

SPATIO-TEMPORAL VARIATION IN THE DIET COMPOSITION OF RED LIONFISH, *PTEROIS VOLITANS* (ACTINOPTERYGII: SCORPAENIFORMES: SCORPAENIDAE), IN THE MEXICAN CARIBBEAN: INSIGHTS INTO THE ECOLOGICAL EFFECT OF THE ALIEN INVASION

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Background. The observed expansion of the red lionfish, *Pterois volitans* (Linnaeus, 1758), in the Caribbean represents one of the most rapid marine fish invasions in the history. The invasion rate of this top predator has resulted in a marked negative effect on local fish populations in the Caribbean by impacting local biodiversity. The main aim of this work was to conduct the morphological identification of prey items from the lionfish diet, and to determine the spatio-temporal variation of the lionfish diet composition in different sites of the Mexican Caribbean, to have a better knowledge of how this invasive species is impacting local species of commercial or ecological importance in the region.

Materials and methods. The Mexican Caribbean study area was divided in three zones; North (one locality Isla Contoy), Central (three locations Xpu-Ha, Akumal and X'cabel), and South (two locations Banco Chinchorro and Xcalak). The fish were collected, from different habitats, using SCUBA diving and Hawaiian harpoon. Collected fish were taxonomically identified, measured for total length (TL) and standard length (SL), and weighed to the nearest gram. Prey items were identified using a dissection microscope. After identification, prey items were separated, counted, and weighted individually. Finally, statistical analyses were made for all the samples using this study database, containing predators and prey items.

Results. A total of 76 prey species were identified in 962 lionfish stomachs; 47 of them represented fishes and 29—crustaceans. Fishes of families Pomacentridae, Labridae, and Scaridae were the most abundant diet components of lionfish. Rhynchocinetidae, Penaeidae, and Solenoceridae were the most representative Crustaceans families among the prey items. Molluscs were present as diet components only as incidental food.

Conclusion. Red lionfish, known for its high competitive capacity, preyed more intensively on fishes than on crustaceans. Therefore, it is evident that the lionfish presence in the Mexican Caribbean may affect mainly the local population of reef fishes. The presently reported results contribute to a better understanding of the red lionfish invasion in the Caribbean.

Keywords: invasive species, diet component, reef fishes, marine protected areas, trophic ecology

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INTRODUCTION

Coral reefs are one of the most productive, diverse, and rich ecosystems in the world, but they are also very vulnerable to the effects of climate change, contamination, and anthropogenic effects. These changes are causing a significant decrease in species richness, and a reduction in fish density and biomass on coral reefs and their adjacent mangrove areas (Davis et al. 2011, Green et al. 2011). The reefs are very important for the local communities, providing high-protein foods, areas for recreational activities, and protection of the coastline. Moreover, they are the home to nearly a third of all marine fish species worldwide (Pimiento et al. 2013). Coral reefs are important spawning areas, and they provide protection, breeding and feeding grounds for many species, therefore, the conservation of the biological and genetic diversity of the species that inhabit coral reefs is a priority for coastal management and conservation (Moberg and Folke 1999).

The most abundant components of coral reef ecosystems are corals, fishes, and crustaceans. They also play an important ecological role in the reef and surrounding areas, being key elements in food webs, and maintaining balance and dynamics in the ecosystem. As a result of migratory movements related to the oceanographic and environmental conditions, changes in the abundance and composition are common on reef communities that have neighbouring distribution areas (Albins and Hixon 2013). In the last two decades, the structure and health of many reefs in the world has diminished dramatically, resulting in the loss of live coral cover and biodiversity. These changes are induced by multiple factors, including pollution, sedimentation, eutrophication, overfishing, and global warming (Moberg and Folke 1999). However, these changes are not always the result of natural events, and there are other factors that contribute to this problem such as habitat destruction and introduction of non native species that can alter dramatically the distribution and abundance of fish species in these areas.

One of the main threats to the Caribbean fauna and their ecosystems as a whole, is the invasion of the red lionfish, *Pterois volitans* (Linnaeus 1758). This species is a voracious predator with a natural distribution in the Pacific and Indian Ocean, where it can be found from Australia and Malaysia to the French Polynesia, including Japan, South Korea, New Zealand, and Micronesia (Green et al. 2011). This species was reported for the first time in the Atlantic in the 1980s (Betancur et al. 2010), but it was in the 1990s when this species was systematically observed in waters of the Atlantic Ocean. It has been documented that the lionfish invasion was probably the result of an accidental release of only few individuals, but their potential for expansion and colonization of local habitats, made the lionfish one of the most abundant species in many affected areas, threatening the integrity and productivity of newly colonized coastal ecosystems (Schofield 2009).

Red lionfish adapted, survived, and invaded all the tropical western Atlantic and the Caribbean, and its arrival and establishment has been considered one of the most successful biological invasions reported (Whitfield et

al. 2007). This invasion is one of the main threats to the Caribbean coral reef ecosystems (Morris 2012). The first sighting of lionfish in the Mexican Caribbean was reported in Cozumel Island in 2009 (Schofield 2009). Since that time, lionfish rapidly invaded the entire marine and some estuarine systems in the area (Vásquez-Yeomans et al. 2011), including deep (>75 m) waters.

Invasive species are able to produce what is called a cascade effect through several trophic levels. For example, when an “alien and exotic” fish enters an ecosystem and preys on the native predator, the loss of this predator often results in an increase in the abundance of its prey. If the proliferation of the latter has a negative impact on the ecosystem, then this outcome becomes an indirect consequence the invasive species occurrence in this ecosystem. Basically, invasive species causes a chain reaction in which each trophic niche in the ecosystem is affected (Green et al. 2012). Although the negative effects of the lionfish in the Caribbean ecosystems seem to be obvious, the majority of the studies have focused in areas such as the Bahamas and Florida and little is known about the basic aspects of the invasion in the Mexican Caribbean. Moreover, most of the research work related to the lionfish diet composition focused in the fish species, but little is known about other groups that also serve as food for the lionfish. Therefore, the main aims of the presently reported study were:

- To identify the diet composition of the lionfish along the Mexican Caribbean, and
- To determine the spatio-temporal variation of their diet in different sites along the Mexican Caribbean.

MATERIALS AND METHODS

Sampling. The Caribbean region features some 26 000 km² of coral reefs distributed mostly in shallow areas with mean depths of 20 m. From these, the Mexican Caribbean has a coral reef extension that covers an area of approximately 650 km², constituting part of the Mesoamerican Barrier Reef System (MBRS). In this work, the study site was divided in three zones identified as (10 km scale):

- North zone;
- Central zone;
- South zone.

For fish collection, zone was subdivided into localities (scale of 1 to 10 km); one locality from the North zone (Isla Contoy), three locations for the Central zone (Xpu-Ha, Akumal and X'cabel), and two locations for the South zone (Banco Chinchorro and Xcalak). Finally, at each location different collection sites were established (scale of 0.1 to 1 km) (Fig. 1). Of the six localities and 54 collection sites; four were located inside Natural Protected Areas, that are identified as priorities by the National Commission for the Knowledge and Use of Biodiversity (CONABIO). These areas are known as the National Park of Isla Contoy, Sea Turtle Sanctuary X'cabel-X'cabelito, National Park Arrecifes of Xcalak, and Biosphere Reserve of Banco Chinchorro. The above mentioned sites plus Xpu-ha and Akumal are all locations which support a high touristic activity and are part of the well known “Riviera Maya”.

