

## Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea

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### Abstract

The Indo-Pacific lionfishes (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]; Family Scorpaenidae) are the first non-native marine fishes to establish in the Western North Atlantic. The chronology of the invasion is reported here using records from the US Geological Survey's Nonindigenous Aquatic Species database. Currently, lionfish are established off the Atlantic coast of the USA from the Florida Keys to Cape Hatteras (North Carolina), the Great Antilles, Bermuda, Bahamas, Cayman Islands and Turks and Caicos. The species have been reported from only one island in the Lesser Antilles (St. Croix), but it is not yet established there. Lionfish are established in Mexico, Honduras and Costa Rica. Reports have come from the Gulf of Mexico (Florida), Belize, Panamá and Columbia; although lionfish are not considered established in these localities at this time (August 2009), invasion is likely imminent.

*Key words:* lionfish, *Pterois volitans*, *Pterois miles*, non-native marine fishes, Scorpaenidae

### Introduction

The Indo-Pacific lionfish species (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]; Family Scorpaenidae) are the first non-native marine fishes to establish in the Western North Atlantic and Caribbean Sea. Although there are both confirmed and unconfirmed (anecdotal) reports of lionfish sightings from decades past, it is only recently (i.e., since 2000) that the species have considerably increased in numbers and spread through the Western North Atlantic (Whitfield et al. 2002, 2007; Freshwater et al. 2009a). At this time it is unclear what effects this new addition will have on native communities, and because the invasion is so recent there are few ecological studies of its impact (but see Albins and Hixon 2008). Nonetheless, there are several reasons to be concerned about their presence: Lionfish are predators that consume native species (Morris

and Akins unpubl. data) and have venomous spines that could injure divers. In this paper, information on the chronology of invasion of the lionfish is provided using records from the US Geological Survey's Nonindigenous Aquatic Species database (USGS-NAS 2009).

### Material and Methods

The USGS-NAS database is the national repository for spatially-referenced sightings information for non-native aquatic species in the USA (USGS-NAS 2009). The Reef Environmental Education Foundation database (REEF 2008) and National Oceanic and Atmospheric Administration (NOAA) are major contributors of lionfish data to the USGS-NAS database. Records in the USGS-NAS database are derived from a variety of sources, including scientific literature, published and unpublished reports, museum specimens and personal communi-

cations. Data provided in this report is as current as possible; however, as lionfish distribution changes through time it is likely to become outdated. Lack of sightings data for a given region should not be inferred as a reduced number of lionfish in that region (see Haiti, below). Additionally, the number of reports for a given area may not be reflective of density of lionfish, as likelihood of reporting varies from place to place. Reporting frequency may be a function of the number of divers or tourists that visit a location, therefore places with well-established dive operations and facilities for tourists are likely to have increased reporting. For the most current information, visit the USGS-NAS database online (USGS-NAS 2009). Individuals who have relevant information concerning lionfish (or other non-native fishes) are encouraged to report their findings to the USGS-NAS database.

In the early stages of the invasion, it was thought that only one species of lionfish was present (*Pterois volitans*). However, recent genetic evidence has indicated that *P. volitans* along with a small number of *P. miles* are present in the Atlantic Ocean (Hamner et al. 2007; Morris and Freshwater 2008; Freshwater et al. 2009a, b). It is not clear whether both species are present in all locations; thus in this paper both species are referred to as “lionfish”.

## Results

### *Locations where lionfish are established*

#### Atlantic Coast of Mainland USA

The first confirmed record of lionfish occurrence in the USA was a specimen taken by a lobster fisherman off Dania, Florida in October 1985 (Morris and Akins *In Press*). The next time lionfish were reported was the liberation of six specimens from a sea-side aquarium in south Florida that was damaged in Hurricane Andrew in August 1992 (Courtenay 1995). Reportedly, these lionfish found their way into Biscayne Bay, where they were observed alive a few days later. In his 1995 report, Courtenay also mentioned that lionfish had been seen in three other south Florida locales (Lake Worth, Palm Beach, Boca Raton) but no additional details are given. After Courtenay’s 1995 report, there were no sightings of lionfish in the USA until 2000, when they were observed off Palm Beach (Florida, n = 4), South Carolina (n = 1), and three locations off

North Carolina (n = 1 fish per locality). In 2001 lionfish were seen in three locations in Florida (Jupiter, n = 1; Palm Beach, n = 3; Jacksonville n = 1), off the Georgia coast (n = 3), at three locations off South Carolina (n = 1 to 4 fish per location), at 14 sites off North Carolina and as far north as Fire Island, New York (n = 2). By 2002, lionfish were considered more or less continuously distributed from Miami, Florida to Cape Hatteras, North Carolina. Assessments of these populations have been reported by Whitfield et al. (2002, 2007), Meister et al. (2005) and Ruiz-Carus et al. (2006).

Occasionally, small lionfish have been collected north of North Carolina (e.g., coastal New Jersey, Rhode Island and New York), presumably swept northward in the Gulf Stream. However, these individuals are not expected to survive due to their intolerance of cold winter temperatures (Kimball et al. 2004).

Lionfish were not found in the Florida Keys (from Miami south to the Marquesas Islands) until relatively recently (January 2009); much later than they were found in significant numbers along the Atlantic coast of Florida north of Miami. The first Florida Keys lionfish was found at Benwood Ledge (near Key Largo) in 66 ft of water. The specimen was collected within 24 hrs of the sighting. Twelve additional lionfish have been seen as of June 2009; most of these have been collected by REEF (REEF 2008).

#### Bermuda Islands

The first lionfish recorded from Bermuda was a juvenile taken from a tide pool on the southern shore of the island in 2000 (Whitfield et al. 2002). It appears the species persisted at low levels for several years, as only a few lionfish were seen each year between 2001 and 2003. By 2004, lionfish were numerous in Bermuda. Although lionfish continue to be seen regularly in Bermuda, their annual densities seem to vary greatly. It is unclear whether lionfish can overwinter in Bermuda, and thus unclear whether the population is established (i.e., a self-supporting reproductive population) or transient (driven by recruitment via the Gulf Stream).

#### Commonwealth of the Bahamas

Lionfish first appeared in the Bahamas in 2004 at Nassau (New Providence Island). By 2005 they had established and spread to the Abacos, Andros, Eluthera, Exumas and San Salvador islands. Lionfish inhabit the whole of the

Bahamas now, including not only the typical coral reef habitats, but also mangrove, seagrass, sandy beach and occasionally even canal habitats.

Lack of genetic differentiation between Bahamian and North Carolina *P. volitans* suggests they share a similar source (e.g., east coast of Florida; Freshwater et al. 2009a). While both *P. miles* and *P. volitans* occur off the US Atlantic coast (Hamner et al. 2007; Morris and Freshwater 2008); thus far only *P. volitans* has been recovered from Bahamian waters (Freshwater et al. 2009a).

The effects of non-native lionfish on invaded ecosystems has not been widely studied. However, Albins and Hixon (2008) showed that lionfish could drastically reduce recruitment of native fishes on small patch reefs in the Bahamas. Green and Côté (2008) documented lionfish densities off New Providence Island that were more than eight times greater than known from the native range. A diet study of Bahamian lionfish was completed by Morris and Akins (in press) that showed lionfish primarily eat teleost fishes (they documented 41 species in 21 families) as well as some crustaceans (about 15 % of the diet by volume). Also in the Bahamas, lionfish were found in the stomachs of groupers (Maljković et al. 2008). However, it is unclear how common predation on lionfish occurs.

#### Turks and Caicos Islands

The initial report of lionfish from the Turks and Caicos islands occurred in May, 2006; however, the specific location of the report was unclear. The first confirmed lionfish report from the Turks and Caicos islands was a single specimen seen in August 2007 off West Caicos. Five additional sightings were reported in 2007. More than 25 sightings of lionfish were reported in 2008 and 23 additional reports have been added to date to the USGS-NAS database in 2009 (through July).

#### Cayman Islands

The first lionfish record for the Cayman Islands was a single juvenile seen in February 2008 off Little Cayman Island. The specimen was removed by government officials a few days later. The second lionfish found in the Cayman Islands was captured from a reef off Cayman Brac in October 2008. The Cayman Islands Department of Environment has begun an aggressive lionfish removal programme, using local divers that are specially trained and

licensed to remove lionfish. As of June 2009, over 200 lionfish have been captured and removed from the Cayman Islands.

#### Republic of Cuba

In 2005, a snorkeler spotted a juvenile lionfish in very shallow water on the Atlantic coast of the island after the passage of Hurricane Katrina, but the report was never confirmed. The first confirmed reports of lionfish in Cuba were in 2007. Chevalier et al. (2008) documented the species at six localities along the Atlantic (northern) coast and two from the province of Santiago de Cuba on the southeastern (Caribbean) coast of the island. Six additional reports of lionfish from the Atlantic coast and two from the Caribbean (Camaguey and Granma) were reported in 2007. In 2008, lionfish were reported from more than twenty localities around the island. Over 20 sightings have been reported in the first six months of 2009, and many of these are from the southwestern (Caribbean) coast where lionfish were not previously found. Sometimes as many as 15 individuals were seen on a single dive.

