

# No detectable effect of lionfish (*Pterois volitans* and *P. miles*) invasion on a healthy reef fish assemblage in Archipelago Los Roques National Park, Venezuela

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**Abstract** There is an increasing concern that invasive lionfish will have dramatic impacts on native reef fish assemblages in the Caribbean. However, the intensity and speed of such changes will probably depend on the initial structure of each assemblage and on the lionfish population characteristics. The species composition of native fishes, diet and size structures were analyzed on a protected Venezuelan reef, through visual census on zones with and without lionfish, 1 and 3 years after the first sighting of *Pterois* (lionfish). Lionfish mean density  $\pm$  SD increased from  $30 \pm 83.5$  ( $n = 22$ ) to  $121 \pm 164$  ind  $\text{ha}^{-1}$  ( $n = 22$ ), with an important increase in lionfish over 30 cm and the near

absence of juveniles. Native species richness and densities remained stable through time. No significant change of native fish assemblage structure, species richness and density of potential *Pterois* prey, predators and competitors was found over time, but zones with lionfish had significantly higher levels of prey and predators, and significantly different fish assemblage structures. Most importantly, there was no interaction between time and the presence of *Pterois* on these metrics. Our results may suggest that: 1—a healthy composition of the initial structure of the reef fish assemblage may moderate the early impact of lionfish, and the observed lionfish densities (mean  $\pm$  SD =  $121 \pm 164$  ind  $\text{ha}^{-1}$ ,  $n = 22$ ) were not sufficient to induce a significant change in the assemblage; and 2—lionfish probably select zones where species richness and density of prey are the highest.

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## Introduction

After two decades of rapid spread, Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) have become the first non-native marine fish species to establish to such an extent in the Western Atlantic (Schofield 2009, 2010; Albins and Hixon 2011). Their range currently extends latitudinally from New York, USA, to the Urabá Chocoano, Colombia, and longitudinally from the western Gulf of Mexico to Barbados (USGS-NAS 2014). This invasion may represent the most important concern for the short-term future of Caribbean coral reefs. It adds considerable stress to an ecosystem already severely disrupted by mass coral bleaching (McWilliams et al. 2005; Bastidas et al. 2012), diseases (Hughes 1994; Aronson and Precht 2001; Bellwood et al. 2004), overfishing (Hughes 1994; Jackson et al. 2001) and pollution (DeGeorges et al. 2010).

**Table 1** *Pterois* densities recorded by underwater visual censuses (UVC) in several localities around the Caribbean

Site (country or island)	First report of lionfish	Date of survey	Mean densities ( ind ha <sup>-1</sup> ) ± SD, n = sample size	Reference
Dos Mosquises, Venezuela	Feb 2010	Mar 2013	121 ± 164, n = 22	This study
Los Roques area, Venezuela	Nov 2009	Mar 2013	90 ± 172, n = 48	Elise—unpubl data
Morrocoy area, Venezuela	Dec 2009	Jan 2013	51 ± 69, n = 54	Galindo—unpubl data
Central coast, Venezuela	Nov 2009	2013	26 ± 67, n = 200	Agudo—pers comm
Bonaire, Netherlands	Nov 2009	2011	9, n = 16 (6 m); 31, n = 16 (12 m); 41, n = 16 (16 m); 228, n = 16 (24 m); 216, n = 16 (32 m)	White (2011)
La Amistad, Costa Rica	Apr 2009	June 2011	92 ± 129, n = 26	Sandel (2011)
Mesoamerican Barrier Belize–Mexico	Dec 2008	May–July 2012	160	Hackerott et al. (2013)
Cozumel, Mexico	Jan 2009	2010	255	Sosa-Cordero et al. (2013)
Little Cayman Island, UK	Feb 2008	Sep 2011	233–650	Frazer et al. (2012)
Jardines de la Reina, Cuba	Late 2007	May–June 2011	150	Hackerott et al. (2013)
New Providence, Bahamas	2004	July 2008	393 ± 144, n = 12	Green and Côté (2009)
Eleuthera, Bahamas	2005	2009	520	Hackerott et al. (2013)
Cape Eleuthera, Bahamas	2007	Feb 2012	300 ± 600, n = 60	Green et al. (2013)
North Carolina, USA	2000	2008	150, n = 8	Morris and Whitfield (2009)

In their native range, lionfishes seldom exceed 10 ind ha<sup>-1</sup>, with a maximum reported density of 26.3 ind ha<sup>-1</sup> (Kulbicki et al. 2012). In the Caribbean, they have locally reached considerably higher densities, up to 650 ind ha<sup>-1</sup> (Table 1).

The success of lionfish in the Western Atlantic may be explained by a combination of factors. These species are characterized by high reproductive and dispersal capacities (Moyer and Zaiser 1981; Freshwater et al. 2009; Morris 2009; Morris et al. 2011; Betancur-R et al. 2011) with in particular massive production of well-protected eggs (Morris et al. 2011) all year long (Fishelson 1975; Morris et al. 2011), making possible fast spread and high larval survival rates (Fishelson 1975; Morris et al. 2011; Côté et al. 2013). Furthermore, both juvenile and adult lionfish appear to be habitat generalists (Côté et al. 2013). Across the Western Atlantic, the species are found in temperate hard-bottom reefs (Whitfield et al. 2002, 2007), several types of coral reefs (Albins and Hixon 2011; Biggs and Olden 2011; Lesser and Slattery 2011), seagrass beds (Biggs and Olden 2011), mangroves (Barbour et al. 2010) and estuarine rivers (Jud and Layman 2012) and were also reported down to 300 m deep by Nemo submarine off Lyford Cay, Bahamas.