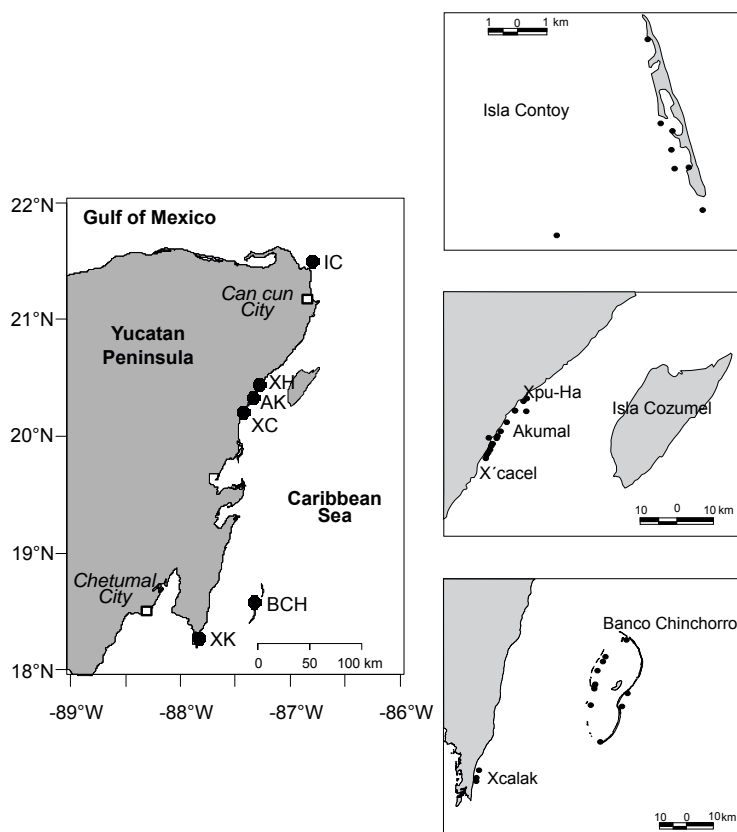


Fig. 1. Map showing the location of the sampling sites in the Mexican Caribbean; Each dot indicates the collection sites distributed along the North-, Central-, and South zones of the Mexican Caribbean

Surveys of red lionfish, *Pterois volitans*, were conducted during the dry- (February–May), rainy- (June–September) and nortes-^{*} seasons (October–January), in 2011 and 2012. The fish were collected using SCUBA diving and a Hawaiian harpoon, and the survey covered different habitats (coral reefs, rocky reef, coral patch, *Thalassia* field, gorgonids field, and laja bottom). Collected specimens were frozen, packed in labelled nylon bags, and transported to the laboratory where they were taxonomically identified following Schultz (1986). Specimens were measured for total length (TL) and standard length (SL) to the nearest centimetre and weighed to the nearest gram.

Sample processing. Prey items present in the stomach and part of the intestine were recovered from each collected lionfish and were then identified using a dissection microscope and taxonomic keys (Abele and Kim 1986, McEachran and Feckhelm 1998, 2005, Carpenter 2002, Humann and DeLoach 2002, Nizinski 2003, Robertson and Van Tassell 2015). After identification, prey items were separated, counted, and individually weighted. In some cases, the level of digestion of prey did not allow the separation of the samples in groups, therefore, such samples were classified as unidentified prey. The classification used here for stomach contents (full, half full, half empty, and empty) was done by volume,

therefore, half empty refers to the apparent volume observed between half full and half empty stomachs.

Data analyses. A sample base rarefaction curve with Estimates (Version 9.1.0.) was made using 500 sample randomization without replacement (Coldwell 2013). To identify if our sample effort fully characterized the lionfish diets, richness was assessed by using 2 non-parametric estimators: Chao2 and Mao Tau. In order to separate the fish collected by size the standard length of all the surveyed fishes and the percentile were used in JMP version 6.0^{**}. Then, the 11 size classes obtained, were assigned to three sizes: small (6–15 cm), medium (15–25 cm), and large (25–39 cm). The repletion index was obtained for all the samples to determine the amount of food found in each stomach (Hyslop 1980).

The percentage by number (%N) and the percentage frequency of occurrence (%F) of each prey was calculated following Hyslop (1980). The percentage by weight (%W) of each prey was calculated following Pinkas et al. (1971). The data obtained was used to calculate the relative importance index (%IRI) following Stevens et al. 1982. The niche amplitude was obtained using the Levin standardized index (Krebs 1999).

Due to the differences in the sample size per habitat, the diet composition by habitat could not be compared,

^{*} The “norte” season brings northerly winds that affect the region during autumn and winter.

^{**} Anonymous 1996. SAS/C compiler and library user’s guide. 4th edn. Release 6.00. SAS Institute Inc., Cary, NC, USA.

therefore, sample localities were separated in North-, Central-, and South zones (Fig. 1). The diet composition was compared between seasons using the Simpson Index, the Shannon Index, and the Student' *t*-test. The Sørensen similarity index, was obtained by a simple league cluster analysis (Moreno 2001). Data were processed using the Bio-DAP software (Gordon and Douglas 1988).

RESULTS

Lionfish diet composition by size. A total of 1482 specimens of *Pterois volitans* were collected. Standard length (SL) of the collected fish was between 60 mm and 390 mm with a mean value (\pm SD) of 194 ± 56 mm. The fish weight was between 9.8 g and 997.3 g with a mean value (\pm ED) of 256 ± 200 g. Out of the total number of the fish collected, 962 specimens (64.9%) were found with prey in their stomachs. The total number of prey items was 1609. Specimens were collected in different habitats, including high profile coral reefs (72.13%), rocky reefs (9.31%), coral patch (6.61%), laja bottom (4.99%), gorgonian fields (3.98%), and *Thalassia* field (2.98%). The rarefaction analyses indicated that sample size was not sufficient to reach the asymptote, indicating that more sampling would be necessary to fully represent the lionfish diet composition. The 2.23% of the stomach analysed were categorized by volume as full, 12.21% as half full, 50.47% as half empty, and 35.09% as empty. Out of the total number of the prey items recovered from the fish

studied only 76 were identified to the species level. In this number there were 47 fishes and 29 crustaceans. A total of 57 prey items were identified to the genus level, including 32 fishes, 22 crustaceans, and 3 molluscs. As many as 38 preys were assigned only to the family level, with 18 families representing fishes, 17—crustaceans, and 3—molluscs (Table 1).

Eleven size classes of fishes showed an ontogenetic variation in the groups consumed, where small lionfish specimens consumed more crustaceans, and larger lionfish consumed more fishes (Fig. 2). Separated by size, the most important prey according with the IRI by genus were:

- For the small size lionfish (6–15 cm): *Cinetorhynchus* (56.98%), *Periclimenes* (24.43%), and *Pleoticus* (2.73%) for crustaceans; and *Coryphopterus* (5.92%), *Scarus* (4.21%), and *Starksia* (1.37%) for fish;
- For medium size specimens (15–25 cm): *Cinetorhynchus* (48.26%), *Pleoticus* (15.79%), and *Trachypenaeus* (1.11%) for crustaceans; and *Stegastes* (8.73%), *Coryphopterus* (7.96%), and *Scarus* (3.83%) for fishes;
- For the large size (25–39 cm): *Cryptosoma* (15.17%), *Collodes* (9.84%), and *Cinetorhynchus* (8.52%) for crustaceans; and *Thalassoma* (5.85%), *Coryphopterus* (7.96%), and *Anchoviella* (2.48%) for fishes (Table 1).