#### Jamaica

The first confirmed report of lionfish in Jamaica was the sighting of a single specimen at Runaway Bay on the northern coast of the island in March 2008. More than 20 additional reports were received in 2008, and an additional 44 reports have been received so far in 2009 (between January and mid-August).

#### Dominican Republic

The first confirmed report of lionfish from the Dominican Republic was from Sosua Bay, Puerto Plata (northern coast), in May 2008 (Guerrero and Franco 2008). There were several unconfirmed reports of lionfish from Sosua Bay previous to this; however, the report of Guerrero and Franco (2008) provided the first photo-documented evidence of the species in the Dominican Republic. The authors reported that more than 20 additional specimens had been observed between the time they photographed the one in May 2008 and the time their paper was published (July 2008). Reports from the USGS-NAS database document the species' spread across both the northern and southern coasts of the island in 2008. Lionfish have been reported from 18 additional locations between January and mid-August 2009.

#### Commonwealth of Puerto Rico

The first confirmed report of lionfish from Puerto Rico was in November 2008, when a single individual was spotted off Vieques Island. Twenty more sightings have been reported between January and mid-August 2009.

#### Mexico

Two lionfish were reported from Cozumel Reefs National Marine Park in January 2009. Since then, 26 more lionfish reports have come from Cozumel. Fourteen additional reports of lionfish have documented their spread along the Mexican mainland west and south of Cozumel in 2009.

#### Honduras

The first lionfish known from Honduras was a specimen captured in May 2009 off the island of Roatán inside the barrier reef about 200 m from shore in 7 m of water. Seventeen additional sightings have been reported from Roatán thus far and 4 reports have come from Utila (as of August 2009).

#### Republic of Costa Rica

Lionfish were first seen in Costa Rica in April, 2009 at the Manzanillo Wildlife Refuge (n=3). Additional specimens were seen the following month at two nearby locations (Puerto Viejo [n=2] and Cahuita National Park [n=4]). An additional 23 reports have come from Cahuita National Park and 12 additional reports from Manzanillo Wildlife Refuge in 2009.

*Locations without enough information to determine establishment*

#### Republic of Haiti

There are only five lionfish records from Haiti. The first was in August 2008, when a specimen was photographed near a jetty in water 2-3 m deep on the western side of Hispaniola (Gulf of Gonâve). Three more reports in April 2009 documented a total of five fish on the northern coast at Labadee (also written as “Labadie”; near Cap Haïtien). A report from June 2009 documented ten more individuals near Baie de l'Acul. The relatively small number of records in the USGS-NAS database is probably not because there are fewer lionfish in Haiti, but likely due to low reporting from this area. Lionfish are classified as established for Hispaniola largely due to the fact that there are reliable records from the Dominican Republic. However, there is

not enough information from Haiti to make a specific determination as to their status there.

*Locations where lionfish have been seen but have not yet established*

#### US Virgin Islands

The first lionfish records from the US Virgin Islands were from a diver who saw and photographed several lionfish at two sites off the north shore of St. Croix in June 2008. However, these records have been disputed. In November 2008 a juvenile lionfish was collected off the Frederiksted Pier, on the western side of St. Croix. Between January and July 2009, seven more fish have been seen or collected from St. Croix. At the time of this publication, no lionfish have been seen in proximity to St. Thomas or St. John.

#### Gulf of Mexico

In October 2006, a dead lionfish was retrieved from waters off Treasure Island (Pinellas County), Florida (FWRI 2008). The fish was found during a bloom of the toxic red-tide organism *Karenia brevis*; however, toxicity testing revealed only minimal exposure of the fish to the brevetoxin. Therefore, it appears the fish was only in Gulf coast waters for a short period of time. Several other reports of lionfish in the northern Gulf of Mexico (from Texas and the Florida panhandle) have been received by the USGS-NAS database; however, to date none of these have been confirmed.

#### Belize

There was an unconfirmed report of a lionfish sighting in Belize from September 2001. The first confirmed report was a single specimen taken in December 2008 from Turneffe Atoll. Subsequently, lionfish have been seen at Glover's Reef (January 2009; n=1), Ambergris Caye (March 2009; n=2) and Lighthouse Reef (June 2009; n=3).

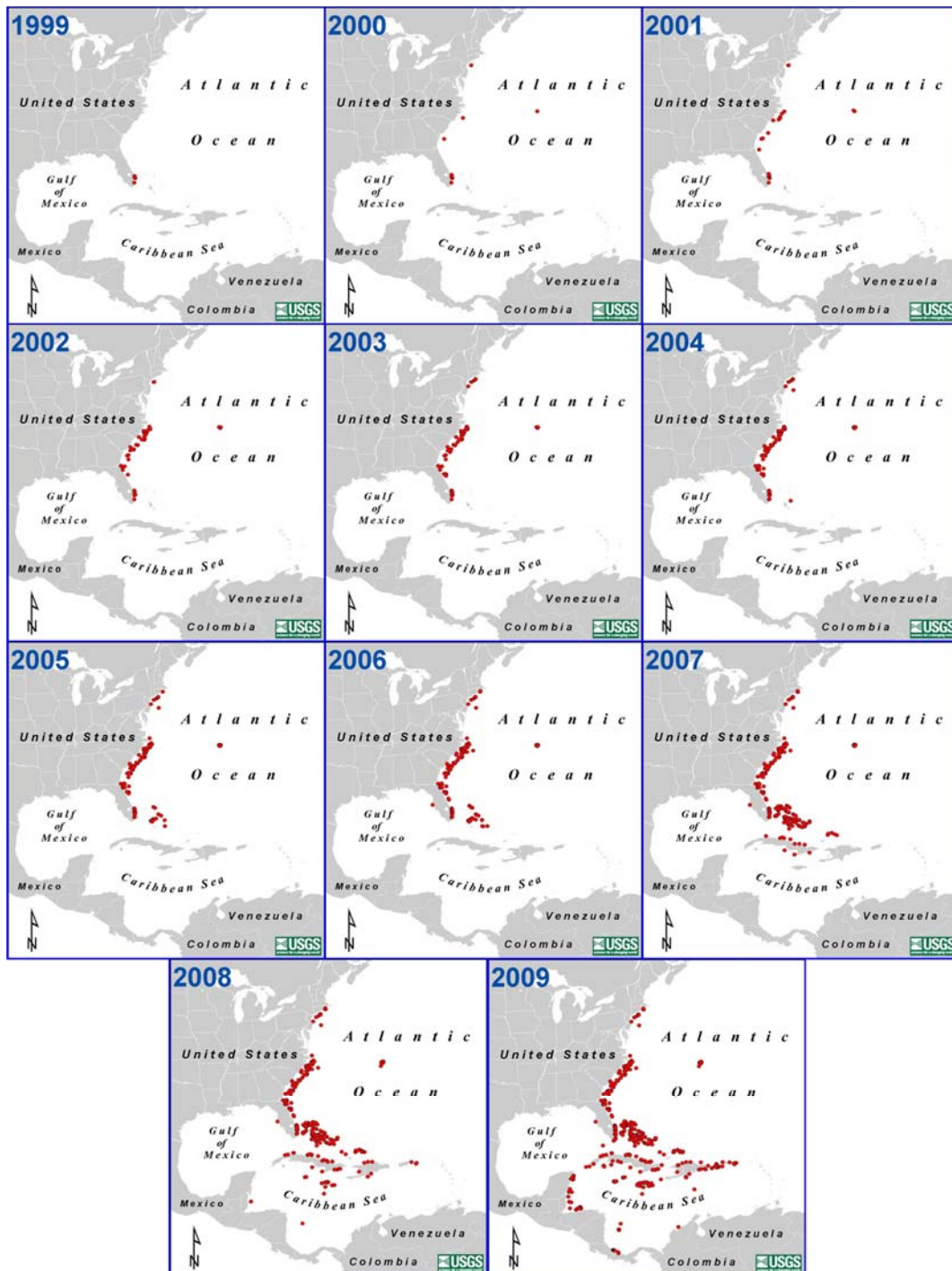
#### Republic of Panamá

Three lionfish have been collected from Bocas del Toro, the first in May 2009 and the second and third in July 2009. All three specimens were donated to the Smithsonian Tropical Research Institute in Bocas del Toro.

#### Republic of Columbia

The first lionfish from Columbia was seen on a shallow (5 m) patch reef in December 2008 at

Lionfish invasion chronology



**Figure 1.** Confirmed lionfish occurrences in the Western North Atlantic and Caribbean Sea (USGS-NAS 2009). The first panel displays all lionfish records in the database through December 1999 ( $n=5$ ). Each subsequent panel displays cumulative occurrences of lionfish for each calendar year. The panel for 2009 includes data through mid-August 2009. All data is available online via the USGS-NAS database (<http://nas.er.usgs.gov>). Alternately, this [direct link](#) is available

Manta City just south of Isla de Providencia in the Seaflower Biosphere Reserve, part of the Archipelago of San Andres (near Nicaragua). Nine additional specimens have been seen off San Andres Island to date. In May 2009 two specimens were collected at Tayrona National Park, Santa Marta. These two fish were the first known from the Columbian mainland; at least one of these is deposited in the Museum of Natural History (INVEMAR). Four additional fish have been seen near Santa Marta off the Columbian (mainland) coast (González et al. 2009).