The success of lionfish invasion is often linked to their trophic generalism: More than 70 native fish species have so far been reported as lionfish prey (Morris and Akins 2009; Côté and Maljković 2010; Valdez-Moreno et al. 2012). The diet of juveniles also includes crustaceans (Morris and Akins 2009). *Pterois volitans* has specific hunting method, by blowing jets of water at its prey

(Albins and Lyons 2012), combined with a behavior and appearance not perceived as a predation threat (Côté et al. 2013), which affords it a high predation success (Côté and Maljković 2010; Cure et al. 2012). This predation may be at the origin of drastic changes in native reef fish assemblages. Such changes have already been noticed in the Bahamas, where lionfish have been present for a decade. Green et al. (2012), for example, showed that an increasing biomass of lionfish—from 23 to 40 % of the total biomass of predator—between 2008 and 2010 coincided with a 65 % decline in the biomass of the lionfish's prey fishes. Moreover, Albins and Hixon (2008) reported a 79 % reduction in the recruitment of native fishes in the presence of lionfish over 5 weeks on small artificial reefs. This result can be in part explained by the targeting of small fish as prey by lionfish, the average prey size being on average less than 20 % of the lionfish size (Morris and Akins 2009; Muñoz et al. 2011; Albins 2013).

The extent to which biotic resistance, through predation, competition, parasitism or diseases (Elton 1958; Levine et al. 2004), can slow the invasion is unclear. Predation on lionfish by native predators has already been reported (Maljković et al. 2008; Spalburg 2014; Mata pers comm). In the Exuma marine protected area (MPA), Bahamas, Mumby et al. (2011) observed an inverse relationship between grouper biomass and lionfish biomass, suggesting lionfish predation by groupers. In contrast, Hackerott et al. (2013) highlighted that biomass of large groupers (and potential native predators) had no measurable effects on lionfish densities on a larger Caribbean scale. Hackerott

et al. (2013) suggested that the lower lionfish densities observed within MPAs were the result of local culling, which is generally focused on protected areas in the region. The grouper effect described by Mumby et al. (2011) could therefore be an MPA effect instead. In addition, lionfish appear to grow faster and have higher predation efficiency than potential native competitors (Albins 2013; Côté et al. 2013), which suggests a limited potential for biotic resistance, at least in terms of predation and competition by native species. The impacts of lionfish invasion are likely to vary greatly among Caribbean localities, according to:

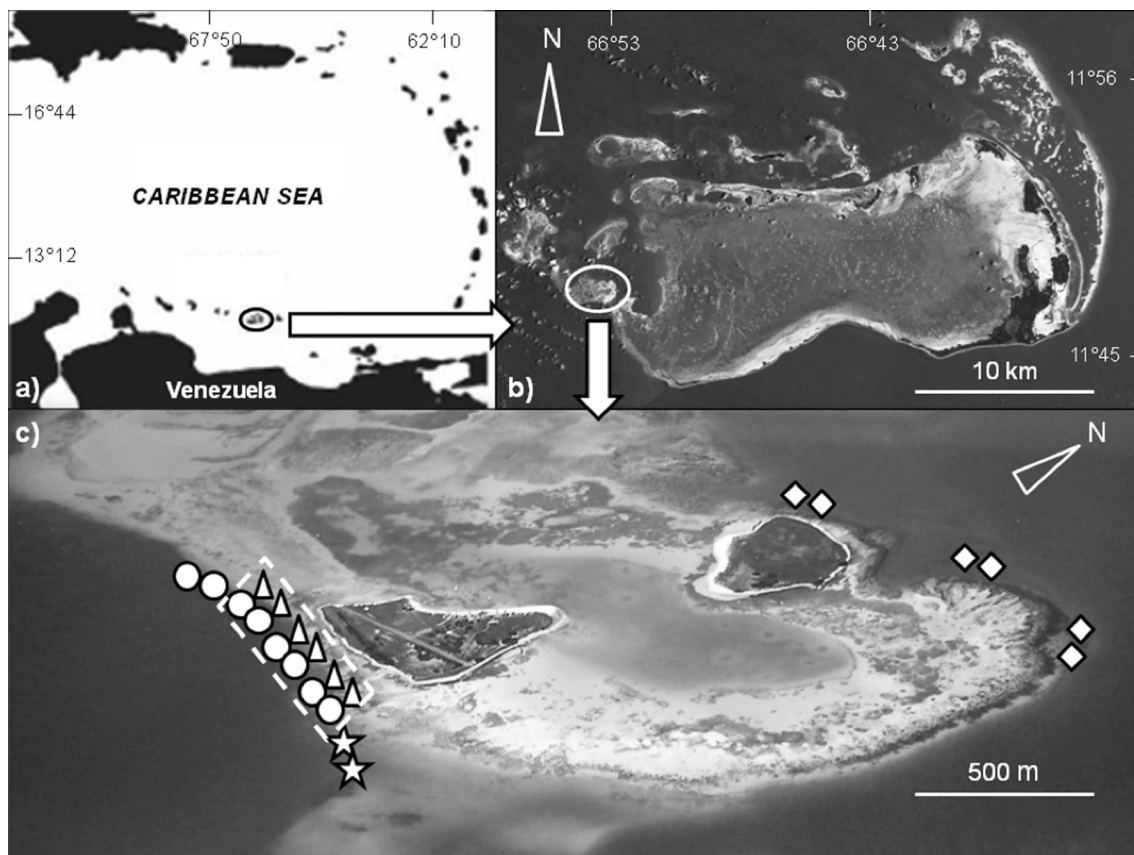
- the initial characteristics of the reef fish assemblage, i.e., species richness, density, size and trophic structure; in particular, “healthy” assemblages, with high fish biodiversity and abundance, may resist better than degraded ones (Levine and D’Antonio 1999)
- the characteristics of the invading *Pterois* spp. population, i.e., density and size structure
- the duration of the exposure of the native assemblage to *Pterois* spp.

