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ORIGINAL PAPER

Parasite diversity and regional variation in invasive red lionfish *Pterois volitans*

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Abstract The invasion of the red lionfish *Pterois volitans* in the western Atlantic has generated widespread concern due to its strong negative effects on native biodiversity. Nevertheless, information on the parasite assemblages associated with this invasive fish and their spatial variability remains scarce. Here, we examined 829 individuals of *P. volitans* collected from 50 coral reef sites in the Mexican Caribbean (MXC) and one in the southern Gulf of Mexico (SGMX). Across these sites, 27 parasite taxa were recorded (27 in the MXC and 8 in the SGMX), most of which were host-generalist species. Among them, five constitute new geographical records and 21 represent new host records. Trematodes were the dominant group in both locations. Overall, parasite richness ranged from 1–15 species/site, and mean intensity from 1–5.6 individuals/host. The higher parasite richness in *P. volitans* from the MXC and SGMX, compared with locations in its native range, suggests its integration into western Atlantic parasite networks, surpassing the initial 'enemy release' stage. A similarity analysis indicated that the MXC parasite

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assemblage was more closely related to those from the southern and southwestern Gulf of Mexico than those from the northern Gulf of Mexico, Cayman Islands, Bahamas, and Puerto Rico, likely reflecting environmental differences, geographic distances and variation in prey composition (potential intermediate hosts). At the local scale, variation among MXC sites was associated with spatial distance and the heterogeneous distribution of adjacent habitats. These findings highlight the rapid incorporation of *P. volitans* into local ecological interactions and its potential influence on parasite transmission dynamics in western Atlantic reef ecosystems.

Keywords Parasite assemblages · Invasive fish · *Pterois volitans* · Mexican Caribbean · Gulf of Mexico

Introduction

Invasive species are becoming an increasingly common threat to coastal communities globally (Bax et al. 2003). Their success is mainly due to a lack of predation and a reduction in ecological or biological constraints that shape the species' density, distribution range, and environmental niche in its native environment (Molnar et al. 2008; Cano-Barbacil et al. 2023). This pattern is frequently explained by the enemy release hypothesis (ERH), which proposes that non-native species experience greater success in invaded environments because they are freed from the pressure of their natural enemies, such as predators and parasites, that regulate their populations in the native range (Tompkins and Poulin 2006; Dunn 2009; Sarabeev et al. 2017).

The species *Pterois volitans* (Linnaeus, 1758) (Scorpaeniformes: Scorpaenidae), for example, is a venomous marine fish native to the Indo-Pacific region that was accidentally introduced to the western Atlantic in the 1980s, where it has become a highly invasive species in coral reef environments (Whitfield et al. 2002, 2007, 2014; Morris and Akins 2009; Schofield 2009; Aguilar-Perera and Tuz-Sulub 2010; Lesser and Slattery 2011; Arias-González et al. 2011; Santander-Monsalvo et al. 2012; Sutherland et al. 2019). Its predatory habits have caused severe ecological and socio-economic impacts, as it has contributed to a decline in the biomass and diversity of native species on local reefs (Arias-González et al. 2011; Green et al. 2012; Palmer et al. 2016).

Other potential effects of this species may include habitat alteration (by disrupting the food web, reducing native fish populations, and impacting coral reef health, Lesser and Slattery 2011; Albins and Hixon 2013) and the introduction of diseases and parasites. Although according to recent studies there is no indication that lionfish introduced Pacific parasites into the Atlantic (Fogg et al. 2016; Tuttle et al. 2017), this aspect, in particular, has received less attention so far, as there is still limited knowledge about the parasite assemblages that these fish host, especially when they are outside their native range (Atlantic coasts of U.S.A.: Ruiz-Carus et al. 2006; Bullard 2010; Fogg et al. 2016; Caiman Islands, Puerto Rico, Bahamas: Ramos-Ascherl et al. 2015; Venezuela: López-Hernández et al. 2017; Gulf of Mexico, Mexico: Montoya-Mendoza et al. 2017). Studies on this topic have shown that the abundance and species richness of parasites on this fish varies widely between locations in the western Atlantic and that species richness has been relatively low compared to some native fish predators (Sellers et al. 2015). However, after an apparent initial release from parasites in the invaded area, evidence suggests that parasite richness has been increasing over time, likely due to the acquisition of local generalist species (Sellers et al. 2015; Tuttle et al. 2017). Therefore, characterizing the parasitic fauna of *P. volitans* in different invaded regions is key to evaluating whether its success follows the expectations of the ERH or reflects an ongoing ecological integration with native communities.

Moreover, knowing the parasitic fauna of this fish is also important given that in different locations in the Caribbean its consumption has been promoted at both local and commercial scales as a strategy to control its populations (Morris et al. 2011; Aguilar-Perera 2013; Chapman et al. 2016; Jimenez-Muñoz et al. 2023; Del Río et al. 2023). In this sense, it is essential to know whether this invasive fish could also act as a vector and transmitter of parasites for humans.

Therefore, the aims of this study were: (1) to identify the parasitic fauna of the red lionfish *P. volitans* from different coral reef locations in the Mexican Caribbean region and from one of the southern Gulf of Mexico, (2) to analyze the intra-location variability

in the parasite assemblages of this fish between the sampling locations of the Mexican Caribbean, and (3) to determine the regional variability by comparing the parasite assemblages reported in this study with those reported in other locations of the western Atlantic.

