackages.htm> (accessed 15 August 2015)
- Jackson JBC, Donovan MK, Cramer KL, Lam VV (eds) (2014) Status and trends of Caribbean coral reefs: 1970–2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland, 304 pp
- Johnston MA, Nuttall MF, Eckert RJ, Embesi JA, Slowey NC, Hickerson EL, Schmahl GP (2015a) Long-term monitoring at East and West Flower Garden Banks National Marine Sanctuary, 2011–2012, volume 1: technical report. U.S. Dept. of Interior, Bureau of Ocean Energy Management (BOEM), Gulf of Mexico Outer Continental Shelf (OCS), New Orleans, Louisiana. OCS Study BOEM 2015–001, 194 pp
- Johnston MA, Gittings SR, Morris JA Jr. (2015b) NOAA national marine sanctuaries lionfish response plan (2015–2018): Responding, controlling, and adapting to an active marine invasion. Marine Sanctuaries Conservation Series ONMS-15-01. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, Maryland, 55 pp
- Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter SR, Galzin R, Green A, Harmelin-Vivien M, Hixon M, et al. (2012) Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. *Marine Ecology Progress Series* 446: 189–205, <http://dx.doi.org/10.3354/meps09442>
- Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with Lionfish (*Pterois volitans*) invasion on a Bahamian Coral Reef. *Biological Invasions* 13: 1855–1868, <http://dx.doi.org/10.1007/s10530-011-0005-z>
- Morris JA Jr., Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific Lionfish: an updated integrated assessment. National Oceanic and Atmospheric Administration Technical Memorandum NOS NCCOS 99, 57 pp
- Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE* 6: e21510, <http://dx.doi.org/10.1371/journal.pone.0021510>
- Nuttall MF, Johnston MA, Eckert RJ, Embesi JA, Hickerson EL, Schmahl GP (2014) Lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) records within mesophotic depth ranges on natural banks in the Northwestern Gulf of Mexico. *Bioinvasions Records* 3: 111–115, <http://dx.doi.org/10.3391/bir.2014.3.2.09>
- Ruttenberg BI, Schofield PJ, Akins JL, 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. *Bulletin of Marine Science* 88: 1051–1059, <http://dx.doi.org/10.5343/bms.2011.1108>
- Schmahl GP, Hickerson EL, Precht WF (2008) Biology and ecology of coral reefs and coral communities in the Flower Garden Banks region, northwestern Gulf of Mexico. In: Riegl B, Dodge R (eds), Coral Reefs of the USA. Springer Netherlands, pp 221–261
- Schofield PJ (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the western North Atlantic and Caribbean Sea. *Aquatic Invasions* 4: 473–479, <http://dx.doi.org/10.3391/ai.2009.4.3.5>
- Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquatic Invasions* 5 (Suppl. 1): S117–S122, <http://dx.doi.org/10.3391/ai.2010.5.s1.024>
- Schofield PJ, Morris JA Jr., Langston JN, Fuller PL (2011) *Pterois volitans/miles*. USGS nonindigenous aquatic species database. Gainesville, FL. <http://nas.er.usgs.gov/queries/factsheet.aspx?speciesid=963> (accessed 13 November 2015)
- Scyphers SB, Power SP, Akins L, Drymon M, Martin CW, Schobernd ZH, Schofield PJ, Shipp RL, Switzer TS (2015) The role of citizens in detecting and responding to a rapid marine invasion. *Conservation Letters* 8: 242–250, <http://dx.doi.org/10.1111/conl.12127>
- Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ (2014) Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. *PeerJ* 2: e348, <http://dx.doi.org/10.7717/peerj.348>
- Switzer TS, Tremain DM, Keenan SF, Stafford J, Parks SL, McMichael RH Jr (2015) Temporal and spatial dynamics of the lionfish invasion in the eastern Gulf of Mexico: Perspectives from a broadscale trawl survey. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 7: 1–8, <http://dx.doi.org/10.1080/19425120.2014.987888>