The aim of our study is to evaluate the relationship between various reef fish assemblage metrics and lionfish densities in a nearly undisturbed reef area in the Archipelago Los Roques National Park (MPA), Venezuela, which belongs to a lesser known Caribbean region. In particular, we will test: 1—whether the preserved status of Los Roques reef fish assemblage brings some protection against the impacts of *Pterois* spp. and 2—whether the impacts of *Pterois* spp. on the characteristics of the native fish assemblage are linked to some thresholds.

## Materials and methods

### Study system

The Archipelago Los Roques National Park was established in 1972 on an area of 221,120 ha, with coral reefs covering approximately 10,000 ha. It is located at the southern edge of the Caribbean Sea ( $11^{\circ}44'–11^{\circ}58'N$ ,  $66^{\circ}32'–66^{\circ}57'W$ ), 160 km north of the central coast of Venezuela (Fig. 1).



**Fig. 1** **a** East Caribbean map; **b** Archipelago Los Roques National Park (adapted from a satellite photography by Japan Aerospace Exploration Agency); **c** Dos Mosquises’ reef aerial photography with approximate position of the transects: *triangle* reef flat–lionfish, *dia-*

*mond* reef flat–no lionfish, *circle* reef slope–lionfish, *asterisk* reef slope–no lionfish. The area where lionfish were culled is indicated by a *dash line*

The archipelago lies over a wide volcanic platform, covered by a thick sedimentary layer (Méndez-Baamonde 1978). On this oceanic platform, two narrow barrier reefs, the East reef and South reef (approximately 20 and 30 km long, respectively), partially enclose a shallow lagoon with a mean depth of 4 m. The lagoon floor is predominantly bare sand or mud with important expanses of seagrass and/or macro-algae beds and numerous patch reefs. Some 42 keys and many sand and coral banks are spread around this lagoon (Fig. 1). Both spearfishing (since 1972) and the use of nets (since 1992) are banned, and with a human population around 1,500 inhabitants ( $0.7 \text{ inhab km}^{-2}$  of MPA), the Archipelago Los Roques National Park is considered to be among the least impacted coral reef systems in the Caribbean (Kramer 2003; Posada et al. 2003). The fish fauna comprises about 370 species, including 21 shark species (Cervigón and Ramírez-Nahím 2003; Tavares 2005).

Our study site, Dos Mosquises' reef ( $11^{\circ}48'03''\text{N}$ ,  $66^{\circ}53'30''\text{W}$ ), is located along the South barrier reef, southwest of the archipelago. Shallow dead *Acropora* colonies form the fringing reef of the island, extending to a reef platform of both hermatypic and octocorals, in a spurs and grooves area to a depth of 8–9 m. Seaward, a steep reef slope, supports live coral colonies down to 20–25 m. The fish densities on this slope are the highest of the whole reef (Elise 2012). Dos Mosquises' reef is under special protection since the creation of the National Park, when the Fundación Científica Los Roques (FCLR) established a marine biology station on the island. Lionfish were first reported on the reef in February 2010 (Lasso-Alcalá and Posada 2010).

### Sampling design

We sampled the Dos Mosquises' reef twice, in March 2011 and in March 2013. Eleven stations were sampled at each period, with two transects per station (Table 2; Fig. 1). No lionfish was recorded or caught on eight of the transects neither in 2011 nor in 2013, while lionfish were recorded or caught along the remaining 14 transects in 2011 and 2013. Twelve transects were set on the reef flat at 6 m depth, and the remaining ten transects were sampled on the reef slope, at a mean depth of 12 m. The same observers performed the dives at each period.

**Table 2** Sampling design. The numbers of transects performed in each zone are shown

	Reef flat Lionfish	Reef slope Lionfish	Reef flat No lionfish	Reef slope No lionfish
2011	6	8	6	2
2013	6	8	6	2

### Reef fish community sampling

Transects were 2 m wide  $\times$  30 m long and encompassed the entire water column from the seafloor to surface. During each census, a diver swam over the transect line identifying and counting all fishes within 1 m on either side of the central line. Mobile and shy species were identified on the first pass as the transect line was laid and then the other species on the second pass. All detected fish were recorded.

### Lionfish population status

The observer inspected any hiding place within the transect width, in order to comply with the recommendations of Green et al. (2013) regarding the detection of lionfish. The size of any sighted lionfish was recorded per 1-cm interval. In addition to the UVC observations, lionfish were caught by handnet and spearfishing over 1.5 ha in 2011 and 2013 (Fig. 1). Any detectable lionfish was targeted. All the catch was measured to the nearest cm.

### Statement of human and animal rights

All lionfish were euthanized in a way minimizing their suffering by trained fishermen and divers. All the study was made with the authorization of the National Parks Institute of Venezuela (INPARQUES).