As clearly shown in Fig. 2, the diet composition of small size lionfish is based mainly on crustaceans, and the diet composition of the large size lionfish is based mainly on fish.

Table 1

List of food items (prey consumed) found in the stomach contents of red lionfish, *Pterois volitans*, collected in the Mexican Caribbean

Higher taxa/Food item	%N	%W	%F	%IRI
Mollusca				
Mesogastropoda				
Littorinidae gen spp.	0.0624	0.0055	0.1225	0.0005
<i>Echinolittorina</i> spp.	0.0632	0.0055	0.1247	0.0007
Neogastropoda				
Muricidae gen spp.	0.0624	0.0131	0.1225	0.0005
<i>Stramonita</i> spp.	0.0632	0.0132	0.1247	0.0007
Columbellidae gen spp.	0.0624	0.0033	0.1225	0.0005
<i>Aesopus</i> spp.	0.0632	0.0033	0.1247	0.0006
Crustacea				
Stomatopoda				
Hemisquillidae gen spp.	0.1248	0.0394	0.2451	0.0023
<i>Hemisquilla</i> spp.	0.1264	0.0397	0.2494	0.0032
Gonodactylidae gen spp.	0.1871	0.0449	0.3676	0.0050
<i>Neogonodactylus</i> spp.	0.1264	0.0287	0.2494	0.0029
<i>Neogonodactylus curacaoensis</i>	0.1553	0.0337	0.3802	0.0040
<i>Gonodactylus</i> spp.	0.0632	0.0165	0.1247	0.0008
Pseudosquillidae gen spp.	0.6862	0.3874	1.4706	0.0919
<i>Pseudosquilla</i> spp.	0.6953	0.3904	1.4963	0.1237
<i>Pseudosquilla ciliata</i>	0.8540	0.4593	2.2814	0.1647

Table continues on next page.

Table 1 cont.

Higher taxa/Food item	%N	%W	%F	%IRI
Isopoda				
Cymothoidae gen spp.	0.4991	0.0109	0.7353	0.0218
<i>Renocila</i> spp.	0.5057	0.0110	0.7481	0.0294
Sphaeromatidae gen spp.	0.0624	0.0011	0.1225	0.0005
<i>Sphaeroma</i> spp.	0.0632	0.0011	0.1247	0.0006
<i>Sphaeroma serratum</i>	0.0776	0.0013	0.1901	0.0008
Decapoda				
Penaeidae gen spp.	5.8016	2.2369	18.3824	8.5984
<i>Metapenaeopsis</i> spp.	1.2010	0.4842	0.3741	0.0480
<i>Metapenaeopsis smithi</i>	1.4752	0.5696	0.5703	0.0641
<i>Parapenaeus</i> spp.	1.5171	0.3055	0.6234	0.0865
<i>Parapenaeus americanus</i>	1.8634	0.3594	0.9506	0.1162
<i>Penaeus</i> spp.	0.6321	0.4268	0.6234	0.0503
<i>Penaeus brasiliensis</i>	0.3882	0.1894	0.3802	0.0121
<i>Penaeus schmitti</i>	0.1553	0.0272	0.1901	0.0019
<i>Trachypenaeus</i> spp.	2.2756	0.7775	16.7082	3.8848
<i>Trachypenaeus constrictus</i>	0.4658	0.1881	0.3802	0.0137
<i>Rimapenaeus similis</i>	2.3292	0.7266	2.0913	0.3513
<i>Litopenaeus</i> spp.	0.2528	0.2603	0.3741	0.0146
Sicyoniidae gen spp.	0.1248	0.0471	0.1225	0.0012
<i>Sicyonia</i> spp.	0.1264	0.0474	0.1247	0.0017
Solenoceridae gen spp.	8.0474	4.7101	10.5392	7.8238
<i>Pleoticus</i> spp.	8.1542	4.7467	10.7232	10.5352
<i>Pleoticus robustus</i>	9.2391	4.9187	14.8289	11.5412
Sergestidae gen spp.	0.0624	0.0109	0.1225	0.0005
<i>Sergestes</i> spp.	0.0632	0.0110	0.1247	0.0007
Stenopodidae gen spp.	0.0624	0.0088	0.1225	0.0005
<i>Stenopus</i> spp.	0.0632	0.0088	0.1247	0.0007
<i>Stenopus hispidus</i>	0.0776	0.0104	0.1901	0.0009
Disciidae gen spp.	0.5614	0.0788	0.1225	0.0046
<i>Discias</i> spp.	0.5689	0.0794	0.1247	0.0062
<i>Discias atlanticus</i>	0.6988	0.0934	0.1901	0.0083
Rhynchocinetidae gen spp.	30.8172	12.0729	15.4412	38.5374
<i>Cinetorhynchus</i> spp.	31.2263	12.1668	15.7107	51.9175
<i>Cinetorhynchus rigens</i>	38.3540	14.3137	23.9544	69.3546
Palaemonidae gen spp.	6.5502	0.8624	3.9216	1.6915
<i>Palaemon</i> spp.	0.0632	0.0055	0.1247	0.0007
<i>Palaemon northropi</i>	0.0776	0.0065	0.1901	0.0009
<i>Palaemonetes</i> spp.	0.2528	0.0154	0.1247	0.0025
<i>Palaemonetes pugio</i>	0.3106	0.0182	0.1901	0.0034
<i>Periclimenes</i> spp.	6.3211	0.8481	3.7406	2.0423
<i>Periclimenes americanus</i>	0.1553	0.0467	0.3802	0.0042
<i>Periclimenes iridescens</i>	0.4658	0.0376	0.3802	0.0105
<i>Periclimenes pedersoni</i>	0.4658	0.1038	0.5703	0.0179
<i>Periclimenes rathbunae</i>	2.5621	0.2530	1.1407	0.1765
<i>Urocaris longicaudata</i>	2.9503	0.2945	1.1407	0.2035
Alpheidae gen spp.	0.1248	0.0317	0.2451	0.0022

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Table 1 cont.