Methodology

Lionfish specimens were collected in 51 reef locations in the Mexican Caribbean between February 2011 and February 2019 (Table 1 of supplementary material and Fig. 1). Fish were caught by spearfishing in coral reef habitats (at depths from 0 to 35 m), placed in adequately labeled plastic bags, and kept in coolers with ice for transport to the different laboratories (Centro de Investigación de Ciencias Ambientales of the Universidad Autónoma del Carmen, Centro de Investigación Científica de Yucatán, Centro de Investigación y de Estudios Avanzados, Unidad Mérida, and Instituto de Ciencias del Mar y Limnología-UNAM). All lionfish individuals were measured for total length using a fish measuring board (cm) and weighed (g) with a digital balance Accu-Lab. Each specimen was placed in a 20 µm sieve-mesh and thoroughly washed under a freshwater tub to dislodge external parasites from the skin and fins. Fish were dissected, and internal structures (gills, heart, liver, gall bladder, intestine, brain, spleen, kidney) were individually separated and placed on Petri dishes with 0.7% saline solution and subsequently reviewed using forceps and by compression between 2 glasses of 10 cm per side. All samples were examined under an Olympus SZ30 stereomicroscope at × 4 magnification. Each parasite was carefully removed using mounted triangular surgical needles (size 16, Barber of Sheffield, UK) or a small brush. Each specimen was then mounted on a glass slide in distilled water, ensuring the parasite was flat. The specimens were then stained and fixed in situ by the addition of a drop (~ 3 µl) of Malmberg's fixative (ammonium picrate glycerine, APG; saturated picric acid and 100% glycerin) to the edge of the coverslip which was drawn under the coverslip by capillary action. The coverslip was then sealed with transparent nail vanish. The parasites were recorded using a compound microscope (MoticBA310E) at 100 X/oil immersion magnification. External parasites were preserved in vials of ethyl alcohol (70%) and appropriately labeled for subsequent definitive identification. Copepods were first fixed, then cleared using a solution of glycerin-alcohol and mounted on slides covered with glycerin-gelatin to their posterior taxonomic identification based on traditional morphological methods (Kabata 1992).

Helminths were fixed in AFA solution (acetic acid–formaldehyde–alcohol) for 2–24 h. Then, they were preserved in ethyl alcohol (70%) and stained with Gomori's trichromic stain. Nematodes were fixed in Berland's liquid, preserved in ethyl alcohol (70%), cleared with phenol–ethanol (Lent's solution) and mounted on slides covered with glycerin-gelatin. After obtaining the morphological data, parasites were identified according to the keys proposed by Siddiqi and Cable (1960) and Williams and Bunkley-Williams (1996). The parasitological material was deposited in the Helminths Collection of the Laboratorio Ambiental de Parasitología (CICA-UNACAR). Species richness, prevalence (%), mean abundance (number of parasite individuals/host), and mean intensity (number of parasite individuals/infected hosts) of parasites were determined according to Bush et al. (1997). The presence of parasite species in the different internal organs of the host was used as habitat preference.

Data analysis

Data on parasite assemblages documented in *P. volitans* from the western central Atlantic region (Puerto Rico, PR, Caiman Islands, CI, and Bahamas, BH, Ramos-Ascherl et al. 2015) and northern and southwestern Gulf of Mexico (NGMX, Fogg et al. 2016; SWGMX, Montoya-Mendoza et al. 2017) were used to compare the parasite assemblage documented in this study (Mexican Caribbean, MXC and Southern Gulf of Mexico, SGMX). The aforementioned investigations employed sampling and parasite identification protocols consistent with those applied herein, facilitating regional comparisons. Notably, while the same organs examined in previous studies were included, the present work expanded the scope of analysis to additional tissues, namely the brain, mesentery, liver, spleen, and kidney, that had not been considered in earlier assessments. A dendrogram was obtained using the unweighted pair-group method with the arithmetic mean (UPGMA) based on

Jaccard's similarity coefficient, which was built from a binary matrix (presence/absence) of species distribution (Bordin et al. 2019; Castellanos-Pérez et al. 2020). At local scale (Mexican Caribbean, MXC), a non-metric multidimensional scaling (nMDS) analysis was used (using the Bray–Curtis similarity matrix built from the square root transformed abundance data of parasite species) to determine the grouping of sites by plotting them in a two-dimensional ordination (Anderson and Underwood 1997). Finally, SIMPER was performed to detect the species that contributed the most to dissimilarity among the groups formed (Clarke and Warwick 1994). The analyses were performed using PAST v. 4.12 (Paleontological Statistics) and Primer v. 7 (Plymouth Routines in Multivariate Ecological Research) programs.

Results

A total of 829 individuals of *P. volitans* (size range: 140–455 mm total length) from 51 reef locations were analyzed (819 individuals from 50 sites in the Mexican Caribbean coasts [MXC] and ten from one site in Alacranes reef in the southern Gulf of Mexico [SGMX]). In the MXC sample, a total of 1443 parasite individuals were found belonging to eight classes, 19 genera, and 27 species. Among the identified species, 23 were endoparasites (16 digeneans, four nematodes, two acanthocephalans and one cestode) and four ectoparasites (three copepods and one Hirudinea) (Table 1). In this assemblage, the acanthocephalans (two species), cestodes (one species), nematodes (three species), and some digeneans (nine species) were also found in the larval stage. The most infested organs were the stomach, intestine, and mesentery, which together hosted 21 species of endoparasites (Table 1). In the case of trematodes (the most diverse group), most species were found in the stomach (n = 1048 trematode individuals). Nematodes (86 individuals), cestodes (23 individuals), and acanthocephalans (8 individuals) were found in the mesentery, stomach and intestine. Crustacean (77 individuals) and annelid (14 individuals) parasites were found in the skin, fins, and buccal cavity (Table 1).