### Benthic community sampling

We assessed benthic composition along the same transects, applying the medium-scale approach (MSA) of Clua et al. (2006), based on the description of 12 quadrats of  $25 \text{ m}^2$  ( $300 \text{ m}^2$  in total), six quadrats on each side of the transect. We collected 11 benthic variables. Depth was the mean depth (m) of all quadrats; depth standard deviation was also estimated across quadrats; slope was defined as the mean difference in depth between the right and the left side of the transect; habitability was evaluated on a 1–6 scale, 1 indicating the absence of refuges and 6 the most complex reef matrix; heterogeneity was evaluated using a Shannon index applied to all the hard substrate variables across quadrats; hard bottom (which included slabs, rocks, boulders, dead and live coral), dead and live coral, turf, octocoral and sponges were evaluated for each quadrat on a 1–5 scale as defined in Clua et al. (2006).

### Analysis

We identified each fish species recorded on the transect as potential prey, competitor or predator of lionfish, based on recent studies in the Caribbean (Morris and Akins 2009; Côté and Maljković 2010; Valdez-Moreno et al. 2012;

Hackerott et al. 2013) (Online resource 1). The objective of this classification was to explain potential changes in the structure of the assemblage linked to the presence of lionfish.

In order to characterize the structure of the assemblage, we compiled several life-history traits for each species. Diet was divided into 6 categories (herbivores H, omnivores OM, sessile invertebrate feeders SI, mobile invertebrate feeders MI, feeding carnivores FC and plankton feeders PK). Species size, based on maximum recorded total length (Froese and Pauly 2013), was divided into six size classes: <7, 7–15, 16–30, 31–50, 51–80 and >80 cm. Schooling was divided into solitary species, species living in pairs, species living in small groups (3–20 fish on average in a group), medium size groups (20–50 fish) and large groups (> 50 fish). Daily activity was divided into species active only during the day, species active only at night and species active either during the day or the night. Adult home range was divided into sedentary species, mobile species (staying within the same reef for several days) and very mobile (constantly moving around and usually changing reefs within a day). Level in the water column was divided into species staying on the bottom (benthic), species hovering just above the bottom (demersal) and species hovering high above the reef (pelagic). Geographical range was defined for each species, with an index based on the number of checklists where the species is known in the Atlantic (Kulbicki et al. 2013). Functional entities were defined as the combination of diet and size classes, resulting into 36 possible entities, of which 22 were represented by at least one species.

Differences in species richness and density of the total fish fauna, potential prey, competitors and predators were tested using factorial type III ANOVAs (calling “Anova” within the CAR package from the R software). Differences in density of life-history traits groups and functional entities were tested using type III MANOVAs (calling “Manova” within the CAR package from the R software). The factors tested were year, habitat (reef flat or reef slope) and zones defined by the presence or absence of lionfish, and their interactions. Year and zone factors were used to test differences in benthic composition. Spatial autocorrelations of the residuals from the ANOVAs and MANOVAs were tested using Moran I tests (calling “Moran.I” within the APE package from the R software). When significant autocorrelations were found, results were re-analyzed using a Spatial Linear Model (SLM: using the “spautolm” module within the SPDEP package from the R software). All the tests were performed using the program R (R Core Team 2014). We analyzed the changes in the structure of the reef fish assemblages according to habitat (reef flat or reef slope), zones defined by the presence or absence of lionfish and year using a PERMANOVA (calling the module “adonis” within the VEGAN package from the R software).

**Table 3** Benthic variables mean values on lionfish and no lionfish zones

Benthic variables	Zone		Effect	
	Lionfish	No lionfish	Zone effect	Year effect
Depth (m)	10.2	6.8	**	NS
Depth SD	0.1	0.11	NS	NS
Slope value	1.7	1	*	NS
Habitability	49	26	***	NS
Heterogeneity	2.8	2.9	NS	NS
Hard bottom (%)	87	75	***	Increase**
Dead coral (%)	37	34	NS	NS
Live coral (%)	49	41	**	Increase***
Turf	28	20	**	Increase*
Octocorals	20	34	***	NS
Sponges	13	29	***	NS

Significance according to an ANOVA of zone effect and year effect on benthic variables: NS not significant; \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

## Results

### Benthic composition

A limited number of significant changes were recorded in the benthic assemblage of Dos Mosquises’ reef between 2011 and 2013. Eight out of 11 benthic variables showed no significant change. Only hard-bottom cover (ANOVA,  $F = 9.13$ ,  $p = 0.0043$ ), live coral cover (ANOVA,  $F = 27.34$ ,  $p < 0.0001$ ) and turf index (ANOVA,  $F = 5.97$ ,  $p = 0.019$ ) significantly increased between years (Table 3). No significant interaction was detected between year and zones defined by the presence or absence of lionfish.

### Native assemblage

Overall, we recorded 91 native fish species, belonging to 29 families, across all transects (2,640 m<sup>2</sup>). We found a mean species richness  $\pm$  SD of  $29 \pm 6$  species 60 m<sup>-2</sup> ( $n = 44$ ) and a mean density  $\pm$  SD of  $4.17 \pm 1.57$  ind m<sup>-2</sup> ( $n = 44$ ). The fish assemblages were significantly different on transects with and without lionfish (Table 4). Transects with lionfish had higher total fish species richness and density, higher species richness of prey, predators and competitors and higher densities of prey and predators but not of competitors. No significant interaction was detected between year and zones defined by the presence or absence of lionfish (Table 4). In addition, there were significant differences between lionfish and no lionfish zones for all life-history groups tested, except for size class groups (Table 5). Densities of the different groups were higher (or at least similar) in lionfish zone than in no lionfish zone for nearly