### Summary

Figure 1 displays cumulative lionfish occurrence information by year, summarized below:

**Atlantic Coast of USA:** Lionfish have been established from Miami to North Carolina since 2002. They have only recently (2009) established in the Florida Keys. Although present in Atlantic waters north of North Carolina, they are not considered established there because they are not likely to survive cold winter temperatures.

**Bermuda, Bahamas, Turks and Caicos and Cayman Islands:** Lionfish were numerous in Bermuda by 2004 and established in the Bahamas by 2005, the Turks and Caicos by 2008 and the Cayman Islands by 2009.

**Greater Antilles:** Lionfish are established off all islands in the Greater Antilles (Cuba [2007], Jamaica [2008], Hispaniola [Haiti and the Dominican Republic; 2008] and Puerto Rico [2009]). Lionfish are classified as established off Hispaniola due to the documentation of their spread in the Dominican Republic; however, data for Haiti is lacking.

**Lesser Antilles:** Currently (July 2009), the only reports of lionfish from the Leeward Islands are those from St. Croix (see above), where lionfish are not considered established. There have been no confirmed reports from Anguilla (UK), Antigua, Barbuda, Montserrat (UK), Nevis, Redonda, Saint Kitts, Saba (Netherlands), Sint Eustatuis (Netherlands), Saint Martin/Sint Maarten (France/Netherlands Antilles) or the French islands of Basse-Terre, La Désirade, Grande-Terre, Marie-Galante, Saint-Barthélemy,

Terre-de-Bas and Terre-de-Haut. However, there is an unconfirmed report from Sint Maarten from 2008. There are no reports of lionfish from the Windward Islands (Dominica, Grenada, Martinique [France], Saint Lucia and Saint Vincent and the Grenadines), Trinidad and Tobago or the Leeward Antilles (Aruba, Bonaire and Curaçao [Netherlands] and Coche, Cubagua, La Tortuga, Margarita Island and the Venezuelan Archipelago [Venezuela]). There have been two unconfirmed reports of lionfish sightings from Barbados (from February 2006 and January 2009).

**Mexico, Central and South America:** Lionfish are currently expanding through Mexican, Central and South American waters. They are considered established in Mexico, Honduras and Costa Rica (2009). Lionfish are not considered established in locations outside these three; however, establishment is likely imminent.

### Acknowledgements

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## Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago

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**Abstract** Feeding ecology of the lionfish (*Pterois volitans*), an invasive species in the Western North Atlantic, was examined by collecting stomach content data from fishes taken throughout the Bahamian archipelago. Three relative metrics of prey quantity, including percent number, percent frequency, and percent volume, were used to compare three indices of dietary importance. Lionfish largely prey upon teleosts (78% volume) and crustaceans (14% volume). Twenty-one families and 41 species of teleosts were represented in the diet of lionfish; the top 10 families of dietary importance were Gobiidae, Labridae, Grammatidae, Apogonidae, Pomacentridae, Serranidae, Blenniidae, Atherinidae, Mullidae, and Monacanthidae. The proportional importance of crustaceans in the diet was inversely related to size with the largest lionfish preying almost exclusively on teleosts. Lionfish were found to be diurnal feeders with the highest predation occurring in the morning (08:00–11:00).

**Keywords** *Pterois* · Diet composition · Stomach content · Invasive species

### Introduction

The lionfishes, *Pterois miles* and *P. volitans*, (Hamner et al. 2007; Morris 2009) are the first non-native marine fishes to become established along the Atlantic coast of the U.S. and the Caribbean. Adult lionfish specimens are now found along the U.S. East Coast from Cape Hatteras, North Carolina, to Florida, and in Bermuda, the Bahamas, and throughout the Caribbean, including the Turks and Caicos, Haiti, Cuba, Dominican Republic, Puerto Rico, St. Croix, Belize, and Mexico (Schofield et al. 2009). The first documented capture of lionfish in the Atlantic was in 1985 off Dania Beach, Florida (J. Bohnsack, NOAA NMFS, pers. comm.). Additional sightings occurred in 1992 following an accidental release of six lionfishes from a home aquarium into Biscayne Bay, Florida (Courtenay 1995). Many other reports of lionfish were documented in southeast Florida between 1999 and 2003 by Semmens et al. (2004), who attributed many of these sightings to releases by home aquarists.

Recreational divers reported the first sightings of lionfish in the Bahamas in 2004 (REEF 2009). Snyder and Burgess (2007) published the first record of lionfish in the Bahamas, suggesting that lionfish were widely distributed throughout Little Bahama and

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Grand Bahama Banks. It is uncertain if lionfish invaded the Bahamas via larval transport by ocean currents or if their introduction was the result of additional aquarium releases. Recent genetic studies by Freshwater et al. (2009) suggest that lionfish invaded the Bahamian archipelago via larval dispersal originating from U.S. waters.

Early efforts to assess the density of lionfish off North Carolina by diver surveys and remotely operated vehicles suggested that lionfish populations were rapidly increasing, with trophic interactions with native reef fishes a concern (Whitfield et al. 2002; Hare and Whitfield 2003). Recently, densities on Bahamian reefs have been documented by Green and Côté (2009) to be in excess of 390 lionfish hectare<sup>-1</sup>; almost five times higher than estimates from the native range. Albins and Hixon (2008) reported the first evidence of the impacts of lionfish on native fish communities by demonstrating that lionfish reduced recruitment of coral reef fishes on experimental reefs in the Bahamas by nearly 80%.

To date, comprehensive assessments of lionfish diets are lacking in their native and invaded ranges. Preliminary observations of lionfish feeding in their native range suggest that lionfish feed primarily on small fishes and some invertebrates (Fishelson 1975, 1997; Harmelin-Vivien and Bouchon 1976). In the Pacific Ocean, the closely related luna lionfish (*P. lumulata*) was found to feed primarily on invertebrates, including penaeid and mysid shrimps (Matsumiya et al. 1980; Williams and Williams 1986). More recently, Albins and Hixon (2008) reported a list of nine species consumed by invasive lionfish in the Bahamas. While these observations suggest general patterns in lionfish diet, quantitative assessments of lionfish feeding habits in their new range are needed to elucidate the impacts of these predators on invaded reef communities. The overall objectives of this study were to 1) assess dietary habits of lionfish collected from various habitats in the Bahamian archipelago, 2) determine the relationship between prey and predator size, and 3) document temporal feeding patterns of this invader.

## Methods

### Collections

Lionfish were collected from the Bahamian archipelago (Fig. 1) between January 2007 and May 2008. All

specimens were collected by fisheries professionals and trained volunteers while snorkeling or using SCUBA gear at sites ( $n=134$ ) comprised of high profile coral reefs, patch reefs, artificial reefs, mangroves, and man-made canals ranging in depth from 1 to 30 m. Sampling sites were chosen opportunistically to optimize sampling success. Most collections utilized hand nets and vinyl collection bags, although some were collected by pole spear. Live captures from nets and bags were euthanized by excess anesthesia in a bath of eugenol (Borski and Hodson 2003). Only two lionfish regurgitated stomach contents during ascension; therefore, stomach content retention measures were unnecessary. Lionfish were placed on ice and dissected the same day as capture.