In these locations, the parasite species richness ranged from 1 to 15 per site (Fig. 2) and from 1 to 15 species per individual parasitized. The species with higher prevalence were the cestode *Prochristianella* sp. (average ± SD = 16.2 ± 13.8%) and the trematodes Zoogonidae sp. and Acanthocolpidae sp. 1, and *Lecithochirium musculus* (14.8 ± 14.3% and 14.8 ± 15.0%, and 14.5 ± 11.7%, respectively). The higher mean abundances (± SD) were in Acanthocolpidae sp. 2 (0.73 ± 0.79 ind/host), *Diphterostomum* sp. (0.65 ± 0.59 ind/host), and Zoogonidae sp. (0.63 ± 0.56 ind/host). The higher mean intensities of infection were in Acanthocolpidae sp. 2 (5.60 ± 7.61 ind/host), Acanthocolpidae sp. 1 (3.97 ± 4.82 ind/host), and Zoogonidae sp. (3.12 ± 2.83 ind/host). In this region, the sites with the highest species richness of parasites were Cabo Catoche (15 species), Cozumel (12 species), Xcacel dos (11 species), and Las Iglesias (ten species), which were in the northern region of the study area (Mexican Caribbean). In contrast, sites with the lower species richness (e.g., Las Redes, Poza, Cayo Centro, Cayo Lobos) were in the southern part of this region, where only one parasite species was recorded.

At the SGMX location, 18 parasite individuals were found, which belong to eight species (Table 1). The species richness ranged from 1 to 2 per individual parasitized. These species had prevalences of 10% as they were only found in one host. The mean abundance of these species ranged from 0.1 to 0.7 ind/host and the mean intensity from 1 to 7 ind/host. In this location, *Diphterostomum* sp. had the highest values of mean abundance and intensity (0.7 ± 0.0 ind/host and 7.0 ± 0.0 ind/host, respectively) (Table 1).

According to the cluster analysis, the parasite assemblages reported in the western Central Atlantic region for *P. volitans* were separated into two main groups (Fig. 3 of supplementary material) that differ significantly (One-way ANOSIM, permutation $N = 999$, $R = 0.90$, $p = 0.021$). Group A includes three Caribbean locations, Puerto Rico (PR), the Bahamas (BH) and the Cayman Islands (CI), and one is in the northern Gulf of Mexico (NGMX). Group B includes two locations in the southern Gulf of Mexico (SGMX and SWGM) and the Mexican Caribbean (MXC). Of a total of 59 parasite species reported for *P. volitans* (including those identified in this work) in the study region, the two groups shared only 26 of them.

A wide inter-site variability in species composition was also detected at the local scale. According to the nMDS analysis, it resulted in three groups for the 50 sampling sites in the MXC (ANOSIM, Global test $R = 0.578$, $p = 0.01$ with 9999

Table 1 List of parasites found in samples of *P. volitans* from the Mexican Caribbean (MXC) and the southern Gulf of Mexico (SGMX), the organ they inhabit, and their respective data on prevalence (*P*%), mean abundance (MA) and mean intensity (MI)

Class	Species	No. of parasites	Organ	*P*%	MA	MI	Host range	References
MXC								
Trematoda	*Diphterostomum* sp. *	110	S	10.9 ± 10.1	0.65 ± 0.59	2.27 ± 1.09	S	
	Zoogonidae sp. *	112	Sk	14.8 ± 14.3	0.63 ± 0.56	3.12 ± 2.83	G	
	Acanthocolpidae sp. 1 *	119	S	14.8 ± 15.0	0.60 ± 0.46	3.97 ± 4.82	G	
	Acanthocolpidae sp. 2 *	200	S	13.7 ± 12.4	0.73 ± 0.79	5.60 ± 7.61	G	
	Siphoderina sp. 1 *	87	S	12.1 ± 9.0	0.51 ± 0.34	2.97 ± 2.15	G	
	Siphoderina sp. 2 *	71	S	10.0 ± 7.7	0.49 ± 0.32	2.72 ± 1.74	G	
	Siphoderina sp. 3 *	52	S	10.7 ± 15.0	0.50 ± 0.29	2.45 ± 1.19	G	
	Siphoderina sp. 4	55	S	12.0 ± 8.5	0.33 ± 0.22	2.93 ± 2.97	G	
	Dollfustrema sp. *	57	F	8.1 ± 4.9	0.41 ± 0.29	2.18 ± 1.50	S	
	Stephanostomum sp.*	61	S	10.6 ± 8.3	0.55 ± 0.66	2.68 ± 1.68	G	Ramos-Ascherl et al. 2015
	Lecithochirium musculus †	57	S	14.5 ± 11.7	0.53 ± 0.46	1.99 ± 1.21	G	López-Hernández et al. 2017
	Lecithochirium microstomum	79	S	12.8 ± 14.6	0.43 ± 0.25	2.20 ± 1.84	G	
	Lecithochirium floridense †	51	S	10.8 ± 10.1	0.55 ± 0.26	1.97 ± 1.16	G	Fogg et al. 2016
	Lecithochirium sp. †	52	S	13.1 ± 17.9	0.55 ± 0.51	1.76 ± 1.39	G	
	Hemiuridae sp.	33	S	12.0 ± 9.2	0.60 ± 0.44	2.08 ± 1.68	G	
	Brachyphallus parvus	21	S	10.2 ± 7.5	0.46 ± 0.29	1.71 ± 0.81	G	
Cestoda	*Prochristianella* sp.*	23	I	16.2 ± 13.8	0.47 ± 0.34	1.28 ± 0.55	G	
Chromadorea	*Ascarophis mexicana**	20	Me, S, I	9.5 ± 5.7	0.19 ± 0.04	1.79 ± 0.40	S	
	Spirocamallanus sp.* †	21	Me, S, I	8.4 ± 3.3	0.40 ± 0.32	1.81 ± 0.75	G	Ramos-Ascherl et al. 2015
	Hysterothylacium sp.* †	10	Me, S, I	8.4 ± 4.7	0.30 ± 0.27	1.50 ± 0.55	G	Montoya-Mendoza et al. 2017
Enoplea	*Capillaria* sp. †	35	Me, S, I	8.5 ± 3.4	0.43 ± 0.26	1.61 ± 0.70	G	Ramos-Ascherl et al. 2015
Palaeacanthocephala	*Gorgorhynchus* sp.*	4	I	7.8 ± 0.9	0.56 ± 0.35	1.33 ± 0.58	G	
	Serrasentis sp.* †	4	I	8.3 ± 0.0	0.61 ± 0.38	1.33 ± 0.58	MG	Simmons 2014
Malacostraca	*Cymothoa excisa* †	20	Bc	11.6 ± 6.1	0.41 ± 0.31	1.19 ± 0.27	G	Aguilar-Perera et al. 2018
Copepoda	*Caligus wilsoni*	33	G, F, Sk	9.6 ± 4.3	0.33 ± 0.17	2.86 ± 1.93	G	