Higher taxa/Food item	%N	%W	%F	%IRI
<i>Alpheus</i> spp.	0.1264	0.0320	0.2494	0.0030
<i>Alpheus heterochaelis</i>	0.1553	0.0376	0.3802	0.0040
Axiidae gen spp.	0.0624	0.3907	0.1225	0.0032
<i>Axiopsis</i> spp.	0.0632	0.3937	0.1247	0.0043
<i>Axiopsis hirsutimana</i>	0.0776	0.4632	0.1901	0.0057
Palinuridae gen spp.	0.0624	0.0547	0.1225	0.0008
<i>Panulirus</i> spp.	0.0632	0.0551	0.1247	0.0011
<i>Panulirus argus</i>	0.0776	0.0649	0.1901	0.0015
Scyllaridae gen spp.	0.0624	0.0186	0.1225	0.0006
<i>Scyllarides</i> spp.	0.0632	0.0187	0.1247	0.0008
<i>Scyllarides nodifer</i>	0.0776	0.0221	0.1901	0.0010
Porcellanidae gen spp.	0.0624	0.1204	0.1225	0.0013
<i>Petrolisthes</i> spp.	0.0632	0.1213	0.1247	0.0018
<i>Petrolisthes galathinus</i>	0.0776	0.1427	0.1901	0.0023
Calappidae gen spp.	0.5614	0.8098	0.9804	0.0782
<i>Cryptosoma</i> spp.	0.5057	0.7830	0.8728	0.0857
<i>Cryptosoma bairdii</i>	0.1553	0.2491	0.3802	0.0085
Inachoididae gen spp.	0.0624	0.0186	0.1225	0.0006
<i>Collodes</i> spp.	0.0632	0.0187	0.1247	0.0008
Majidae gen spp.	0.0624	0.1007	0.1225	0.0012
<i>Ala</i> spp.	0.0632	0.1015	0.1247	0.0016
<i>Ala cornuta</i>	0.0776	0.1194	0.1901	0.0021
Portunidae gen spp.	1.5596	1.1983	1.9608	0.3147
<i>Callinectes</i> spp.	1.3274	0.8735	1.7456	0.2926
<i>Callinectes similis</i>	1.2422	0.5748	1.9011	0.1899
<i>Portunus</i> spp.	0.2528	0.3342	0.2494	0.0111
Actinopterygii				
Clupeiformes				
Engraulidae gen spp.	6.1135	3.7690	1.7157	0.9866
<i>Anchoviella</i> spp.	6.1947	3.7983	1.7456	1.3284
Aulopiformes				
Synodontidae gen spp.	0.0624	0.0317	0.1225	0.0007
<i>Synodus</i> spp.	0.0632	0.0320	0.1247	0.0009
<i>Synodus synodus</i>	0.0776	0.0376	0.1901	0.0012
Gasterosteiformes				
Aulostomidae gen spp.	0.1248	0.1412	0.2451	0.0038
<i>Aulostomus</i> spp.	0.1264	0.1423	0.2494	0.0051
<i>Aulostomus maculatus</i>	0.1553	0.1674	0.3802	0.0067
Perciformes				
Serranidae gen spp.	1.1853	6.3593	2.3284	1.0222
<i>Cephalopholis</i> spp.	0.0632	0.1996	0.1247	0.0025
<i>Cephalopholis cruentata</i>	0.0776	0.2348	0.1901	0.0033
<i>Hypoplectrus</i> spp.	0.1896	3.7486	0.3741	0.1122
<i>Hypoplectrus nigricans</i>	0.0776	1.9592	0.1901	0.0213
<i>Hypoplectrus puella</i>	0.1553	2.4509	0.3802	0.0545
<i>Liopropoma</i> spp.	0.1264	0.1765	0.2494	0.0058
<i>Liopropoma rubre</i>	0.1553	0.2076	0.3802	0.0076

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Table 1 cont.

Higher taxa/Food item	%N	%W	%F	%IRI
<i>Paralabrax dewegeri</i>	0.0776	0.6111	0.1901	0.0072
<i>Serranus</i> spp.	0.8217	2.2840	1.6209	0.3834
<i>Serranus tigrinus</i>	0.3882	1.5920	0.9506	0.1035
Grammatidae gen spp.	0.1871	0.7606	0.3676	0.0203
<i>Gramma</i> spp.	0.1896	0.7665	0.3741	0.0272
<i>Gramma loreto</i>	0.0776	0.0350	0.1901	0.0012
<i>Gramma melacara</i>	0.1553	0.8667	0.3802	0.0214
Carangidae gen spp.	0.0624	0.0328	0.1225	0.0007
<i>Alectis</i> spp.	0.0632	0.0331	0.1247	0.0009
<i>Alectis ciliaris</i>	0.0776	0.0389	0.1901	0.0012
Lutjanidae gen spp.	0.0624	0.0044	0.1225	0.0005
<i>Lutjanus</i> spp.	0.0632	0.0044	0.1247	0.0006
Haemulidae gen spp.	1.0605	1.2301	1.1029	0.1470
<i>Haemulon</i> spp.	1.0746	1.2396	1.1222	0.1978
<i>Haemulon flavolineatum</i>	1.3200	1.4500	1.7100	0.2000
Apogonidae gen spp.	0.9357	0.4640	1.1029	0.0898
<i>Apogon</i> spp.	0.8850	0.4555	0.9975	0.1018
<i>Apogon planifrons</i>	0.0776	0.0324	0.1901	0.0012
<i>Apogon maculatus</i>	0.3106	0.3270	0.3802	0.0133
<i>Phaeoptyx</i> spp.	0.0632	0.0121	0.1247	0.0007
<i>Phaeoptyx pigmentaria</i>	0.0776	0.0143	0.1901	0.0010
Mullidae gen spp.	0.0624	2.9000	0.1225	0.0211
<i>Mulloidichthys</i> spp.	0.0632	2.9226	0.1247	0.0284
<i>Mulloidichthys martinicus</i>	0.0776	3.4383	0.1901	0.0367
Pomacentridae gen spp.	5.4897	28.4948	8.2108	16.2372
<i>Chromis</i> spp.	1.1378	6.2643	1.8703	1.0543
<i>Chromis cyanea</i>	1.1646	5.6440	2.2814	0.8539
<i>Chromis multilineata</i>	0.2329	1.7256	0.5703	0.0614
<i>Stegastes</i> spp.	4.2351	22.0418	6.1097	12.2263
<i>Stegastes adustus</i>	0.0776	1.3572	0.1901	0.0150
<i>Stegastes leucostictus</i>	0.1553	0.2452	0.3802	0.0084
<i>Stegastes partitus</i>	3.7267	18.2528	5.7034	6.8913
<i>Stegastes planifrons</i>	0.0776	1.9112	0.1901	0.0208
<i>Microspathodon</i> spp.	0.0632	0.1743	0.1247	0.0023
<i>Microspathodon chrysurus</i>	0.0776	0.2050	0.1901	0.0030
Labridae gen spp.	7.9226	19.3296	7.8431	12.4376
<i>Clepticus</i> spp.	2.5284	9.4868	2.6185	2.3959
<i>Clepticus parrae</i>	3.1056	11.1608	3.9924	3.1311
<i>Halichoeres</i> spp.	1.4539	2.4439	1.2469	0.3701
<i>Halichoeres bivittatus</i>	0.6211	0.3672	0.5703	0.0310
<i>Halichoeres garnoti</i>	0.6211	1.5310	0.1901	0.0225
<i>Thalassoma</i> spp.	2.9077	7.0407	2.7431	2.0783
<i>Thalassoma bifasciatum</i>	3.5714	8.2831	4.1825	2.7256
Scaridae gen spp.	6.3007	8.7548	6.9853	6.1196
<i>Nicholsina</i> spp.	1.1378	0.7433	0.9975	0.1429
<i>Nicholsina usta</i>	1.3975	0.8745	1.5209	0.1900
<i>Scarus</i> spp.	3.0973	7.0815	4.1147	3.1896

Table continues on next page.

Table 1 cont.