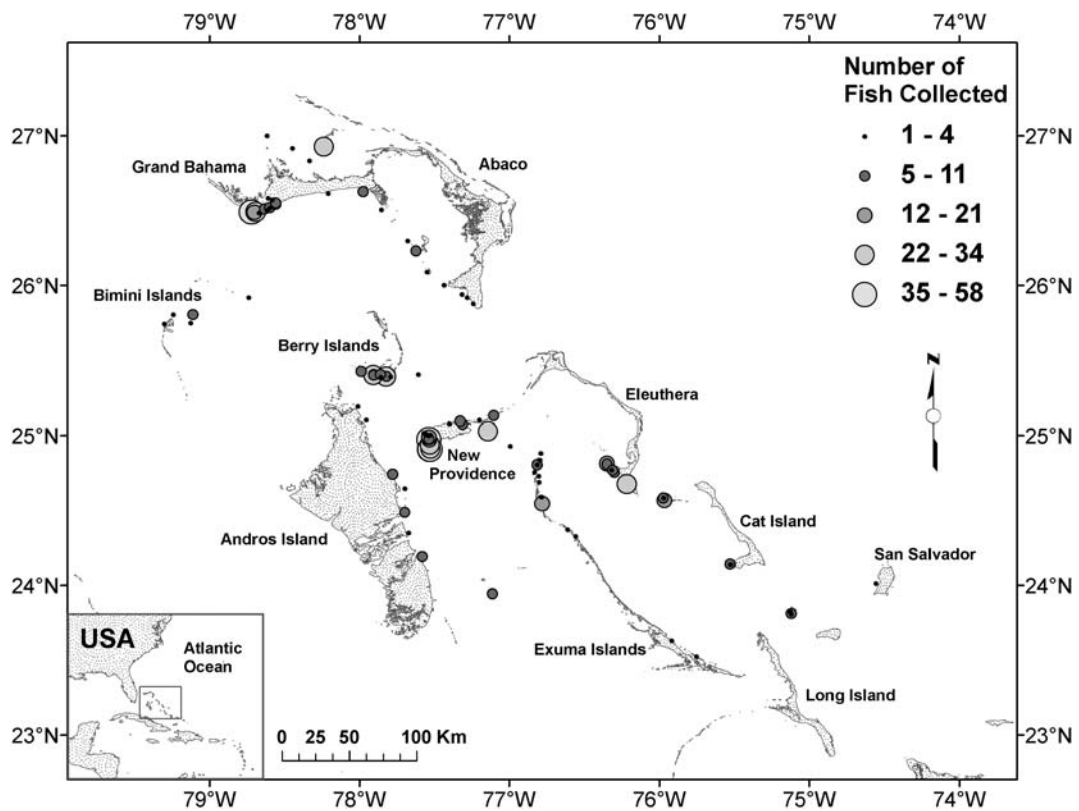
Lionfish were collected every month of the calendar year ( $\bar{X} = 111 \pm 28$  individuals per month), with the smallest sample size collected during June ( $n=10$ ) and the largest collected during February ( $n=368$ ). Collections of lionfish were achieved from 07:00 to 21:00; the majority of collections (99.1%) occurred between 08:00 and 17:00.

### Cumulative prey curve

A cumulative prey curve was used to assess sample size sufficiency of lionfish stomachs containing identifiable prey. Prey taxa were grouped by family and cumulative numbers of novel prey were determined following 1,000 randomizations (Bizzarro et al. 2007). Mean and standard deviation of the cumulative number of novel prey was calculated and sufficiency of sample size was assessed statistically using the linear regression method of Bizzarro et al. (2007) that compares the slope from a regression of the last four stomach samples to a slope of zero using a Student's *t*-test of equality of two population regression coefficients (Zar 1999). A *p*-value >0.05 was considered to demonstrate sampling sufficiency. To determine the minimum number of stomach samples (with identifiable prey) required to adequately describe lionfish diet, one sample was removed sequentially until the Student's *t*-test *p*-value fell below 0.05 indicating that asymptote was not achieved.

### Stomach content analyses

Stomach contents were identified to lowest possible taxon (without fixation), counted, and measured for



**Fig. 1** Sampling locations and number of lionfish collected along the Bahamian archipelago

total length (TL). No adjustment of prey TL due to partial digestion was performed, thus the estimated prey sizes are potentially underestimated. Volumes of diet items taken from contents were measured by water displacement in a graduated cylinder. The contribution of each prey taxon to the overall diet was assessed using the following three relative metrics of prey quantity: percent frequency of occurrence (%F), percent composition by number (%N), and percent composition by volume (%V) (Hyslop 1980; Bowen 1996). Variations in prey size and diet composition across lionfish sizes were examined statistically by conducting a significance test on the slope of a linear regression. An  $\alpha$ -level  $\leq 0.05$  was considered significant.

Dietary importance indices or hybrid diet indices have been widely-employed in the study of fish food habits (Bowen 1996), yet their specific use has been criticized (Windell and Bowen 1978) and subject to controversy (Hyslop 1980; Cortés 1997; Hansson 1998). For a robust assessment of

prey importance, three indices of importance were calculated:

- (1) the Index of Relative Importance (IRI) (Pinkas et al. 1971),

$$IRI_a = F_a \cdot (N_a + V_a)$$

- (2) the Index of Importance (IOI<sub>a</sub>) (Gray et al. 1997; Hunt et al. 1999),

$$IOI_a = \frac{100 \cdot (F_a + V_a)}{\sum_{a=1}^s (F_a + V_a)}$$

- (3) the Index of Preponderance (IOP) (Natrajan and Jhingran 1962; Sreeraj et al. 2006),

$$IOP_a = \frac{F_a \cdot V_a}{\sum_{a=1}^s (F_a + V_a)}$$

where  $s$  is the number of prey types,  $F_a$  is the frequency of occurrence of species  $a$ ,  $V_a$  is the percent

composition by volume of species  $a$ , and  $N_a$  is the percent composition by number of species  $a$ .

## Results

The size of lionfish ranged from 62 to 424 mm TL with a mean size ( $\pm$ SE) of  $217 \pm 7$  mm. A total of 1,876 prey items from 1,069 stomachs were assigned to taxa. Volumetric measurements of prey by taxon were determined for 699 stomachs. Lionfish were sampled from diverse habitat types including high profile coral reefs (68%), canals (11%), artificial reefs (9%), other (predominately blue holes) (5%), patch reefs (4%), and mangrove habitats (3%). Cumulative prey curve analysis indicated sample size sufficiency reached asymptote for stomachs with identifiable prey ( $p > 0.58$ ). A large number of stomachs were required to attain sufficient sample size as  $p < .05$  occurred at sample 706.

### Prey composition

Twenty-one families of teleosts, four families of crustaceans, and one family of mollusks were represented in the diets of lionfish (Table 1). Teleost fishes dominated lionfish diet comprising 78% by volume (%V), 71.2% by number (%N), and 61.6% by occurrence (%F). Crustaceans were also represented at 14.4%V, 28.5%N, and 24.7%F, while mollusks comprised  $< .01\%$ V, %N, and %F. Approximately 21% ( $n=225$ ) of the stomachs were empty.

Teleost prey included 41 species and exhibited a wide-range of body shapes and morphological characteristics (Table 1). The families with the greatest number of species included Labridae (8), Pomacentridae (6), Gobiidae (5), and Serranidae (4). Eight families comprised 38% of lionfish diet by volume and 48% of the volume of identifiable teleosts. These included Pomacentridae (7.2%), Labridae (6.7%), Mullidae (5.5%), Grammatidae (5.0%), Serranidae (4.3%), Gobiidae (4.2%), Apogonidae (3.6%), and Blenniidae (1.1%). Unidentified prey accounted for 42.1%N, 38.1%V, and 36.5%F of all food items. The following teleost families had the greatest representation in percent number: Gobiidae (8.4%), Labridae (4.4%), Grammatidae (4.3%), Apogonidae (3.1%), Pomacentridae (1.8%), Serranidae (1.5%), Blenniidae (1%), and Atherinidae (1%). In terms of %F, the same familial order applied with only minor changes in the percentages.

The majority of crustacea prey were identified as shrimps: 25.5%N, 22.1%F, and 12.7%V of the total prey. Of the remaining crustacean prey, 3%V, %F, and %N were represented by four families (Corallanidae, Squillidae, Rhynchocinetridae, Stenopodidae) along with items from the categories of unidentified crab, and unidentified crustaceans (Table 1).

### Rankings of importance indices

The same ten families of teleosts ranked as the top ten for all three indices (IRI, IOI, IOP) (Table 2). Top three rankings (gobiids, labrids, and grammatids) occurred in the IRI and IOP lists; whereas, the IOI ranked labrids, pomacentrids, and gobiids as most important of the teleost prey.

### Diet composition and size of lionfish

The importance of teleosts in the diet of lionfish increased significantly with size in all three dietary metrics (%F  $R^2=0.86$ ,  $p=0.0003$ ; %N  $R^2=0.55$ ,  $p=0.02$ ; %V  $R^2=0.76$ ,  $P=0.005$ ) (Fig. 2). The mean sizes of teleosts and crustaceans in the diet increased with the size of lionfish (teleost prey  $R^2=0.46$ ,  $p=.01$ ; crustacean prey  $R^2=0.36$ ,  $P=0.002$ ) (Fig. 3). The maximum number of crustacean prey per lionfish was 50, whereas the maximum number of teleost prey was 21. The mean ratio of prey size (TL) to lionfish size (TL) was  $14.5\% \pm 0.003$  standard error of the mean. The maximum prey size was 48% of the total length of lionfish, whereas the minimum prey size was 0.02%.

### Feeding activity

Stomachs of lionfish contained the highest volume of prey during the morning hours of 07:00–11:00 with a significant decrease in mean prey volume towards the evening ( $R^2=-0.39$ ,  $P=.01$ ) (Fig. 4). Few lionfish were collected at dusk or immediately after dark; therefore the prevalence of feeding at this time is uncertain.