Table 1 (continued)

Class	Species	No. of parasites	Organ	*P%*	MA	MI	Host range	References
	Caligus xystercus	24	G, F, Sk	7.9 ± 5.2	0.52 ± 0.20	2.15 ± 1.26	G	
Clitellata	*Trachelobdella lubrica* †	14	Sk, Bc	8.5 ± 2.9	0.51 ± 0.30	1.06 ± 0.14	G	Bullard et al. 2011
SGMX								
Trematoda	*Diphterostomum* sp.	7	S	10	0.7 ± 0.0	7.0 ± 0.0	S	
	Acanthocolpidae sp. 2	1	S	10	0.1 ± 0.0	1.0 ± 0.0	G	
	Siphoderina sp. 1	2	S	10	0.2 ± 0.0	2.0 ± 0.0	G	
Chromadorea	*Ascarophis mexicana*	1	Me, S, I	10	0.1 ± 0.0	1.0 ± 0.0	S	
	Spirocamallanus sp. †	2	Me, S, I	10	0.2 ± 0.0	2.0 ± 0.0	G	Ramos-Ascherl et al. 2015
	Hysterothylacium sp. * †	1	Me, S, I	10	0.1 ± 0.0	1.0 ± 0.0	G	Montoya-Mendoza et al. 2017
Enoplea	*Capillaria* sp. †	3	Me, S, I	10	0.3 ± 0.0	3.0 ± 0.0	G	Ramos-Ascherl et al. 2015
Palaeacanthocephala	*Serrasentis* sp. †	1	I	10	0.1 ± 0.0	1.0 ± 0.0	MG	Simmons 2014

Dispersion values after means indicate the standard deviation. *: larval stage, Sk: skin, G: gill cavity, F: fins, Bc: buccal cavity, Me: mesentery, S: stomach, I: intestine. †: previous recors (species/genus) for *P. volitans* in the Western Atlantic

permutations) (Fig. 4 of supplementary material). Group A (average similarity: 48.7%) comprised 5 sampling sites, group B (average similarity: 34.8%) by 15 sites, and group C (average similarity: 33.5%) by 30 sites (Fig. 4 of supplementary material). In group A the sites were characterized by relatively low abundance (1–4 parasites/site) and species richness (a total of 5 parasite species), compared to those in groups B (2–15 parasites/site and 11 species) and C (1–134 parasites/site and 25 species). Overall, the clustering of sites observed in the nMDS was not consistent with their geographic location, i.e., some sites in group A were in the central and southern zones of the study area, while those in groups B and C were in the northern, central, and southern zones (Fig. 2). Groups A and B had an average dissimilarity of 88.6% and the species that contributed most to this dissimilarity were *Siphoderina* sp. 2 (21.6%), *Siphoderina* sp. 1 (14.8%), and *Zoogonidea* sp. (13.8%). Groups A and C had an average dissimilarity of 87.0% and the species that contributed most to this dissimilarity were *Diphterostomum* sp. (25.9%), *Siphoderina* sp. 2 (10.5%), and Zoogonidea sp. (9.7%). Groups B and C had an average dissimilarity of 82.2% and the species that contributed most to this dissimilarity were *Diphterostomum* sp. (21.0%), Zoogonidea sp. (10.6%), and Acanthocolpidae sp. 2 (8.6%).