Higher taxa/Food item	%N	%W	%F	%IRI
<i>Scarus iseri</i>	2.3292	4.8928	3.4221	1.3586
<i>Scarus taeniopterus</i>	0.3106	1.1379	0.7605	0.0606
<i>Sparisoma</i> spp.	2.1492	0.9981	1.9950	0.4782
<i>Sparisoma atomarium</i>	0.9317	0.3088	0.9506	0.0648
<i>Sparisoma radians</i>	0.2329	0.2556	0.1901	0.0051
<i>Sparisoma viride</i>	0.1553	0.1220	0.3802	0.0058
Tripterygiidae gen spp.	0.0624	0.0285	0.1225	0.0006
<i>Enneanectes</i> spp.	0.0632	0.0287	0.1247	0.0009
<i>Enneanectes pectoralis</i> spp.	0.0776	0.0337	0.1901	0.0012
Dactyloscopidae gen spp.	0.1248	0.1510	0.1225	0.0020
<i>Gillellus</i> spp.	0.1264	0.1522	0.1247	0.0026
<i>Gillellus greyae</i>	0.1553	0.1791	0.1901	0.0035
Labrisomidae gen spp.	2.4953	0.8514	3.5539	0.6921
<i>Malacoctenus</i> spp.	2.2124	0.8007	2.9925	0.6867
<i>Malacoctenus macropus</i>	0.1553	0.2569	0.1901	0.0043
<i>Malacoctenus triangulatus</i>	1.7081	0.3555	2.4715	0.2804
<i>Starksia</i> spp.	0.1896	0.0331	0.3741	0.0063
<i>Starksia nanodes</i>	0.0776	0.0143	0.1901	0.0010
<i>Labrisomus</i> spp.	0.1264	0.0243	0.2494	0.0029
<i>Gobioclinus gobio</i>	0.1553	0.0285	0.3802	0.0038
Chaenopsidae gen spp.	0.0624	0.0022	0.1225	0.0005
<i>Acanthemblemaria</i> spp.	0.0632	0.0022	0.1247	0.0006
<i>Acanthemblemaria maria</i>	0.0776	0.0026	0.1901	0.0008
Gobiidae gen spp.	9.2327	2.4557	6.8627	4.6677
<i>Bathygobius</i> spp.	0.1264	0.1963	0.2494	0.0061
<i>Bathygobius soporator</i>	0.1553	0.2309	0.3802	0.0081
<i>Coryphopterus</i> spp.	8.9760	2.2642	6.4838	5.5501
<i>Coryphopterus dicrus</i>	0.8540	0.4827	0.9506	0.0698
<i>Coryphopterus glaucofraenum</i>	0.3882	0.1894	0.7605	0.0241
<i>Coryphopterus lipernes</i>	4.1149	0.7837	1.3308	0.3584
<i>Coryphopterus personatus</i>	2.6398	0.3283	2.8517	0.4653
<i>Gnatholepis</i> spp.	0.2528	0.0143	0.2494	0.0051
Pleuronectiformes				
Bothidae gen spp.	0.3119	0.0897	0.4902	0.0115
<i>Bothus</i> spp.	0.3161	0.0904	0.4988	0.0154
<i>Bothus lunatus</i>	0.0776	0.0091	0.1901	0.0009
Tetraodontiformes				
Monacanthidae gen spp.	1.7467	0.8722	2.3284	0.3548
<i>Monacanthus</i> spp.	1.7067	0.8183	2.2444	0.4316
<i>Monacanthus tuckeri</i>	2.0963	0.9627	3.4221	0.5755
<i>Cantherhines</i> spp.	0.0632	0.0607	0.1247	0.0012
<i>Cantherhines pullus</i>	0.0776	0.0714	0.1901	0.0016

%N = percentage by number, %W = percentage by weight, %F = frequency of occurrence, %IRI = index of relative importance; Bold print denotes the most important values of each index.

Prey composition. Results showed that crustaceans dominated the lionfish diet by number (%N) with a total of 56.13%; fishes represented 43.5%, and molluscs 0.31%. Fishes dominated the lionfish diet by weight (%W) with a 77%, followed by crustacean with 20.46%, unidentified organic matter (MONI) with 2.42% and molluscs with 0.13%. By frequency of occurrence (%F) 61.18% corresponded to teleost fishes, 34.83% were crustaceans, 3.34% MONI and 0.58% molluscs. According with the IRI teleost fishes were the most important prey type with a total of 72.35%, followed by crustaceans with 27.16%, MONI with 0.49% and molluscs included in the MONI percentage (Table 1). The total of unidentified prey accounted for 35.38 %W and 51.41 %F of all food items, and for the analyses they were grouped as partial undigested parts of fishes or crustaceans. For some samples, the level of digestion of prey did not allow the separation of the samples in groups.

The most important families in the lionfish diet were: Pomacentridae, Labridae, Scaridae, Gobiidae, Rhynchocinetidae, Penaeidae, Solenoceridae, and Palaemonidae (Table 1 and Fig. 3). Whereas the fish families with more genera represented in the diet of lionfish were: Serranidae (4), Pomacentridae (3), Labridae (3), Scaridae (3), Labrisomidae (3), and Gobiidae (3). The families with more species represented as part of the diet components were: Pomacentridae (7), Scaridae (6), Serranidae (6), Gobiidae (5), and Labrisomidae (4). For the crustaceans the families with more genera were: Penaeidae (5), Palaemonidae (3), Gonodactylidae (2), and Portunidae (2). The families with more species were: Palaemonidae (7) and Penaeidae (6). The most abundant genera found as diet components were *Cinetorhynchus*, *Pleoticus*, *Periclimenes*, *Trachypenaeus*, *Callinectes*, *Coryphopterus*, *Anchoviella*, *Stegastes*, *Clepticus*, and *Scarus* (Table 1 and Fig. 4).

The most important species identified in the diet of lionfish were: *Coryphopterus lipernes* Böhlke et Robins, 1962; *Stegastes partitus* (Poey, 1868); *Thalassoma bifasciatum* (Bloch, 1791); *Clepticus parrae* (Bloch et Schneider, 1801); *Pleoticus robustus* (Smith, 1885) for fish, and *Cinetorhynchus rigens*, *Urocaris longicaudata*, *Rimapenaeus similis*, and *Pseudosquilla ciliate* for crustaceans (Table 1 and Fig. 5).

The lionfish predation on teleost fish was found to be greater as compared to the predation of crustaceans and molluscs. Therefore, from these results it is clear that the lionfish presence in the Mexican Caribbean is affecting mainly the local population of reef fish.

Diet composition by season. A total of 201 lionfish specimens were collected during the dry season. A minimum length of 60 mm SL and maximum of 300 mm SL; and minimum weight of 10 g and maximum of 835 g were found. Eighteen families, 26 genera (one mollusc, eight crustaceans, and 17 fishes), and 24 species were identified, of which 20 were fishes and four were crustaceans.

During the rainy season a total of 286 lionfish specimens were collected. Their length (SL) ranged from 60 mm through 290 mm, while their weight was within 9.8–642 g. Twenty-four families, 38 genera (two molluscs, 17 crustaceans, and 19 fishes), and 36 species (19 fishes and 17 crustaceans) were found.

During the nortes season a total of 995 lionfish specimens were collected, with a standard length ranging from 60 to 390 mm, and the weight—from 10 to 977 g. Thirty three families, 48 genera (28 fishes and 20 crustaceans), and 57 species were identified (38 fishes and 19 crustaceans) (Table 2).