## Discussion

In the Bahamian archipelago, invasive lionfish feed predominantly on teleosts and crustaceans. The large

**Table 1** Identifiable lionfish prey sorted by taxa

	Frequency (stomachs)	%F (n=1,069)	%N (n=926)	%V (n=699)
Mollusca	3			
Unidentified spp.	2	0.2	0.2	
Octopodidae				
Octopoda	1	0.1	0.1	
Crustacea	264			
Unidentified crustacean	2	0.2	0.2	
Unidentified shrimp	236	22.1	25.5	13.8
Unidentified crab	8	0.7	0.9	0.5
Corallanidae	3	0.3	0.3	
Stenopodidae				
<i>Stenopus hispidus</i>	4	0.4	0.4	
Rhynchocinetidae				
<i>Rhynchocinetes rigens</i>	5	0.5	0.5	1.0
Squillidae	6	0.6	0.6	0.2
Teleosts	659			
Unidentified fish	390	36.5	42.1	41.3
Atherinidae	9	0.8	1.0	0.6
Lutjanidae				
<i>Ocyurus chrysurus</i>	1	0.1	0.1	
Labridae	4	0.4	0.4	0.3
<i>Thalassoma bifasciatum</i>	13	1.2	1.4	0.6
<i>Halichoeres pictus</i>	2	0.2	0.2	0.7
<i>Halichoeres bivittatus</i>	3	0.3	0.3	1.1
<i>Clepticus parrae</i>	4	0.4	0.4	2.6
<i>Halichoeres garnoti</i>	13	1.2	1.4	1.9
<i>Halichoeres maculipinna</i>	1	0.1	0.1	0.1
<i>Bodianus rufus</i>	1	0.1	0.1	
<i>Xyrichtys</i> sp.	1	0.1	0.1	
Opistognathidae	3	0.3	0.3	0.3
Gobiidae	20	1.9	2.2	1.1
<i>Coryphopterus personatus/hyalinus</i>	39	3.6	4.2	1.6
<i>Coryphopterus eidolon</i>	14	1.3	1.5	1.5
<i>Coryphopterus dicrus</i>	3	0.3	0.3	0.4
<i>Coryphopterus glaucofraenum</i>	1	0.1	0.1	
<i>Priolepis hipoliti</i>	1	0.1	0.1	
Scaridae	2	0.2	0.2	
<i>Scarus iserti</i>	3	0.3	0.3	
<i>Scarus viride</i>	1	0.1	0.1	0.1
Blenniidae	1	0.1	0.1	
<i>Lucayablennius zingaro</i>	4	0.4	0.4	0.1
<i>Malacoctenus triangulatus</i>	4	0.4	0.4	0.8
<i>Malacoctenus boehlkei</i>	1	0.1	0.1	0.3
Tripterygiidae				
<i>Enneanectes</i> sp.	1	0.1	0.1	0.1

**Table 1** (continued)

	Frequency (stomachs)	%F (n=1,069)	%N (n=926)	%V (n=699)
Serranidae	5	0.5	0.5	1.0
<i>Epinephelus striatus</i>	2	0.2	0.2	0.6
<i>Serranus tigrinus</i>	4	0.4	0.4	0.9
<i>Hypoplectrus</i> sp.	1	0.1	0.1	1.4
<i>Liopropoma rubre</i>	3	0.3	0.3	0.8
Grammatidae	1	0.1	0.1	0.1
<i>Gramma loreto</i>	36	3.4	3.9	5.2
<i>Gramma melacara</i>	3	0.3	0.3	0.1
Synodontidae	3	0.3	0.3	0.4
Pomacentridae	4	0.4	0.4	
<i>Chromis insolata</i>	1	0.1	0.1	
<i>Chromis cyanea</i>	7	0.7	0.8	0.6
<i>Chromis multilineata</i>	2	0.2	0.2	5.1
<i>Stegastes partitus</i>	1	0.1	0.1	0.2
<i>Stegastes leucostictus</i>	1	0.1	0.1	
<i>Stegastes variabilis</i>	1	0.1	0.1	1.9
Apogonidae	21	2.0	2.3	3.1
<i>Apogon townsendi</i>	4	0.4	0.4	0.1
<i>Apogon binotatus</i>	4	0.4	0.4	0.6
Tetradontidae				
<i>Canthigaster rostrata</i>	1	0.1	0.1	
Syngnathidae	2	0.2	0.2	0.1
Acanthuridae				
<i>Acanthurus bahianus</i>	2	0.2	0.2	
Monacanthidae	2	0.2	0.2	0.1
<i>Monacanthus tuckeri</i>	3	0.3	0.3	0.4
Holocentridae				
<i>Sargocentron vexillarium</i>	1	0.1	0.1	
Cirrhitidae				
<i>Amblycirrhitus pinos</i>	1	0.1	0.1	0.2
Aulostomidae				
<i>Aulostomus maculatus</i>	1	0.1	0.1	0.3
Mullidea				
<i>Pseudupeneus maculatus</i>	2	0.2	0.2	5.9

number of teleostean families in lionfish diet indicates that lionfish feed upon a wide variety of available prey, but feed primarily on abundant teleosts and crevice dwelling species. The proportion of teleosts in the diet was size-dependent, with larger lionfish feeding more heavily on teleosts. Smaller size classes of lionfish had a higher proportion of crustaceans in their diet, primarily shrimps.

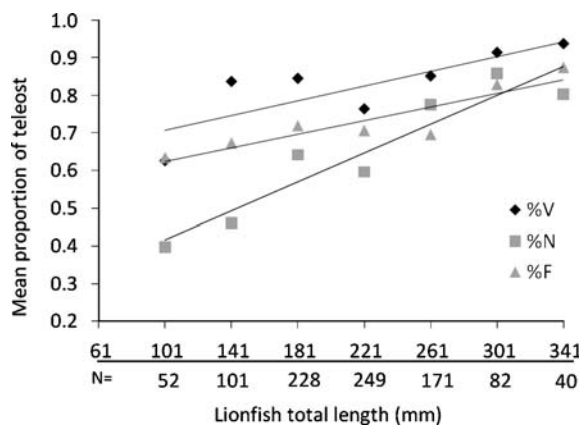
The amount of prey in lionfish stomachs over the course of the day suggest that lionfish feeding is highest in the morning (07:00–11:00), or the hours prior, with a decrease in feeding activity throughout the day. Diurnal visual observations of lionfish feeding further support this conclusion (L. Akins, S. Green, unpubl. data). Fishelson (1975) reported that lionfish (*Pterois volitans*) in the Red Sea are primarily

**Table 2** Rankings of importance indices for each fish family for each importance index

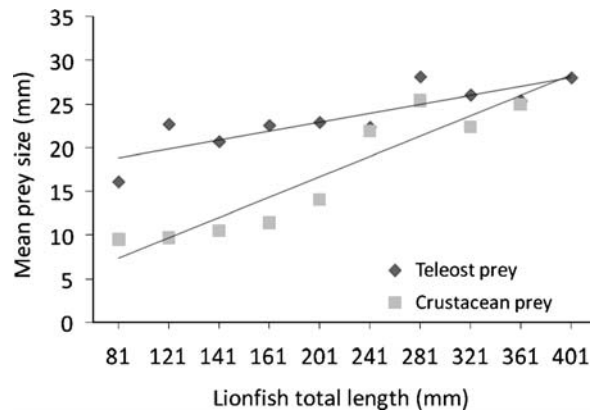
Rank	IRI	IOP	IOI
1	Gobiidae	Gobiidae	Labridae
2	Labridae	Labridae	Pomacentridae
3	Grammatidae	Grammatidae	Gobiidae
4	Apogonidae	Apogonidae	Grammatidae
5	Pomacentridae	Pomacentridae	Mullidea
6	Serranidae	Serranidae	Serranidae
7	Blenniidae	Blenniidae	Apogonidae
8	Atherinidae	Atherinidae	Blenniidae
9	Mullidea	Mullidea	Atherinidae
10	Monacanthidae	Monacanthidae	Monacanthidae

nocturnal and become active during crepuscular periods of dawn and dusk. Given the lack of samples in this study from the hours of 21:00 to 07:00, feeding activity during the late night hours (or nocturnal period) is unknown.