**Table 4** Mean species richness (SR on 60 m<sup>2</sup> transects) ± SD and densities (DENS in ind m<sup>-2</sup>) ± SD of lionfish's prey, predators and competitors on Dos Mosquises' reef. Effects of zone (presence/absence of lionfish), habitat (reef flat and reef slope), year and interactions between factors on prey, predators and competitors species richness and densities (*p* values of factorial ANOVAs)

	Lionfish zone				No lionfish zone			
	Reef flat		Reef slope		Reef flat		Reef slope	
	2011	2013	2011	2013	2011	2013	2011	2013
Mean prey SR	19.2 ± 1.9	19.3 ± 2.0	21.4 ± 2.1	19.4 ± 2.7	17.2 ± 1.2	17.0 ± 1.7	17.5 ± 2.1	17.0 ± 2.8
Mean pred. SR	2.7 ± 0.5	2.7 ± 0.5	4.1 ± 1.2	5.0 ± 0.9	1.0 ± 0.0	2.0 ± 1.3	3.0 ± 0.0	2.5 ± 2.1
Mean comp. SR	9.7 ± 2.1	9.5 ± 2.7	12.4 ± 3.3	13.8 ± 1.3	7.7 ± 1.2	9.5 ± 2.8	10.5 ± 0.7	9.0 ± 2.8
Mean total SR	31.2 ± 3.7	30.3 ± 5.3	32.9 ± 4.1	33.3 ± 4.5	23.2 ± 1.9	23.5 ± 4.0	26.5 ± 3.5	24 ± 4.2
Mean prey DENS	4.1 ± 1.0	3.1 ± 0.9	5.0 ± 2.0	3.9 ± 1.2	3.4 ± 0.7	2.3 ± 0.4	3.4 ± 0.4	3.3 ± 0.1
Mean pred. DENS	0.07 ± 0.03	0.08 ± 0.03	0.14 ± 0.08	0.22 ± 0.19	0.03 ± 0.02	0.05 ± 0.04	0.10 ± 0.0	0.06 ± 0.06
Mean comp. DENS	0.63 ± 0.56	0.40 ± 0.31	1.36 ± 1.02	1.17 ± 0.75	0.37 ± 0.13	0.59 ± 0.23	1.14 ± 0.11	0.93 ± 0.53
Mean total DENS	4.5 ± 1.1	3.7 ± 1.2	5.7 ± 2.1	4.7 ± 1.5	3.6 ± 0.7	2.5 ± 0.4	3.7 ± 0.4	3.5 ± 0.1

	Zone	Habit	Year	Zone × Habit	Zone × Year	Habit × Year	Zone × Year × Habit
Mean prey SR	***	NS	NS	NS	NS	NS	NS
Mean pred. SR	***	***	NS	NS	NS	NS	NS
Mean comp. SR	*	**	NS	NS	NS	NS	NS
Mean total SR	***	NS	NS	NS	NS	NS	NS
Mean prey DENS	*	NS	NS	NS	NS	NS	NS
Mean pred. DENS	*	*	NS	NS	NS	NS	NS
Mean comp. DENS	NS	**	NS	NS	NS	NS	NS
Mean total DENS	**	NS	NS	NS	NS	NS	NS

**Table 5** Effects of zone (presence/absence of lionfish), habitat (reef flat and reef slope), year and interactions on groups densities (*p* values of MANOVAs). Densities for each group are detailed per class in the Online resource 2

Groups	Zone	Habitat	Year	Zone × habitat	Zone × year	Habitat × year	Zone × year × habitat
Functional entities (diet × size)	***	***	*	*	NS	NS	NS
Diet	*	***	*	***	NS	NS	NS
Species size class	NS	**	NS	NS	NS	NS	NS
Schooling behavior	*	NS	NS	***	NS	NS	NS
Adult home range (mobility)	*	NS	NS	*	NS	NS	NS
Daily activity	*	NS	NS	NS	NS	NS	NS
Level in the water column	**	***	*	**	NS	NS	NS
Geographical range	*	NS	NS	NS	NS	NS	NS

all the groups tested: Only the densities of herbivorous taxa were higher in the zone without lionfish (Online resource 2). Most of the functional entities and trophic groups' densities decreased between 2011 and 2013. Pelagic, demersal and benthic species densities also decreased between years. No significant interaction was detected between year and lionfish presence/absence (Table 5). A PERMANOVA (Table 6) on the abundances of all native species confirmed the significant differences in the structure of the assemblage between zones defined by the presence or absence of lionfish ( $F = 8.79$ ,  $p = 0.001$ ). Differences between 2011 and

2013 were marginally significant ( $F = 2.43$ ,  $p = 0.019$ ). No significant interaction was detected between these two factors (Table 6).

Overall species richness and densities, as well as prey species richness and densities, were not significantly different between reef flat and reef slope (Table 4). Reef slope carried higher species richness and densities of predators and competitors than reef flat, whether lionfish are present or not (Table 4). Differences in the structure of the fish assemblage between flat and slope, zones being taken into account or not, were also significant (see Table 5 and

**Table 6** Results of the PERMANOVA performed on the abundances of the overall native fish assemblage

	<i>Df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Zone	1	0.9653	0.96533	8.791	0.001***
Habitat	1	0.7242	0.72415	6.5946	0.001***
Year	1	0.2664	0.26643	2.4263	0.019*
Zone × habitat	1	0.4701	0.47009	4.2809	0.001***
Zone × year	1	0.1734	0.1734	1.5791	0.12
Habitat × year	1	0.1144	0.11445	1.0422	0.388
Zone × year × habitat	1	0.1011	0.10107	0.9204	0.482
Residuals	36	3.9531	0.10981		
Total	43	6.7681			

Online resource 2 for details), but no significant interaction was detected with year (Table 5). The PERMANOVA (Table 6) corroborated the significant differences in the structure of the assemblage between flat and slope ( $F = 6.59$ ,  $p = 0.001$ ) and between flat and slope depending on the zone ( $F = 4.28$ ,  $p = 0.001$ ). Interaction with year was not significant (Table 6).