During the dry season the genera *Cinetorhynchus*, *Sparisoma*, *Pleoticus*, *Coryphopterus*, *Thalassoma*, *Stegastes*, *Serranus*, *Anchoviella*, and *Renocila* were the most represented components of the lionfish diet (Fig. 6).

During the rainy season the genera *Cinetorhynchus*, *Periclimenes*, *Trachypenaeus*, *Parapenaeus*, *Metapenaeopsis*, *Mulloidichthys*, *Chromis*, *Clepticus*, *Hypoplectrus*, *Monacanthus*, and *Haemulon* were the most represented items of the lionfish diet components (Fig. 7).

During the nortes season only the genera *Cinetorhynchus*, *Coryphopterus*, *Pleoticus*, *Anchoviella*, *Stegastes*, *Clepticus*, and *Scarus* were identified as the most important components of the diet (Fig. 8).

Results showed that there is an evident variation in the composition of the diet which seems to be associated with the climatic season. Even though that the numbers of lionfish collected during the three seasons were not the same, it is evident that the most abundant prey, in spite of the season, were the fishes. The presently reported study demonstrated that the increase in the number of lionfish captured was

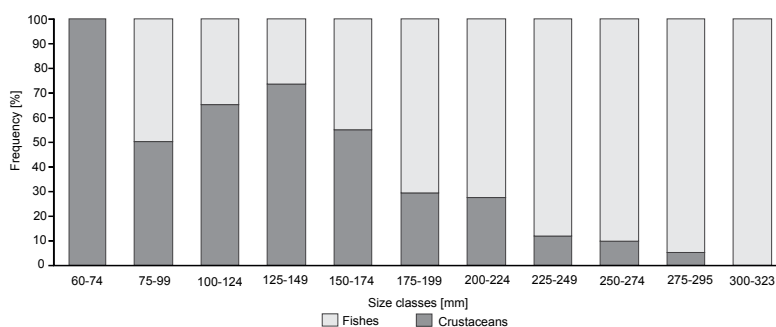


Fig. 2. Variations in two major prey groups (fishes and crustaceans) consumed by red lionfish, *Pterois volitans*, in eleven length classes

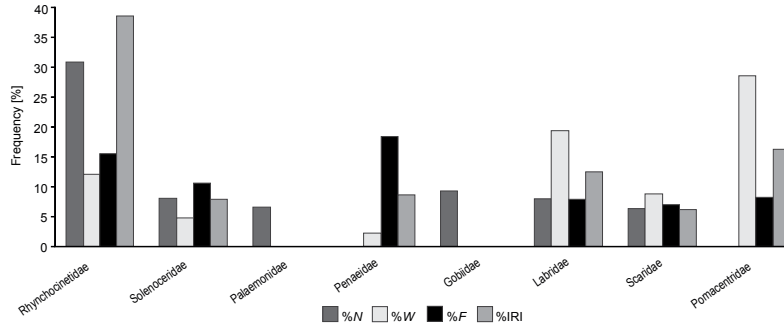


Fig. 3. Diet composition of red lionfish, *Pterois volitans*, on the family level; %N = percentage by number, %W = percentage by weight, %F = frequency of occurrence, %IRI = index of relative importance %IRI

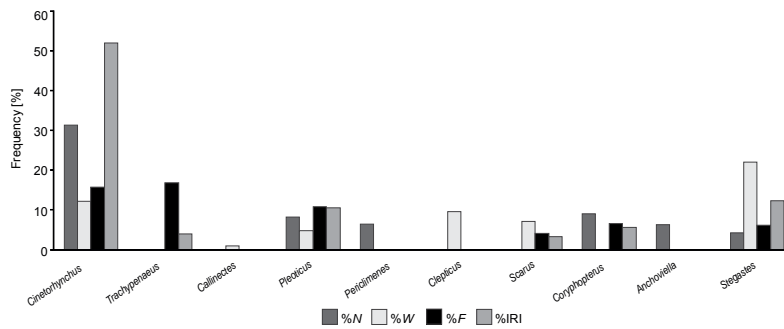


Fig. 4. Diet composition of red lionfish, *Pterois volitans*, on the genus level; %N = percentage by number, %W = percentage by weight, %F = frequency of occurrence, %IRI = index of relative importance %IRI

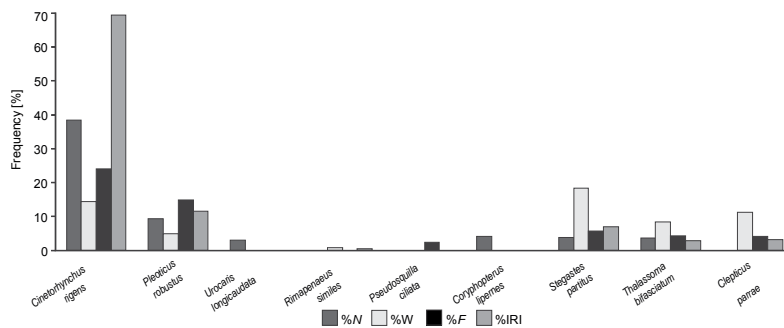


Fig. 5. Diet composition of red lionfish, *Pterois volitans*, on the species level; %N = percentage by number, %W = percentage by weight, %F = frequency of occurrence, %IRI = index of relative importance %IRI

directly associated with the number of families, genera, and species found in their diet. It should also be emphasized that the composition of prey species in general, was different in each season (Figs. 6–8). Overall, species of the genus *Cinetorhynchus* seems to be the most available and preferred food component of the lionfish diet in the three seasons. However, the total number of consumed fish was higher and the diversity of fish prey was higher compared to the diversity of crustacean preys. It is important to mention that the sampling intensity was partially lower during the dry and rainy season, due to a function of time/visibility during these seasons, which limited the total catch by period.

Diversity measurements. The Shannon diversity index (H') (bits · individual⁻¹) showed that the highest diversity of the diet composition was found during the nortes

season ($H' = 2.66$ bits · ind⁻¹), followed by the dry season ($H' = 2.38$), and the rainy season ($H' = 2.37$). The diet composition during the dry season showed high evenness with a value of 0.73, and the rainy season showed the high dominance with a value of 0.65. The Sørensen test showed that the most similar values found in the rainy season were diversity and abundance (0.558 and 0.379 qualitative and quantitative, respectively). The less similarity was found during the dry season and the nortes season (0.486 and 0.248 qualitative and quantitative, respectively) (Table 3).

The highest diversity of the diet composition was found during the nortes season, and the lowest value during the rainy season. The lowest value of species similitude was found also in the rainy season, being understandable to find the value of higher dominance over the same period.

Table 2

Basic biometric parameters of red lionfish, *Pterois volitans*, caught per season and number of its prey items representing different levels of identification and different taxonomic groups

Season	Biometric parameters of <i>Pterois volitans</i>							No. of identified prey items of <i>Pterois volitans</i>				
	Fish No.	Fish length [mm]			Fish weight [g]			Level of identification			Spp. breakdown	
		Min	Max	Mean	Min	Max	Mean	Family	Genus	Species	<i>F</i>	<i>C</i>
Dry	201	60	300	19.25	10	835	202.72	24	26	24	20	4
Nortes	286	60	290	137.18	9.8	642	60.67	24	38	36	19	17
Rainy	995	60	390	15.91	10	977	147.54	33	48	57	30	19

F = number of prey species representing fishes, *C* = number of prey species representing crustaceans; Nortes season = October–January.