Lionfish are suction feeders, a common teleostean feeding technique comprised of rapid expansion of the buccal and opercular cavities coupled with quick forward motion (Van Leeuwen and Muller 1984). Lionfish also use a variety of feeding strategies, including ambush predation and corralling prey with their large, frilly pectoral fins. Lionfish also use their pectoral fins to flush benthic invertebrates from the substrate by palpation (Fishelson 1975). Specialized bilateral swim bladder muscles in lionfish provide novel control of their pitch in the water column,



**Fig. 2** Mean proportion of lionfish diet comprised of teleosts by lionfish 40 mm total length size classes



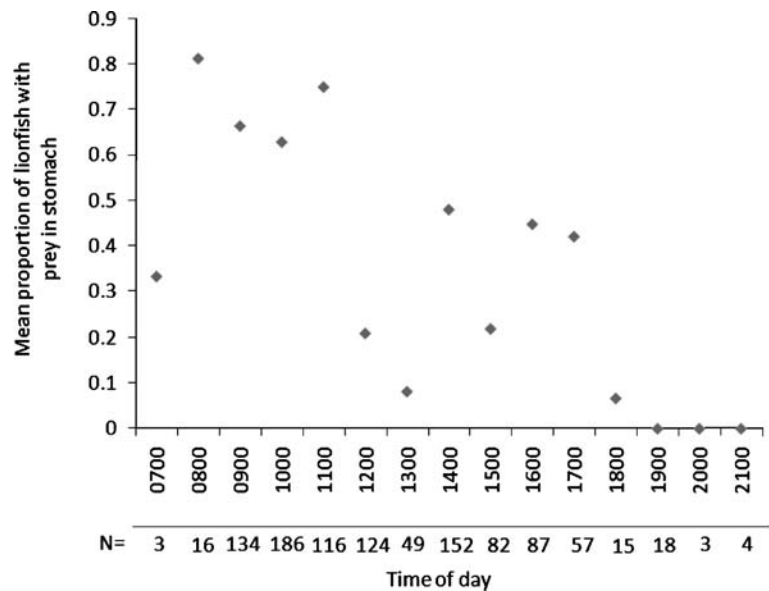
**Fig. 3** Mean teleost and crustacean prey size consumed by lionfish. Lionfish size displayed in 40 mm total length size classes

which allows lionfish to alter their center of gravity and provides fine-tuning of position prior to striking prey (Homstra et al. 2004). Lionfish also use this mechanism to orient and hover; they are frequently observed in an up-side-down position under ledges and on the lateral face of structure. Hovering behavior, hunting, ambush predation, and the flushing of prey from the benthos enable lionfish to employ a diverse array of feeding strategies well-suited for feeding on benthically-associated and cryptic fauna.

The relative importance of teleost families in the stomachs of lionfish was similar among the three indices of importance, suggesting a high degree of confidence in the rankings of the top ten teleost prey (Table 2). Similar rankings of the top two families (gobiids and labrids) among all three indices is evidence that these fishes are of highest importance in the diet of lionfish.

All three indices used here engage at least two of the dietary metrics %F, %N, and %V, but place different weight on the importance of each metric. The IRI, for example, places equal weight on %N and %V, and higher weight on %F. The IOI does not include %N and increases bias towards high volume, but infrequently found prey items. The IOP also does not incorporate %N, but employs a weighted mean approach. The IRI and IOP indices resulted in identical rankings. The IOI reported a different ranking order when compared to the IRI and IOP. The teleost family exhibiting the highest difference in ranking was Mullidae (ninth in the IRI and IOP and fifth in the IOI), probably because of its low %N and %F, but relatively high %V. The IRI and IOP are the

**Fig. 4** Proportion of lionfish stomachs containing prey throughout the day



more appropriate indices for investigating importance of prey items in lionfish diet because these indices require prey ranked high in importance to be both high in %F and %V.

This study suggests that lionfish feed primarily upon small-bodied teleost fishes, which are an important component of the diet of many economically important fishes of the tropical and western north Atlantic such as serranids (Lindquist et al. 1994; Eggleston et al. 1998) and lutjanids (Rooker 1995; Duarte and García 1999; Ouzts and Szedlmayer 2003). The diet of lionfish is diverse and includes 21 families and 41 species of teleosts. Direct predation by lionfish on economically-important species, including yellowtail snapper (*Ocyurus chrysurus*) and Nassau grouper (*Epinephelus striatus*), was observed, but these specific species were in relative low frequency.

The scale of ecological or economic impact of lionfish predation is uncertain and multiple scenarios are plausible: 1) prey are abundant because many top-level predators are removed by fishing, thus lionfish could have no direct impact; 2) lionfish will reduce prey communities causing a diminution of prey for native predators; 3) reduced levels of prey will slow, but not inhibit, stock rebuilding efforts for native fishes; and 4) lionfish predation on economically important species will cause direct impacts and possibly cascading effects. Although the likelihood of any of these scenarios occurring is unknown,

lionfish appear to be steadily increasing in both abundance and distribution. Recent evidence suggests that lionfish are capable of removing significant proportions (78%) of the prey community on isolated patch reefs (Albins and Hixon 2008). Future studies that quantify the biomass of the prey community and the seasonality of their abundance are needed to clarify direct and indirect impacts of lionfish on native species.

Our sampling did not include quantitative assessments of the prey communities; therefore prey preference cannot be derived from this study. Further, it is possible that lionfish diet may shift over time if predation by lionfish reduces or alters the abundance of the prey fish communities. Seasonal bias could also be present in our sampling as our sample size did vary among months and tropical reef fish recruitment is known to vary seasonally (Luckhurst and Luckhurst 1977; McFarland et al. 1985). Future assessments of the seasonality of lionfish diet, coupled with assessments of native reef fish recruitment across locales in the Southeast U.S., Caribbean, and Gulf of Mexico are needed to further elucidate the trophic impacts of lionfish. Additional research directed towards understanding the metabolic demands of lionfish coupled with dietary analysis and prey density surveys could quantify consumptive removal of native species by lionfish. These efforts would then allow scaling trophic impacts of lionfish at the individual and population level.

## Conclusion

This study provides the first comprehensive assessment of feeding habits of the invasive lionfish (*Pterois volitans*) in the tropical Western North Atlantic. Future research is needed to quantify the impacts of lionfish on forage fish communities in various habitats. Given the ecological and economical importance of higher trophic level predators such as serranids, increased efforts to remove lionfish through fishery development and/or control strategies are needed to mitigate the present and future impacts of lionfish.

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## **Biology and Ecology of the Invasive Lionfishes, *Pterois miles* and *Pterois volitans***

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### **ABSTRACT**

The Indo-Pacific lionfishes, *Pterois miles* and *P. volitans*, are now established along the U.S. southeast coast, Bermuda, Bahamas, and are becoming established in the Caribbean. While these lionfish are popular in the aquarium trade, their biology and ecology are poorly understood in their native range. Given the rapid establishment and potential adverse impacts of these invaders, comprehensive studies of their biology and ecology are warranted. Here we provide a synopsis of lionfish biology and ecology including invasion chronology, taxonomy, local abundance, reproduction, early life history and dispersal, venomology, feeding ecology, parasitology, potential impacts, and control and management. This information was collected through review of the primary literature and published reports and by summarizing current observations. Suggestions for future research on invasive lionfish in their invaded regions are provided.

KEY WORDS: Lionfish, invasive species, *Pterois*

### **Biología y Ecología del Pez León Invasor, *Pterois miles* y *Pterois volitans***

Los peces león del Indo-Pacífico, *Pterois volitans* and *Pterois miles*, se están estableciendo a lo largo de la costa sur oriental de los Estados Unidos, Bermuda, Bahamas y han comenzado a invadir el Caribe. Aunque los peces leones son populares en el comercio de acuarios, poco es conocido de su biología y ecología. Dado el rápido establecimiento de los peces león y su impacto potencial de estos invasores, los estudios comprensivos acerca de su biología y ecología son necesarios. Aquí proporcionamos una sinopsis de la biología y ecología del pez león incluyendo la cronología de la invasión, taxonomía, abundancia local, reproducción, historia temprana de la vida y dispersión, venomology, ecología de alimentación, parasitología, los impactos potenciales, y control y gerencia. Esta información fue recogida por medio de la revisión de la literatura primaria y informes públicos y resumiendo observaciones actuales. Las sugerencias para la investigación futura sobre el invasor pez león en las regiones invadidas son proporcionadas.

PALABRAS CLAVES: Peces león, especie invasora, *Pterois*

### **Biologie et Ecologie de Rascasses volantes Invasives, *Pterois miles* et *Pterois volitans***

Les rascasses volantes, *Pterois volitans* et *Pterois miles*, originaires de la zone tropicale indo-Pacifique sont aussi retrouvées le long des côtes sud-est américaines, aux Bermudes, aux Bahamas, et sont actuellement entrain d'envahir les Caraïbes. Alors que ces poissons sont très demandés dans le commerce des poissons d'aquarium, peu de données relatives à leur biologie et à leur écologie sont connues. Dans ce contexte, d'invasion rapide de ce poisson et des impacts potentiels sur les communautés de poissons récifaux endogènes, nous essayons de mettre en évidence la biologie de reproduction, les habitudes alimentaires et les caractères venimeux en utilisant les observations menées en laboratoire et sur le terrain. Concernant la reproduction de ce poisson, les observations menées montrent que c'est un animal itéropare, asynchrone avec de multiples pontes par saison (le nombre de ponte étant indéterminé). Les mesures visant à déterminer la périodicité de ponte montrent que ces poissons pondent mensuellement, avec des périodes de ponte au cours de la plupart des mois du calendrier d'où le caractère invasif de cette espèce. Les expérimentations conduites au laboratoire sur la prédation des rascasses juvéniles ont montré que ces derniers ne constituent pas de véritables proies pour les poissons récifaux endémiques à cause de leurs défenses venimeuses. L'analyse du contenu stomacal révèle essentiellement des crustacés et des poissons des espèces fourragères incluant les poissons dévolus à la pêche commerciale ou de loisirs, comme le vivaneau et le mérour. Ces travaux fournissent un nouvel éclairage en ce qui concerne la biologie intégrée et l'écologie des rascasses volantes non endémiques, et démontrent le besoin d'une détection précoce et systématique de cette espèce et la mise en œuvre de solution rapide pour faire face à cette invasion dans l'écosystème marin.