Discussion

Parasite richness, new records, and implications for the enemy release hypothesis

The total parasite species richness recorded here for *P. volitans* was 27 species (including 27 for the Mexican Caribbean and 18 for the southern Gulf of Mexico), ranging from of 1 to 15 species per sampling site. This species richness was relatively higher to that registered previously in other locations of the western Atlantic, e.g., northern Gulf of Mexico, USA (nine species) (Fogg et al. 2016), Cayman Islands (seven species), the Bahamas (six species), Puerto Rico (13 species) (Ramos-Ascherl et al. 2015), and

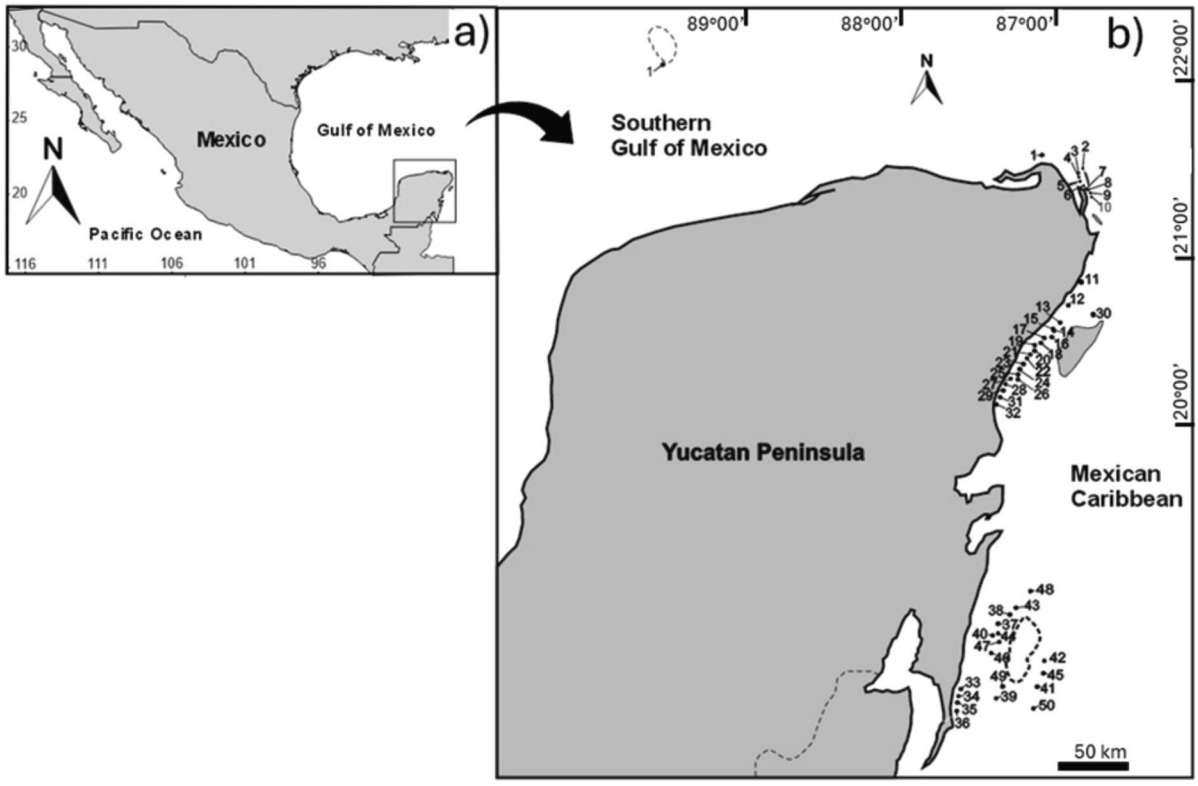

Fig. 1 **a** Location of the study area and sampling sites at Yucatan Peninsula, Mexico. **b** Map of the Yucatan Peninsula showing the sampling sites where *P. volitans* was collected. At the top is the sampling site on the Arrecife Alacranes, which corresponds to the south of the Gulf of Mexico, and on the right the sampling sites in the Mexican Caribbean

southwestern Gulf of Mexico, Mexico (eight species) (Montoya-Mendoza et al. 2017).

In addition, five of the parasite species recorded in this study constitute new geographical records (*Stephanostomum* sp., *T. lubrica*, *Capillaria* sp., *Spirocamallanus* sp., *Histerothylacium* sp.) and 21 represent new host records for the study area (*C. xystercus*, *C. wilsoni*, *C. excisa*, *Serrasentis* sp., *Diphterostomum* sp., Zoogonidae sp., Acanthocolpidae sp. 1, Acanthocolpidae sp. 2, *Siphoderina* sp. 1, *Siphoderina* sp. 2, *Siphoderina* sp. 3, *Siphoderina* sp. 4, *Dollfustrema* sp., *L. musculus*, *L. microstomum*, *Lecithochirium* sp., Hemiuridae gen. sp., *B. parvus*, *Prochristianella* sp., *A. mexicana*, and *Gorgorhynchus* sp.). Of the total taxa recorded, only the acanthocephalans of the genus *Serrasentis* had previously been reported from *P. volitans* in its native range (the Philippines; Tuttle et al. 2017).

According to the Enemy Release Hypothesis (ERH), invasive species are expected to exhibit reduced parasite loads and lower diversity in invaded regions compared to their native range, as they leave behind many of their natural enemies during translocation (Keane and Crawley 2002; Torchin et al. 2003). However, contrasting with this expectation, our findings reveal a different pattern: the parasite richness recorded in *P. volitans* in the MXC and SGMX exceeds that documented in its native Indo-Pacific range (seven taxa; Tuttle et al. 2017). This indicates that, rather than maintaining a persistent release from parasites, *P. volitans* has progressively incorporated new local generalist species, likely through trophic transmission from native hosts that share similar prey and habitats or through interactions with other hosts and free-living parasitic larvae. Such results provide evidence that *P. volitans* is gradually integrating into local parasite networks in the western Atlantic, suggesting that, in line with classic ERH predictions, its invasion has progressed beyond the initial stages.