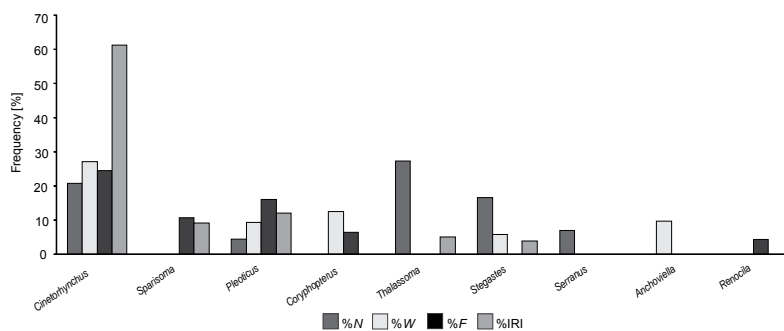


Fig. 6. Diet composition of red lionfish, *Pterois volitans*, by genus during the dry season; %*N* = percentage by number, %*W* = percentage by weight, %*F* = frequency of occurrence, %*IRI* = index of relative importance %*IRI*

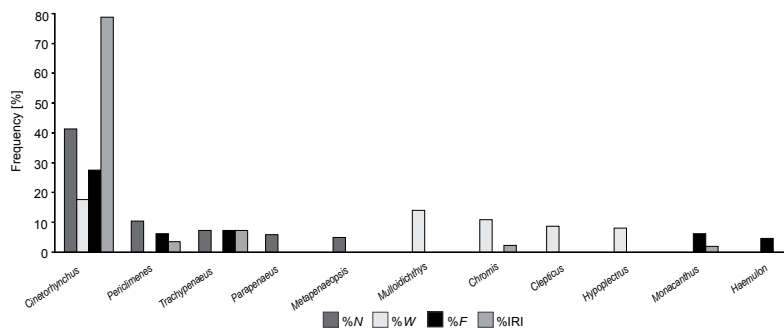


Fig. 7. Diet composition of red lionfish, *Pterois volitans*, during the rainy season; %*N* = percentage by number, %*W* = percentage by weight, %*F* = frequency of occurrence, %*IRI* = index of relative importance %*IRI*

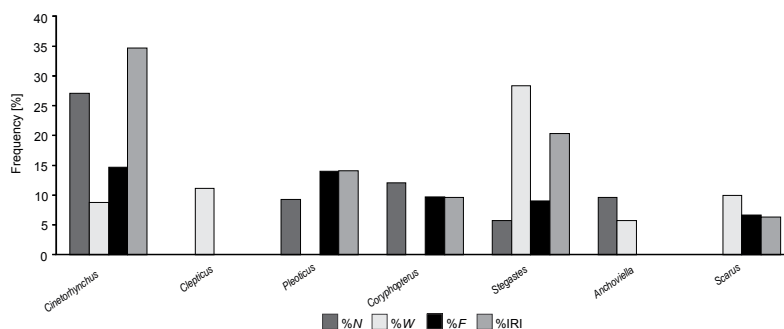


Fig. 8. Diet composition of red lionfish, *Pterois volitans*, during the nortes season; %*N* = percentage by number, %*W* = percentage by weight, %*F* = frequency of occurrence, %*IRI* = index of relative importance %*IRI*

Table 3
Diversity index and Sørensen similarity analysis per seasons of the diet composition of red lionfish, *Pterois volitans*

Index	Season	Season		
		Dry	Rainy	Nortes
<i>s</i>		201	286	995
<i>H'</i>		2.38	2.37	2.66
<i>E</i>		0.73	0.65	0.69
Var <i>H'</i>		0.00812	0.00582	0.00157
	Dry	1	0.531	0.486
Sørensen	Rainy	0.338	1	0.558
	Nortes	0.248	0.379	1

Nortes season = October–January *s* = richness, *H'* = Shannon–Wiener, *E* = evenness, Var *H'* = variance of Shannon–Wiener index.

DISCUSSION

Red lionfish, *Pterois volitans*, demonstrates a high competitive capacity, high reproduction, and high growth rates (Albins and Hixon 2013), all of which makes this species as one of the most efficient predators and a dangerous invasive species that could, in a very short time, affect the ecology relations of coral reefs in the Mexican Caribbean, as well as in other parts of the world. The invasion in the Mexican Caribbean is relatively recent, the first lionfish sighting was reported in 2009 in Cozumel island (Schofield 2009), and although in other areas such as Florida and Bahamas this species was systematically reported as early as 1992 (Albins and Lyons 2012), few studies have been done to understand the impact of the lionfish in the ecology and local populations, by analysing its diet composition in natural and invaded areas.

Although Hamner et al. (2007) showed that two species of *Pterois* are present in the Atlantic, *P. volitans* represented around 93% of the population, and *P. miles* only 7%. In the presently reported study the 1482 specimens collected were identified as *P. volitans*, based in traditional measurements and identification analyses, however, 57 specimens were classified as taxonomically uncertain. Overall results presented in this paper are consistent with the results reported by Valdez-Moreno et al. (2012), where they used a barcode molecular method for identification of lionfish in the Caribbean and found only the species *P. volitans*. This is also supported by unpublished data obtained from our collaborators, that used DNA barcode (*COI* sequences) and obtained at least 15 sequences from different specimens that shared a 99% of nucleotide identity with the sequence published at GenBank for *P. volitans* (Hernandez-Zepeda et al. unpublished data). Therefore, to date the only species of lionfish identified in the Mexican Caribbean is *P. volitans*.

Lionfish is characterized by a slow movement, a camouflaged coloration, and elongated fin ray projections that results in a low detectability by predators (Albins and Hixon 2008). As a consequence of these features, lionfish may be escaping from significant top-down control predators, with only few occasional predators (Pimiento

et al. 2013). Another possible reason for the lionfish success is their efficient reproduction and the movement of the larvae with the currents where there are not natural predators (Morris et al. 2009, Morris and Akins 2009). It has been proposed that lionfish preferentially (but not exclusively) settle in shallow habitats before moving to deep reefs when they reach larger sizes (Claydon et al. 2012). This pattern is often a consequence of fish ontogeny (Mumby et al. 2011). In the presently reported work, results showed that lionfish is more abundant in areas resembling cracks and caves of shallow reef areas (2 to 35 m).