MOTS CLÉS: Rascasses volantes ,espèce invasion, *Pterois*

### **INTRODUCTION**

The lionfish invasion in the Northwestern Atlantic and the Caribbean represents one of the most rapid marine finfish invasions in history. Despite being a popular member of the marine ornamental aquarium trade, little

was known regarding the biology and ecology of these lionfishes prior to this invasion. Information on lionfish abundance, dietary habits, predators, and seasonality of reproduction are scarce. Most of what has been published on lionfish relates largely to lionfish envenomations, which

commonly occur during aquarium husbandry or as a result of poor handling by home aquarists.

Invasive lionfish are a concern to coastal managers due to their potential threat on fisheries resources, native fish communities, and human health. Since 2000, National Oceanic and Atmospheric Administration (NOAA) researchers have partnered with non-governmental organizations, academics, and other federal and state agencies to develop a programmatic response to the lionfish invasion. The following provides a synopsis of information on the biology and ecology of the invasive lionfishes that have invaded the Northwestern Atlantic and Caribbean, and a discussion of future research needs and management options.

### Invasion Chronology

Many non-native marine ornamental fishes have been reported along the U.S. East Coast, with a “hotspot” of introductions occurring in South Florida (Semmens *et al.* 2004). Lionfish have been documented off Palm Beach, Boca Raton, and Miami, Florida beginning in 1992; and Bermuda, North Carolina, South Carolina and Georgia beginning in 2000 (Hare and Whitfield 2003, REEF 2008, USGS 2008, Whitfield *et al.* 2002). Since 2004, lionfish have become widespread in the Bahamas (REEF 2008, USGS 2008, Whitfield *et al.* 2007). More recently, lionfish were reported in the Turks and Caicos and Cuba (Chevalier *et al.* 2008) in 2007, and in the Cayman Islands, Jamaica, Dominican Republic (Guerrero and Franco 2008), U.S. Virgin Islands, Belize, and Barbados in 2008 (REEF 2008, USGS 2008). Juvenile lionfishes have also been reported along the U.S. northeast coast including Virginia, New York, Rhode Island, and Massachusetts since 2001. These northeastern specimens are incapable, however, of overwintering due to thermal intolerance (Kimball *et al.* 2004), and they are not considered established.

It is nearly impossible to determine which introduction event(s) allowed lionfish to become established. Research on the genetic variation of the lionfish populations is providing insight into the minimum number of lionfish and the geographic origin of founder population(s) (Hamner *et al.* 2007). Interestingly, this is not the first documented invasion of *Pterois* sp. as Golani and Sonin (1992) reported a Mediterranean invasion of *P. miles* from the Indian Ocean via the Suez Canal.

### Taxonomy

*Pterois miles* and *P. volitans* are morphologically similar and distinguishable in their native range by meristics, with *P. volitans* exhibiting one higher count of dorsal and anal fin rays when compared to *P. miles*. This difference was documented by Schultz (1986) who reported that *P. miles* is found in the Red Sea, Persian Gulf, and Indian Ocean (excluding Western Australia) and *P. volitans* is found in the Western and Central Pacific and Western Australia. Kochzius *et al.* (2003) used mitochon-

drial DNA analyses to show that specimens identified as *P. miles* and *P. volitans* were genetically distinct. Their geographic sampling did not allow the determination of whether this distinction was at the species or population level. Hamner *et al.* (2007) analyzed specimens identified as *P. miles* and *P. volitans* from additional areas of their native range, including Indonesia, where they are sympatric. They found that the two taxa are clearly distinct supporting the designation of two species. Analyses with different molecular markers and additional geographic samples of species in *Pterois* and the out-group comparison with the closely related genus *Dendrochirus*, support the classification of *P. miles* and *P. volitans* as separate species. Recent efforts by Hamner *et al.* (2007) have confirmed that:

- i) Both *P. miles* and *P. volitans* were introduced along the U.S. East Coast,
- ii) *P. volitans* comprises approximately 93% of the population, and
- iii) A strong founder effect (*i.e.* low genetic diversity) is evident among Atlantic specimens.

The genetic structure of invasive lionfish in the Caribbean is presently unknown. Only one species (*P. volitans*) has been confirmed along the Bahamian archipelago. Documentation of genetic change and adaptation of lionfish populations in their invaded range is warranted (*e.g.*, Morris and Freshwater 2008). Greater understanding of lionfish genetics could assist with validation of reef fish dispersal and connectivity models in the Northwestern Atlantic, Caribbean, and Gulf of Mexico.

### Local Abundance

Whitfield *et al.* (2007) provided the first assessment of lionfish densities off North Carolina and reported an average of 21 lionfish per hectare across 17 locations in 2004. Lionfish densities off North Carolina have continued to increase. Recent assessments off New Providence, Bahamas indicate lionfish densities are more than 18 times higher than the 2004 North Carolina estimates (Green and Côté 2008). The cryptic nature of lionfish make them difficult to census. It is likely that estimates of lionfish on complex coral reef habitats under-represent local abundance of juveniles. Thus, these density estimates should be considered conservative. Further, lionfish densities in the Bahamas are more than eight times higher than estimates from their native range (Green and Côté 2008). Few published data are available, however, from the Indo-Pacific region providing high uncertainty for this comparison. In their invaded Atlantic and Caribbean ranges, it is unclear when lionfish densities will reach carrying capacity. Given that many reef fishes along the east coast of the U.S. and Caribbean are overfished (Hare and Whitfield 2003), lionfish might be utilizing vacated niche attributes such as increased availability of forage fishes and reef space.

Monitoring of lionfish densities across habitat types using standardized indices of abundance is needed to determine when lionfish abundances reach carrying capacity. Lionfish densities are expected to vary depending on such factors as seasonality, local recruitment, local niche availability, and fishing pressure. Studies assessing the drivers controlling lionfish densities in specific habitats are needed to support lionfish control measures and to identify potential pathways for new invaders.

### Reproduction

The Pteroinae, including *P. miles* and *P. volitans*, are gonochoristic; males and females exhibit minor sexual dimorphism only during reproduction (see Fishelson 1975). Lionfish courtship has been well described by Fishelson (1975) who provided a detailed description for the pigmy lionfish, *Dendrochirus brachypterus*, and reported similar courtship behaviors for *Pterois* sp. According to Fishelson, lionfish courtship, which includes circling, side winding, following, and leading, begins shortly before dark and extends well into nighttime hours. Following the courtship phase, the female releases two buoyant egg masses that are fertilized by the male and ascend to the surface. The eggs and later embryos are bound in adhesive mucus that disintegrates within a few days, after which the embryos and/or larvae become free floating.

*P. miles* and *P. volitans* ovarian morphology is similar to that reported for *D. brachypterus* (Fishelson 1978) in that these fishes exhibit cystovarian type ovaries (Hoar 1957) with oocytes developing on stalks or peduncles. The oocytes are terminally positioned near the ovary wall, which secretes the encompassing mucus shortly before spawning. The seasonality of lionfish reproduction throughout their native range is unknown. Invasive lionfish collected off North Carolina and in the Bahamas suggests that lionfish are reproducing during all seasons of the year.

### Early Life History and Dispersal

Larval stage descriptions for *P. miles* and *P. volitans* are incomplete with only one report by Imamura and Yabe (1996) describing five *P. volitans* larvae collected off northwestern Australia. Scorpaenid larvae exhibit two morphologically distinct groups characterized as “morph A” and “morph B” by Leis and Rennis (2000). Pteroinae larvae are grouped among the “morph B” morphotypes, whose traits include: large head, relatively long and triangular snout, long and serrated head spines, robust pelvic spine, and pigment confined to the pectoral fins (Leis and Rennis 2000) and postanal ventral and dorsal midlines (Washington *et al.* 1984). *Pterois* sp. meristic characters are reported as 12 - 13 dorsal spines, 9 - 12 dorsal rays, three anal spines, 5 - 8 anal rays, 12 - 18 pectoral rays, one pelvic spine, five pelvic rays, and 24 vertebrae (Imamura and Yabe 1996; Leis and Rennis 2000).

The size of *P. miles* or *P. volitans* larvae at hatching is unmeasured, but is likely to be approximately 1.5 mm based on reports for *P. lunulata* (Mito and Uchida 1958; Mito 1963). The specific planktonic larval duration of lionfish is also unknown, although Hare and Whitfield (2003) estimated it to be between 25 to 40 days based estimates for *Scorpaena* (Laidig and Sakuma 1998).