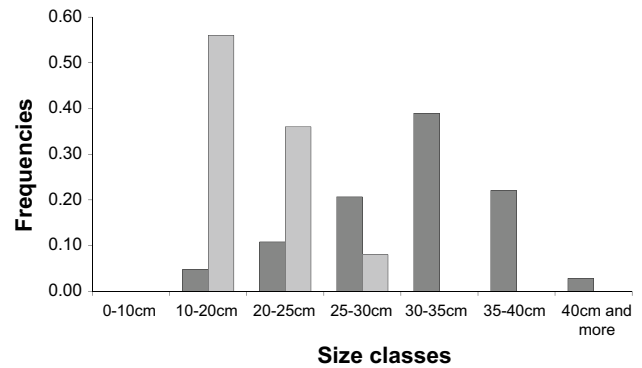
Spatial autocorrelation was tested using Moran I index for 61 variables (total species richness and densities, prey/predators/competitors species richness and densities, densities of each group of life-history traits and functional entities): 46 were not significant and 8 marginally significant (Online resource 3). Most of the significant spatial autocorrelation was for the density of lionfish competitors and its derivatives and to a lesser extent to prey densities. A Spatial Linear Model (SLM) was therefore fitted to prey density and competitor densities (Online resource 4). It indicated that the density of competitors varied significantly with habitat but was not related to lionfish presence. Similarly, prey density changed with years but was not significantly affected by lionfish.

### Lionfish population

Lionfish were observed at sites characterized by a greater depth, higher habitability, higher percentages of hard bottom and live coral cover (Table 3), but lower octocoral and sponge indices.

Between 2011 and 2013, lionfish densities recorded by UVC (mean  $\pm$  SD =  $30 \pm 83.5$  ind  $ha^{-1}$ ,  $n = 22$  and  $121 \pm 164$  ind  $ha^{-1}$ ,  $n = 22$ ; Mann–Whitney  $U$  test,  $U = 163$ ,  $N_1 = 22$ ,  $N_2 = 22$ ,  $p = 0.022$ ) and catches (17 and 143 ind  $ha^{-1}$ ) on Dos Mosquises' reef increased, by a factor of 4 and 8, respectively. The maximum density observed on a transect was 500 ind  $ha^{-1}$ .

The size frequency of lionfish changed between 2011 and 2013 (Fig. 2). In particular, in 2011, no lionfish caught was more than 30 cm TL, whereas in 2013, more than half was over 30 cm ( $G$  test,  $X^2_2 = 120.21$ ,  $p < 0.0001$ ).

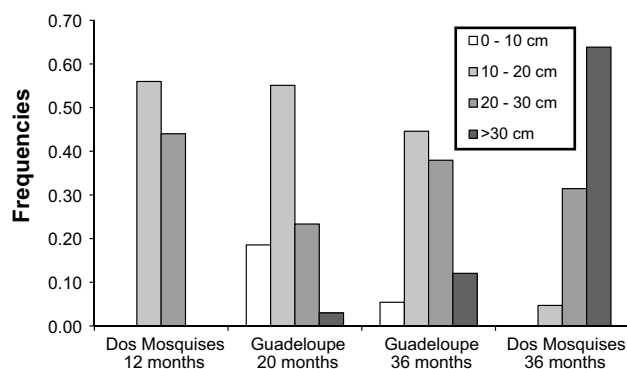
**Fig. 2** Histogram of lionfish (obtained by fishing) size frequencies in 2011 ( $n = 25$ , light gray) and 2013 ( $n = 215$ , dark gray)

### Discussion

On Dos Mosquises' reef, lionfish were found preferentially on the leeward reef slope, which offers a diverse and highly structured habitat. Partially dead coral colonies create overhanging structures on the slope, with important capacities for refuges. Characterized by low turbidity and low hydrodynamic conditions, the slope carries the highest species richness and density of prey of the whole reef and therefore represents a favorable habitat for lionfish. This brief habitat description agrees with the preferred lionfish habitat sketched in the literature for the Caribbean (Côté and Maljković 2010; Biggs and Olden 2011; White 2011; Hackerott et al. 2013).

Lionfish population increased fourfold to eightfold in 2 years, illustrating the success of the invasion on Dos Mosquises' reef. The change in lionfish population structure on Dos Mosquises, when compared with another Caribbean locality (Fig. 3), reveals striking facts.

- Twelve months after the invasion of Dos Mosquises' reef, up to 44 % of lionfish measured between 20 and 30 cm, whereas this size class represented only 23 % in Guadeloupe (Mazeas, DEAL Guadeloupe, pers comm) after 20 months. This suggests either a faster growth of individuals, which could be due to favorable conditions (e.g., high prey density) on the Dos Mosquises' reef or immigration of adult fish from afar. In Guadeloupe, culling effort during that period was low, therefore excluding an effect due to fishing.
- After 36 months, lionfish of more than 30 cm only accounted for 12 % of the Guadeloupe's population, whereas they made up 64 % of the Dos Mosquises' population. One possible explanation is that the increase in culling effort in Guadeloupe at that period had limited the presence of large individuals in this area. Alternatively, Guadeloupe reefs might not be as healthy as the



**Fig. 3** Histogram of lionfish size frequencies (catch data) at several time intervals (in months) after the first sightings of a lionfish within 2 localities. Culling actively started in Guadeloupe 20 months after the beginning of the invasion

Dos Mosquises' reef and offer less favorable conditions for lionfish growth.