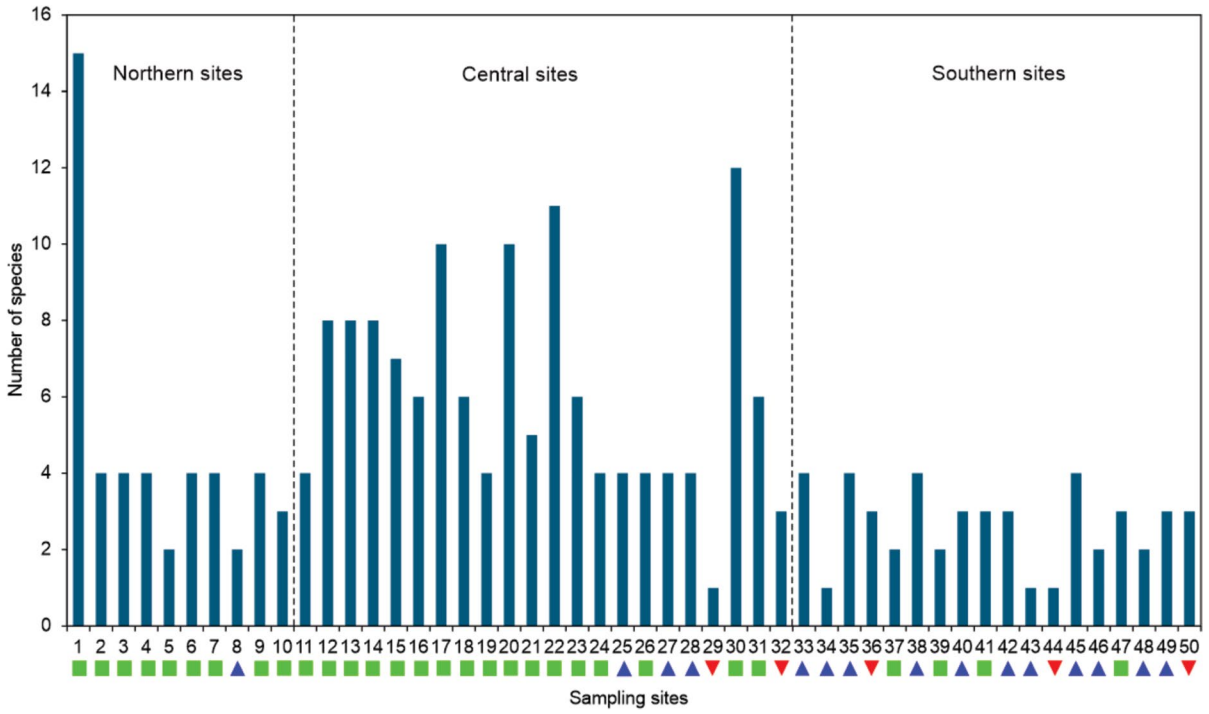

Fig. 2 Number of parasite species recorded at study sites in the Mexican Caribbean. The sites are arranged from north to south according to their location within the study area. The colored symbols below the site number correspond to those generated in the nMDS plot

A similar process of parasite acquisition from the recipient environment has also been reported in other invasive species, such as the silver-cheeked toadfish *Lagocephalus sceleratus* (Tetraodontidae), a Lessepsian invader introduced into the Mediterranean Sea through the Suez Canal (Bakopoulos et al. 2017). This fish has been identified as a new host for several native generalist parasites in the Mediterranean, providing an additional niche that favors the success and proliferation of local parasite populations. However, given the low levels of infection, the authors recommended further investigations to determine whether these parasites could influence the invasion success of *L. sceleratus* (Bakopoulos et al. 2017). Likewise, in the case of *P. volitans*, the parasite species reported from the invaded western Atlantic also show generally low infection intensities (Ramos-Ascherl et al. 2015; Fogg et al. 2016; Montoya-Mendoza et al. 2017; present study). Therefore, to determine whether the parasites currently infecting the lionfish may contribute to regulating its populations in this area, specific investigations on the different parasitic groups are required, since it is known that some native parasites may have different effects on native and non-native hosts (Dunn 2009).

Taxonomic composition, dominant parasite groups, and infection patterns of P. volitans in the western Atlantic

It is noteworthy that the taxonomic groups of parasites recorded for this fish in both native and non-native environments are practically the same (Tuttle et al. 2017). Although a broader set of organs was examined in this study compared to previous investigations conducted in the western Atlantic (e.g., liver, gall bladder, brain, spleen, kidney), no additional parasite taxa were detected. This consistency suggests that the diversity of metazoan parasites infecting *P. volitans* remains stable across regions.