The cumulative curve for the 1482 stomachs with prey analysed indicated that the sample size was insufficient to reach asymptote, therefore more sample effort is required to be able to fully describe the lionfish diet. However, it is important to notice that this work represents the highest collection effort compared to other similar studies conducted in the area. This could be a consequence of the opportunistic feeding behaviour, since lionfish can eat at almost any species that it can gulp (Mumby et al. 2006, 2011) and, since in this work specimens were collected in six different habitats, the variety of prey that the lionfish may consume increased. The lionfish diet in the Atlantic is composed by fishes and crustaceans as the most representative groups, and accidentally some molluscs (due to the low frequency found in the stomachs revised) (Morris 2009, Arias-González et al. 2011, Muñoz et al. 2011, Valdez-Moreno et al. 2012). In the presently reported study the largest number of prey items in the lionfish diet were fish and crustacean (76 species), compared with 43 species reported by Morris and Akins, (2009), 18 species in Muñoz et al. (2011), 34 in Valdez-Moreno et al. (2012), and 42 species in Green et al. (2012). The differences observed in the lionfish diet composition could be explained because in previous published studies, few stomachs were analysed (Morris and Akins 2009), and other studies used different techniques to identify preys such as molecular tools (Valdez-Moreno et al. 2012). Also, the number of crustaceans previously reported as lionfish diet components was low, compared with the 29 species identified in the present study. The total of 48 species of fish found as main components of lionfish diet in this study can be considered higher than those obtained in studies that included a larger sampling area (Morris and Akins 2009), where a total of 41 fish species were reported. In this work an ontogenetic lionfish diet composition variation was found, with crustaceans as the more abundant/important prey for small specimens, whereas as lionfish grows the more abundant/important prey were found to be fish. These results are similar to other studies that also reported a relation between size-diet in lionfish (Cure et al. 2012). Many reef fish species use seagrass and mangrove as juvenile habitat (Mumby et al. 2006). Lionfish in a juvenile nursery may reduce the recruitment pool available to colonize reefs through predation or competition (Barbour et al. 2010) acting in concert with lionfish predation on coral reefs (Albins and Hixon 2008, Barbour et al. 2010) to further stress reef fish

populations. Additionally, lionfish may differentially use habitats throughout their ontogeny. Lionfish in mangrove habitat, for example, may be smaller than in reef habitat (Barbour et al. 2010) suggesting mangroves may function as lionfish nurseries.

The large array of prey consumed indicated that lionfish is a top predator, as the same level as sharks and groupers (Arias-González et al. 2011). All previous studies remark the negative impacts of lionfish in native fish groups, as a predator or competitor with the native fauna (Albins and Lyons 2012, Albins and Hixon 2013). In this work, as in most of the previous reports, the most important fish species that are components of the lionfish diet are the families Labridae, Pomacentridae, Gobiidae, Serranidae, and Scaridae. Also, the parrotfishes (Scaridae) were one of the most important families in the lionfish diet; this group of fishes are mainly herbivorous, and feed on algae that grow in the coral reefs, therefore, they have a very important ecological role maintaining the algae population, acting as a “gardeners” of the reef, preventing the invasion of algae and the subsequent coral damage. The ecological role of parrotfish is more relevant in areas where there is an increase in nutrients in the water as a result of human pollution, which can be the case for the Mexican Caribbean, where one of the main economic activities is tourism. Results presented in this paper suggest that lionfish predation on parrotfish could decrease their numbers in coral reefs, resulting in the subsequent affectation to the coral reef community health, however, more studies regarding fish abundance are necessary to corroborate this hypothesis. As an example striped parrotfish, *Scarus iseri* (Bloch, 1789), which was found as the most important parrot fish species in the lionfish diet, is recognized as one of the most important species associated to the health of coral reefs, because they have the highest consumption rate of algae, making more important their presence in disturbed areas, where the algae production increases considerably (Mumby et al. 2006 Durán and Claro 2009).

Muñoz et al. (2011) discussed that although the pomacentrids are the most abundant prey in the environment, this group show a low importance in the diet of lionfish in locations of Carolina, USA, explaining that this results were related with the high substrate association in the Pomacentridae, making this group less vulnerable to predation. Also, in the Bahamas (Morris et al. 2009) and Florida (Jud et al. 2011) Pomacentridae does not appear to be an important item. In contrast, the results presented in our paper showed the Pomacentridae as the most important (IRI) fish family in the lionfish diet. This can be explained by a lionfish “learning behaviour” where they adapted to eat new available/abundant preys. This possibility is based in the well investigated learning process that territorial fish showed in other areas, for example pomacentrids, can decide if to attack or avoid an invader according with the level of the threat that the new invader possess (Helfman and Winkelman 1997, McCormick and Holmes 2006).

The predation of all grouper species (Family Serranidae) found in this work, suggests that lionfish

might decrease the recruitment of economically important species affecting the already stressed fisheries in the area. For example “cherna”, *Cephalopholis cruentata* (Lacepède, 1802), was found in this work as component of the lionfish diet; cherna has a high economic value due to the quality of its meat. Also chernas feed mainly on *Chromis multilineata* (Guichenot, 1853) (Family Pomacentridae), which is a species with an important ecological role in the area, and is also a recurrent food for lionfish. This work showed that economically important crustaceans (being a possible competitor) such as shrimps and lobsters and other groups (molluscs) are present in the diet of lionfish, highlighting a nested effect that directly or indirectly affect species and regional biodiversity.

The data analysis conducted by seasons, determined that during the dry period crustaceans of the genus *Cinetorhynchus* were abundant preys where *Cinetorhynchus rigens* was the more abundant prey. This species is widespread in the region, it has nocturnal habits and its usually located in the vicinity of the cracks and caves that serve as shelter during the day. It is well known that lionfish also prefers to refuge in cracks and caves where there is a greater chance of finding crustaceans for feeding. Another important genus found as component of the lionfish diet was *Pleoticus*. The highest record of this crustacean as part of the diet in the period coincided with the peak of the crustacean reproduction (Fernández et al. 2012). For the rainy season, again the most important prey was *Cinetorhynchus*, followed by the species of the genus *Periclimenes*. During the nortes season also the genus *Cinetorhynchus* was the most representative component of the diet, followed by genus *Stegastes* (Pomacentridae), with *Stegastes partitus* (Poey, 1868) as the most frequent species.

Previous studies reported the diet composition of the red lionfish, *Pterois volitans*, in the Caribbean, demonstrating that this invader ate mainly fishes, which represented between 78% and 99% of its food volume. The most representative prey groups were the fish families: Gobiidae, Labridae, Grammatidae, Apogonidae, and Pomacentridae followed by a low number of crustaceans (Morris and Akins 2009). The families Scaridae and Serranidae were the most represented components of the lionfish diet in a 2004 (Morris and Akins 2009) and fishes Haemulidae and Carangidae, and crustaceans were identified in another survey during 2006 as the most important diet components (Muñoz et al. 2011). Recently, using molecular techniques, Valdez-Moreno et al. (2012) identified Gobiidae, Apogonidae, Labridae, and Scorpaenidae as the most important fish family groups in the lionfish diet, whereas Côté et al. (2013) used visual and molecular methods to identify 17 fish prey species. It is evident from all these previous works, that the crustaceans did not represent an important component of the lionfish diet. Some authors did not even consider them as part of the lionfish diet. Therefore, this work is the first to acknowledge the importance of crustacean and molluscs in the diet composition of lionfish.

The Mexican Caribbean is part of the second largest coral reef barrier in the world, and supports the most important touristic area in Mexico, where this is the main economic activity that relies on a very significant demand of coastal and marine resources, including fishes and crustaceans. These resources are highly vulnerable to natural and anthropogenic changes, such as habitat destruction, pollution, overfishing, and introduction of non-native species (Albins and Hixon 2008). Therefore, it is very important to monitor and generate new data related to the effect of the lionfish invasions in the area. Results from this work and many others have pointed out the lionfish as an economic risk because its diet habits not only include juveniles of commercially important species such as lobsters, but because it also competes with snappers (Lutjanidae) and grouper (Serranidae) for food and habitat. This factor is aggravated by the strong fisheries exploitation that exists for these and other groups of marine organisms. It is a threat to the tourism industry that revolves around the reef.

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