- There were few very small (0–10 cm) lionfish in the Dos Mosquises' population, as only three individuals under 10 cm were observed in this area. Three hypotheses may support this observation: (1) detection of the smallest individuals in the highly structured habitat of this reef is low (see Green et al. 2013), although culling and in situ observations were performed by trained fishermen and divers; (2) this reef is not a favorable habitat for juveniles and lionfish migrated from other nearby reefs, seagrass or mangroves. Such differences in habitat use between juveniles and adults were found by Barbour et al. (2010) and Biggs and Olden (2011) and (3) there was predation of young lionfish by native predators or large lionfish; Hackerott et al. (2013) considered that if biotic resistance occurs (predation, competition and parasitism), it would be more evident on earlier life stage.

Lionfish have widely colonized the Dos Mosquises' reef in 3 years, but we found no significant changes in the structure of the reef fish assemblage that could be attributed with confidence to lionfish, as indicated by the absence of significant interaction between year and lionfish presence/absence. The differences in the functional structure of the assemblage between reef flat and reef slope and the interaction with zones with and without lionfish confirm the spatial patterns found in a previous study on this reef (Elise 2012), but cannot be directly related to the increase in lionfish density as no significant interaction with year was detected. Additionally, the results of the Moran I tests indicated spatial autocorrelation mainly for the density of competitor and prey of lionfish, but an SLM demonstrated that lionfish could not be directly linked to variations in these parameters. The first hypothesis to explain the absence of lionfish effect is that the densities of *Pterois* were too low

to induce a significant change in the initial assemblage. Green et al. (2012) recorded important variations in the structure of the reef fish assemblage next to the invasion by lionfish on New Providence reef, Bahamas. As in our study, they studied a 2-year period, but their survey took place 4 years after the first lionfish sighting (2004), whereas it was after 1 year in our study. Lionfish populations were much more important in the Bahamas in 2008 than in 2011 in Los Roques (Table 1). It may therefore still be too early to observe structural changes in Dos Mosquises' reef fish assemblage. Green et al. (2014) developed a model of predation by lionfish on native fish communities to predict threshold densities of lionfish beyond which native fish biomass should decline. The use of the model on our data would have certainly helped us to answer to this first hypothesis, but it required data of biomass which we could not survey in our study. A second hypothesis is given by the quality of the reef fish assemblage at Dos Mosquises. This can be assessed by a comparison with other reef fish assemblages across the Caribbean (Table 7).

Numerous studies have highlighted abundance and biomass of piscivores as an evidence of reef fish assemblage health (Newman et al. 2006; Sandin et al. 2008; Stallings 2009). The densities of piscivores on Dos Mosquises' reef, and moreover in Los Roques area, greater than in other Caribbean localities, suggest that the local reef fish assemblage is in good condition (Table 7). Only Navassa Island's assemblage, considered trophically intact by Miller and Gerstner (2002), reveals a similar density of piscivores. The abundance of large species of grazers (Scaridae) in Dos Mosquises' fish assemblage can be interpreted as another evidence of its health (Mumby et al. 2006).

Several other Caribbean MPAs were evaluated after 3 or 4 years of colonization, as in our study, by Hackerott et al. (2013). They found similar low densities of lionfish (Table 1) and high species richness and density of predators, but they did not find a relationship between these observations. They evoked culling effort as the most likely explanation for the low lionfish densities within these reserves, whereas there was no fishing for lionfish in Dos Mosquises' area until the 2013 experiment, except for the 25 individuals caught in March 2011. Consequently, one could expect higher lionfish densities on Dos Mosquises' reef compared to the MPAs of Hackerott et al. (2013) study. The absence of difference in the densities observed (Table 1) could be due to many reasons, which cannot be tested at present, such as differences in the sampling techniques (Kulbicki et al. 2012; Green et al. 2013), differences in the carrying capacities of each location or a higher level of control by the native fish assemblage.

If we cannot test these reasons, we can at least discuss them. Lionfish densities on Dos Mosquises' reef were recorded with two different techniques, UVC and catches



**Table 7** Average densities (ind.100 m<sup>-2</sup>) of six trophic groups in nine localities of the Caribbean

Locality	FC	PK	MI	SI	OM	H	Total	References
<i>Dos Mosquises</i>	13	197	67	7	73	72	428	This study
<i>Los Roques</i>	20	220	52	7	82	47	427	Elise—unpubl data
Barbados	2	141	35	0	5	71	256	Rakitin and Kramer (1996)
Martinique	3	184	36	1	154	36	414	Rousseau (2010)
Guadeloupe	6	321	13	5	54	34	433	Bouchon et al. (1994)
<i>Puerto Rico</i>	6	108	197	13	52	207	582	Aguilar-Perera and Appeldoorn (2008)
<i>Navassa island</i>	11	339	48	2	77	78	555	Sandin (2003)
Bahamas	5	146	82	2	15	34	285	Lamb and Johnson (2010)
Florida keys	2	28	36	1	20	17	104	Bohnsack et al. (1999)