In samples from the MXC and SGMX, trematodes were the dominant group, a pattern consistent with previous reports from the Cayman Islands, Bahamas, Puerto Rico (Ramos-Ascherl et al. 2015), and in the northern Gulf of Mexico (Fogg et al. 2016). In the present study, all parasites exhibited low prevalence, intensity, and abundance (Table 1), with the cestode *Prochristianella* sp. showing the highest prevalence and the trematode Acanthocolpidae sp. 2 the highest intensity and abundance. Cestodes of the genus *Prochristianella* and trematodes of the family Acanthocolpidae are commonly associated with marine teleost fishes, although members of the order Trypanorhyncha, to which *Prochristianella* belongs, can also parasitize sharks and rays (Palm et al. 2009). In general, Trypanorhyncha cestodes exert mild effects on their hosts and are considered of low pathogenicity (de Sales-Ribeiro et al. 2021). In contrast, trematodes may have greater ecological relevance, as their effects on the host depend on whether they occur as larval or adult stages, potentially reducing host fitness under stressful conditions (McGladdery et al. 1990; Paperna 1996; Barber et al. 2000; Esch et al. 2002; Lafferty and Kuris 2005; Woo and Buchmann 2012).

Among the remaining taxa, only the isopod *Cymothoa excisa* has published evidence of causing direct damage to *P. volitans*, having been recorded parasitizing the buccal cavity of individuals from Alacranes Reef in the southern Gulf of Mexico (Aguilar-Perera et al. 2018). This species is known to degenerate or replace the tongue and cause oral lesions that may compromise feeding. Although its prevalence was relatively low (11.6% on average), it was comparable to that reported for native fish species from the SGMX such as the yellowtail snapper *Ocyurus chrysurus* (11.5%) (Borges-Casas et al. 2025). In addition, individuals of *T. lubrica* were also observed in the buccal cavity of *P. volitans* from the Mexican Caribbean, although no lesions were recorded.

Another noteworthy finding was the presence of larval stages of *Histerothylacium* sp. (2–17% prevalence), which deserve special attention due to their zoonotic potential, particularly because lionfish are consumed raw in dishes like 'ceviche' (Quintana et al. 2023), a preparation where fish-borne nematodes can survive and possibly infect humans (Eiras et al. 2016). Although this nematode was found in the stomach, mesentery, and intestine of the host, it is known that such larvae can migrate into the musculature, even post-mortem (Felizardo et al. 2009) and, once embedded in this tissue, they can be ingested by humans.

Overall, most taxa identified in this study appear to have broad ecological distributions, not restricted to a particular latitude or habitat (WoRMS Editorial Board 2025), with the exception of a few regionally limited species, such as *Ascarophis mexicana*, which seems restricted to the Gulf of Mexico (Moravec et al. 1995). When comparing the dominant species across regions, clear geographic differences emerge: the parasites with the highest prevalence in this study differed from those reported in other Caribbean areas and the northern Gulf of Mexico. For instance, in the Greater Antilles, *Lecithochirium floridense* was dominant (Ramos-Ascherl et al. 2015; Fogg et al. 2016), while *Pseudocapillaria* sp. prevailed in the southwestern Gulf of Mexico (Montoya-Mendoza et al. 2017). Although *L. floridense* was also detected here, its prevalence (2–33%) was lower than that reported elsewhere (Bullard et al. 2011; Ramos-Ascherl et al. 2015; Fogg et al. 2016). Conversely, *Capillaria* sp. and *Spirocamallanus* sp. showed higher prevalence and intensity in the SGMX than in the MXC, whereas *Stephanostomum* sp. was notably abundant in the MXC. The prevalence of *Trachelobdella lubrica* and *L. floridense* in the MXC was intermediate relative to other Atlantic regions (Ramos-Ascherl et al. 2015; Fogg et al. 2016), and *Serrasentis* sp. was less frequent than in the native range (8–10% vs. 27%; Tuttle et al. 2017). Altogether, these discrepancies in parasite composition and infection levels likely reflect differences in feeding ecology, environmental conditions, and the local availability of intermediate hosts (Cirtwill et al. 2016).

Regional and local variability in parasite assemblages

The regional variability observed in the parasite assemblages of *P. volitans* in this study agrees with previous findings. For example, Sellers et al. (2015) documented considerable variation in the species richness and abundance of parasites in this invasive fish across locations of the western Atlantic. Such variation may be associated with geographical distance among sites, regional differences in physicochemical conditions, and/or variation in the intermediate hosts to which these fish and their parasites are exposed. The geographical distances separating the areas of group B were relatively shorter than those

of group A, which included more distant subregions such as the Greater Antilles, the Bahamas, and the northern Gulf of Mexico (Fig. 3 of supplementary material). In addition to the relatively short distances among group B locations, the Loop Current, a major oceanic circulation system connecting the Caribbean with the Gulf of Mexico (Oey et al. 2005), enhances biological connectivity between these regions (Johnson and Perry 2009). This current facilitates the passive transport of larvae and adults of marine organisms (including fish) from the Caribbean to the Gulf of Mexico. Therefore, the proximity among these sites, combined with potential population connectivity of reef-associated fishes and their prey, may explain the relatively higher similarity in parasite assemblages.

These results are consistent with other parasitological studies showing that similarity in parasite assemblages tends to decrease as the geographical distance between host populations increases (Oliva and González 2005; Poulin et al. 2011). Intra-specific variation in parasite assemblages has also been reported for the scorpionfish *Sebastes capensis*, which shows differences in parasite composition between distant Chilean coastal sites (Oliva and González 2004). This pattern was attributed to low host mobility and to environmental and ecological factors, such as temperature, diet, and habitat use, that influence parasite communities (Granath and Esch 1983; Zander 2003; Gonzalez and Poulin 2005). Similarly, lionfish exhibit high site fidelity, moving of up to 1.35 km over 15 days across patch reefs (Jud and Layman 2012; Tamburello and Côté 2015), a behavior that may limit parasite exchange and contribute to regional differentiation.