Dispersal of lionfish presumably occurs during the pelagic larval phase during which larvae can be dispersed across great distances. For example, lionfish eggs released in the Bahamas are capable of dispersing to New England via the Gulf Stream. Larval connectivity models for reef fishes (*e.g.*, Cowen *et al.* 2006) provide insight into lionfish larval dispersal and are valuable for predicting the spread of lionfish as evidenced by the recent establishment of lionfish in the Caribbean. Further lionfish dispersal into the lower Caribbean and the Gulf of Mexico seems imminent. Assuming a planktonic larval duration of 25 to 40 days (Hare and Whitfield 2003), the Caribbean and Yucatan currents are capable of dispersing lionfish larvae into the Gulf of Mexico from locations in the Caribbean where lionfish are already resident (*i.e.*, Cuba, Jamaica, Cayman Islands) (Cowen *et al.* 2006). Based on the rapidity of lionfish establishment along the U.S. East Coast and the Bahamas, lionfish establishment along the southern edges of Central America (Nicaragua, Costa Rica, and Panama), the Yucatan peninsula, and the western Gulf of Mexico is likely within a few years or less. Establishment would also be facilitated by gyres such as the Columbia-Panama Gyre and the Gulf of Mexico loop current, which could provide a mechanism for lionfish to become established in the Florida Keys.

### Venomology

Lionfish are venomous with their spines containing apocrine-type venom glands. Each spine of the lionfish (except caudal spines) is venomous including 13 dorsal spines, three anal spines, and two pelvic spines. The spines are encased in an integumentary sheath or skin and contain two grooves of glandular epithelium that comprises the venom producing tissue. Spine glandular tissue extends approximately three quarters the distance from the base of the spine towards the tip (Halstead *et al.* 1955).

Lionfish envenomation occurs when the spine's integumentary sheath is depressed as it enters the victim. This process tears the glandular tissue allowing the venom to diffuse into the puncture wound (Saunders and Taylor 1959). The toxin in lionfish venom contains acetylcholine and a neurotoxin that affects neuromuscular transmission (Cohen and Olek 1989). Lionfish venom has been found to cause cardiovascular, neuromuscular, and cytolytic effects ranging from mild reactions such as swelling to extreme pain and paralysis in upper and lower extremities (Kizer *et al.* 1985). Antivenom of the related stonefish (*Synanceia* spp.) is highly effective in neutralizing lionfish venom activity (Shiomi *et al.* 1989, Church and Hodgson 2002).

The severity of sting reactions in humans is dependent upon such factors as the amount of venom delivered, the immune system of the victim, and the location of the sting. Records of home aquarists stung by lionfish provide a comprehensive assessment of how lionfish stings affect humans (Kizer *et al.* 1985, Vetrano *et al.* 2002). The probability of lionfish envenomation is higher when handling smaller-sized lionfish because the venom glandular tissue is closer to the tip of the spine (Halstead *et al.* 1955).

The effectiveness of lionfish venom defense in their invaded range is in question. Maljković *et al.* (2008) reported that lionfish were found in the stomachs of groupers; however, this observation provides no assessment of the frequency of lionfish consumption by grouper. Furthermore, laboratory behavioral experiments suggest that groupers actively avoid lionfish, even during periods of extreme starvation. Additional research is needed towards understanding predatory interactions between lionfish and native predators.

Work by Sri Balasubashini *et al.* (2006a, 2006b) indicated that lionfish (*P. volitans*) venom contains antitumor, hepatoprotective, and antimetastatic effects in mice suggesting a promising application for cancer research. Depending on the outcome of this research and the subsequent demand for lionfish venom, bioprospecting of venom from invasive lionfish could assist with fishery development.

### Feeding Ecology

In the Red Sea, lionfish (*P. miles*) have been reported to feed on assorted taxa of benthic fishes including damselfish, cardinal fish, and anthias (Fishelson 1975, Fishelson 1997). However, in the Pacific Ocean, *P. lunulata* were observed to feed primarily on invertebrates including penaeid and mysid shrimps (Matsumiya *et al.* 1980, Williams and Williams 1986). Assessments of invasive lionfish feeding suggests that lionfish are largely piscivorous, but also feed on a number of crustaceans. The particular taxa of highest importance in invasive lionfish diet will likely vary by habitat type and prey availability.

Feeding, growth, and starvation of *P. volitans* from the Red Sea was investigated by Fishelson (1997) who reported that lionfish stomachs can expand over 30 times in volume after consuming a large meal. This capability supported Fishelson's hypothesis that lionfish were capable of longterm fasting, and demonstrated their ability to withstand starvation for periods of over 12 weeks without mortality. Fishelson (1997) also measured daily consumption rates in the laboratory for six size classes of lionfish ranging from 30 - 300g and found that lionfish consumed approximately 2.5 - 6.0% of their body weight per day at 25 - 26 °C. Preliminary observations suggest that lionfish in their invaded range can consume piscine prey at rates greater than reported earlier by Fishelson (1997). Quantification of the feeding ecology of lionfish including

consumption rates and prey selectivity will permit better assessment of the impacts of their predation on local reef fish communities.

### Parasitology

Knowledge of the parasites infecting native and non-native lionfish is scant. No comprehensive survey of protozoan or metazoan parasites of either host (*P. miles* or *P. volitans*) has been published. There are, however, a few isolated records of single parasite species such as monogeneans from the Red Sea (Paperna 1972, Colorni and Diamant 2005) and Japan (Ogawa *et al.* 1995), copepods also from Japan (Dojiri and Ho 1988), and leeches from Japan (Paperna 1976) and the Florida coast (Ruiz-Carus *et al.* 2006). Most published records of lionfish parasites are of ectoparasites; the only record of an endoparasite is of a new myxosporean species, *Sphaeromyxa zaharoni* which was found in a lionfish gall bladder from the Red Sea (Diamant *et al.* 2004). Recent observations of invasive lionfish collected off North Carolina and in the Bahamas have found low prevalence of endo- and ectoparasites when compared to parasites of native reef fishes. Future research describing parasites of invasive lionfish will provide a unique study of opportunistic parasitism by common parasites of marine reef fishes.

### Potential Impacts

Potential ecological impacts of lionfish on local reef fish communities will vary depending on the abundance of top level predators, the forage fish community, the density of lionfish, and the geographic location. Local studies that provide observations of lionfish impacts on community structure and the abundance of forage fishes are needed. The first evidence of lionfish impacts in their new range was provided by Albins and Hixon (2008) who reported a 79% reduction in forage fish recruitment on experimental patch reefs in the Bahamas during a five week observation period. Analysis of the potential impact of lionfish consumption on whole coral reef fish communities is also being documented in the Bahamas, where data on stomach contents are being combined with abundance estimates of the prey community across various habitat types and seasons. Given the high levels of lionfish biomass found at some locations (Whitfield *et al.* 2007), the predatory removal of forage fishes is a growing concern, because many other top level predators (i.e., potential food competitors with lionfish) are overfished or in low abundance (Hare and Whitfield 2003).

It is unclear if lionfish predation on economically important species such as juvenile serranids will harm stock rebuilding efforts. Economically important species were relatively low in importance in the lionfish diet of the Bahamas, but this could be a direct result of their low abundance in the forage fish community. Research that monitors lionfish predation on economically important species is needed.

Lionfish impacts on tourist recreational activities have been observed. Some locations have posted warning signs advising of the potential for lionfish envenomation. As lionfish densities increase, so too does the risk of envenomations. It is unknown whether increasing lionfish densities will reduce recreational activities and cause economic hardship. This will be dependent on factors such as the prevalence of warning signs, the density of lionfish, and the effectiveness of education and outreach.

### Control and Management

Management of marine finfish invasions are confounded by highly diverse and wide-ranging habitats, swift ocean currents, and jurisdictional constraints. Prevention is the least expensive and most effective management option. There are currently two lionfish management and control efforts in Bermuda and the Bahamas. Bermuda initiated a lionfish culling program in 2006 that included a training program, collecting license, and a special dive flag allowing commercial and recreational fishers to spear lionfish along nearshore reefs. A video description of this program can be seen at <http://www.youtube.com/watch?v=LNbKjiUCGRU>. Bahamian fisheries officials instituted a lionfish kill order to fishermen in 2005. They have also actively engaged the public with educational seminars devoted to promoting lionfish as a food fish with the hopes that human consumption will support fishery development. Grassroots, "adopt a reef programs", are being developed in Eleuthra (see [www.lionfishhunter.com](http://www.lionfishhunter.com)) that encourage local citizens to take ownership of small reefs and to protect them from lionfish impacts. Some tourist locations, such as resorts, are physically removing lionfish by spearfishing and handnets to reduce the risk of swimmer interaction. It is unclear how effective these approaches will be, because too little is known about the rate of lionfish recruitment and movement among the various habitat types. Recently, NOAA researchers have developed techniques to trap lionfish, thus providing a means of removal from deeper waters and larger areas that are impractical for diver removal.

### CONCLUSIONS

The lionfish introduction provides a reminder of how rapid a non-native species can become established and potentially compete with native fishes for resources. Early detection and rapid response efforts are of utmost importance in the marine environment due to the complexity and ineffectiveness of eradication measures. An early detection and rapid response program has been developed in south Florida (a hotspot for marine introductions), which utilizes and coordinates resources from over thirty state, federal, and non-governmental organizations in the region. Programs such as this represent the first line of defense for marine introductions and should be endorsed and supported by local managers. Future research on invasive lionfish should focus on understanding and reducing their ecologi-

cal impacts, the scale of which is yet to be determined.

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