*FC* piscivores, *PK* plankton feeders, *MI* mobile invertebrates feeders, *SI* sessile invertebrates feeders, *OM* omnivores, *H* herbivores  
Marine protected areas at sampling date are in italics

by spearfishing, leading to very similar results (respectively, 121 and 143 ind ha<sup>-1</sup>). As indicated by Kulbicki et al. (2012), the detectability of lionfish decreases with transect width, with a good detection within the first meter, which was the width of our transects. Green et al. (2013) showed that transects which were not specifically designed to count lionfish limited the detection to 28 % of the density recorded by focused searches. To characterize “non lionfish transects”, they had, however, a faster swimming speed (5 m min<sup>-1</sup>) than with our method (1.5 m min<sup>-1</sup>), and their transect width (2 m) was wider than ours (1 m). As spearfishing was performed intensively and over a short period (1 day) in our study, it is likely that the avoidance behavior of lionfish toward spearfishermen had no time to fully develop. In our opinion, the convergence of UVC and spearfishing densities in our survey therefore suggests that our lionfish density estimates are reliable. Given the high number of replicates in Hackerott et al. (2013) study, and even if the transects they used were larger and longer than ours, the densities of 150 and 160 ind ha<sup>-1</sup> that they observed in Jardines de la Reina (Cuba) and the Mes-oamerican Barrier (Belize and Mexico) can probably be compared with ours. They found that at these lionfish densities no relationship could be detected with native predator densities as in the present study. In addition, we found that lionfish prey, predator and competitor species richness did not change significantly with the arrival of lionfish. However, species richness is the most stable parameter in a reef fish assemblage (Kulbicki et al. 2007), and it may take a much larger lionfish density to generate a significant impact on diversity. Moreover, species richness of lionfish predators and competitors and density of lionfish predators were higher in the lionfish zone. This can be explained by the habitat characteristics we described above and the good abiotic conditions, carrying high species richness and density of prey. The lionfish zone is thus a favorable habitat not only for lionfish but also for both native predators and competitors. The densities of mobile species schooling in medium size and large groups high in the water column, such as plankton feeders, are far higher in this zone and

represent an important prey resource, including for lionfish that we observed feeding on *Chromis cyanea* and *C. multi-lineata* when individuals from those species came close to the bottom.

The decrease in lionfish prey density was marginally not significant between 2011 and 2013. Since there is no interaction between zone and year in our data, the decrease cannot be attributed with certainty to the presence of lionfish, even if this decrease is of 22 % in lionfish zone. In fact, the decrease was more important (24 %) in the zone where lionfish were not recorded, and although lionfish have certainly frequented this latter zone, they have probably never established durably there because of the characteristics of the habitat (more exposed conditions, with higher turbidity, current and less refuge capacities). In addition, it is unlikely that this zone constitutes a specific feeding area for lionfish considering their highly sedentary behavior (Jud and Layman 2012) and the higher availability of prey in the zone where we found them. These observations let us think that the decrease in lionfish prey is probably not mainly driven by lionfish. Nevertheless, considering that recruits of lionfish prey (and other species) on Dos Mosquises’ reef may come from the reef as a whole and even from the wider archipelago, the decrease could be an effect of the invasion at the reef and/or archipelago scales. Additional surveys would be needed to detect whether the decrease in lionfish prey is due to natural factors or to the lionfish invasion. In particular, the action of lionfish, which feed mainly on small fish (Morris and Akins 2009), could be indirectly detected by a general decrease in prey recruits (Albins and Hixon 2008).

Lionfish tend to target small prey fish, on average less than 20 % of the lionfish body length (Morris and Akins 2009; Muñoz et al. 2011; Albins 2013). This means that 30-cm lionfish will target prey on average less than 6 cm. Therefore, the effect of lionfish on the assemblage may take some time to become detectable, the time for recruits to become established adults. Juveniles are subjected to very heavy mortality (Doherty et al. 2004), and the predation by lionfish may not have a detectable effect on the resulting

adults: first, because they may target the most vulnerable juveniles, which would probably die even without lionfish, and second, because the proportion of juveniles eaten by lionfish may only be a small fraction of the total mortality undergone by juvenile reef fish.

We could detect no effect of lionfish presence on Dos Mosquises' reef fish assemblage in 3 years of presence, although its population is well established and healthy. We found no relationship between lionfish density and predators/competitors species richness and density, but highlighted that the native reef fish assemblage was healthy and carried high lionfish prey density. Lionfish prey decreased between years in the same proportion on the zones where lionfish were found and where they were not, suggesting that lionfish may not be the main factor in explaining the decrease in prey. It seems that lionfish have not reached the threshold density beyond which their impact could be significant on this reef, or that their effect, through the predation of juveniles, may not be yet detectable. The alternative hypothesis that lionfish impact must be evaluated at the whole system scale (reef complex and archipelago) should also be considered. Lionfish densities could be limited by several factors, including in particular a low larval recruitment due to connectivity patterns and factors of biotic resistance.

No evidence for biotic resistance was found. Nevertheless, our results must encourage the local and regional authorities to maintain healthy populations of native predators and competitors and to develop active culling so as to minimize the possible impacts of lionfish invasion. These objectives can be reached by promoting lionfish as an alternative resource, which would release fishing pressure on the native assemblage. In that sense, several fishing events have been organized to date across Venezuela, and we can hope it will go on. Additionally, we can expect the development of a regional strategy (for both fighting the invasion and study the effects of lionfish) with the Netherlands Antilles, off the coast of Venezuela, where eradication efforts are quite successful (Vermeij 2012).

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**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical standard** Our study complies with the current laws of Venezuela and was allowed by the National Parks Institute of Venezuela (INPARQUES).

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