Despite the ichthyofaunistic connectivity between the Gulf of Mexico and the Caribbean Sea (McEachran and Fechhelm 2010; González-Gándara 2015), the dissimilarity detected between the parasite assemblages of *P. volitans* from the southwestern and southern Gulf of Mexico and those of the Caribbean likely reflects differences in environmental conditions and host diet between these regions. Unlike the Caribbean, the Gulf of Mexico exhibits more pronounced seasonal variations in water temperature and lacks extensive reefs, which can reduce the availability of stenothermal and reef-dependent prey commonly consumed by lionfish in the Caribbean (Backus et al. 1977; McEachran and Fechhelm 2010). Moreover, previous studies have shown that lionfish diet composition varies significant across the western Atlantic, largely influenced by prey availability and the proximity of alternative habitats, such as mangroves, soft bottoms, and seagrass meadows, where these predators forage daily (Arredondo-Chávez et al. 2016; Eddy et al. 2016; Peake et al. 2018; Aguilar-Medrano and Vega-Cendejas 2020). These aspects highlight the need for detailed studies on the feeding habits of *P. volitans* along the Mexican Caribbean coast to better understand how trophic interactions shape endoparasite acquisition.

At a finer spatial scale, the parasite assemblages recorded at the 50 sampling sites in the MXC clustered into three main groups based on species abundance data. This grouping did not follow a clear geographical or latitudinal pattern, as it included sites from the northern, central, and southern portions of the coast. However, sites with the highest and lowest species richness were located in the north-central and southern areas, respectively. One possible explanation for this spatial structure, in addition to the distances between sites, is the heterogeneous distribution of adjacent habitats other than the coral reefs that lionfish use for foraging. For instance, mangroves are more prevalent in the southern region, whereas seagrass meadows dominate the northern coasts (Cerdeira-Estrada et al. 2023). Differences in the availability of these habitats may influence the diversity of trophically transmitted parasites, through exposure to different prey, ectoparasites or free-living parasitic larvae. Indeed, in the western Atlantic, lionfish have been reported to occupy multiple shallow feeding habitats, including mangroves and seagrass meadows adjacent to coral reefs (Barbour et al. 2010; Claydon et al. 2012).

When comparing parasite assemblages among the three regions of the MXC (north, central, and south), notable differences were observed in species composition and abundance. In the north (10 sites), 17 parasite species were recorded, totaling 270 individuals and ranging from 2 to 15 species per site. In the central region (22 sites), 20 species were identified, with 792 individuals and a range of 1–12 species per site. In the south (18 sites), 10 species were found, with a total abundance of 110 individuals and a range of 1–4 species per site. Regarding similarity among regions, northern and central sites shared 60% of the species (15 in total: 13 trematodes, 1 cestode,

and 1 nematode); northern and southern shared 35% (7 trematodes); and central and southern sites shared 43% (10 in total: 7 trematodes, 2 copepods, and 1 isopod). These results indicate that geographic distance and habitat heterogeneity are key factors structuring parasite communities at the local scale within the MXC. Overall, the regional and local variability observed in the parasite community of *P. volitans* illustrates how parasitological data can serve as valuable indicators of ecological connectivity, adaptation, and biotic integration of an invader within recipient ecosystems. The observed patterns reinforce the idea that parasitic interactions are dynamic components of biological invasions, influencing both the establishment success and the long-term ecological impact of marine invaders.

From a broader invasion ecology perspective, the patterns observed for *P. volitans* further support the notion that parasites act as both indicators and modulators of invasion processes. The progressive acquisition of local generalist parasites by lionfish suggests an increasing ecological integration into recipient communities, potentially diminishing the initial advantages conferred by enemy release. This transition, from a parasite-depleted invader to a species embedded within local host-parasite networks, exemplifies the dynamic nature of biotic interactions during the establishment and spread of marine invaders. Understanding these dynamics is essential to predict the long-term ecological consequences of biological invasions and to incorporate parasitological indicators into management and monitoring strategies across invaded ecosystems.

Conclusion

The results of this study demonstrate that *Pterois volitans* has achieved a remarkable ecological integration within the ecosystems of the Mexican Caribbean and the southern Gulf of Mexico, as reflected by its high parasite richness and the incorporation of numerous local generalist species, many of which represent new geographical and host records. This pattern contrasts with the predictions of the Enemy Release Hypothesis, suggesting that the lionfish has surpassed the initial stage of invasion and has actively integrated into the trophic and parasitic networks of the western Atlantic. The observed parasite composition, dominated by trematodes and showing regional and local variations associated with environmental, trophic, and marine connectivity differences, reveals ongoing processes of adaptation and ecological exchange between regions. Thus, this study highlights that parasites are valuable indicators of biogeographic connectivity and biotic integration of invasive species, providing essential information to understand their population dynamics, ecological interactions, and potential impacts on recipient ecosystems.

Supplementary information

Link to Supporting data (Rodríguez-Santiago et al.). https://drive.google.com/drive/folders/15QgKsYhQMZmTlOBahBLrXrCQoRdvPVkV?usp=sharing

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Author contributions MARS and JACV conceived and designed the study. MARS, JSI, LAM, and JPP developed the methods and collected the data. JIO, DTV, EA and RGF analysed the data. JACV and MARS acquired the funding for the project. MARS was the lead writer of the original draft of the manuscript and all co-authors provided feedback and edits.

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Data availability The data used to perform the analysis are available to the corresponding author upon request.

Declarations

Competing interests The authors declare that they have no conflict of interest.

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