

4-1-2014

Evidence of the Enemy Release Hypothesis: Parasites of the Lionfish Complex (*Pterios volitans* and *P. miles*) in the Western North Atlantic, Gulf of Mexico, and Caribbean Sea

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Nova Southeastern University Oceanographic Center

Evidence of the Enemy Release Hypothesis: Parasites of the Lionfish
Complex (*Pterios volitans* and *P. miles*) in the Western North Atlantic,
Gulf of Mexico, and Caribbean Sea

By

Kayelyn Regina Simmons

Submitted to the faculty of the
Nova Southeastern University Oceanographic Center
in partial fulfillment of the requirements for the degree of
Master of Science with a specialty in:

Marine Biology

April 2014

Abstract

Invasive species are becoming more common as human interactions within coastal waters and the aquarium trade continues to increase. The establishment of the invasive lionfish complex *Pterois volitans* and *P. miles* from the Indo-Pacific to the Western Atlantic, Gulf of Mexico, and the Caribbean Sea has had significant negative effects on reef fish biodiversity and economically important species. Their rapid colonization and success has been attributed to their biological and ecological life history traits as well as their absence of predation. Past research has highlighted these characteristics; however, there is a knowledge gap in lionfish parasitism. This research explored the enemy release hypothesis as a key success factor in rapid establishment in the invaded range on a biogeographical scale. The diversity of lionfish parasitism was compared among 15 geographically diverse sites within the invaded range, incorporating the time of introduction at each site. Eight new parasites are described for the first time in the invasive lionfish: (1) a Cymothoid isopod: *Rocinela stignata*, (2) four nematodes: *Raphidascais* sp., *Contraceacum* sp., *Paracuria adunca* and *Hysterothylaceum* sp., (3) one digenean: *Tergestia* sp., (4) two acanthocephalans: *Serracentis* sp. and *Dollfusentis* sp., and (5) two cestodes: *Nybelinia* sp. and *Tentacularia* sp. Lionfish from the east coast of Florida exhibited the highest abundance in parasite fauna while other invaded areas yielded low abundance and diversity. Comparisons between lionfish parasitism from the past native range studies and the invaded range suggest that vectors of time, life history traits, and trophic interactions structure the lionfish parasite community. Lionfish in the Western Atlantic and Caribbean were found to be host for generalists parasite species within the coastal ecosystem. Consequently, lionfish have relatively low parasite abundance, supporting the enemy release hypothesis and its direct relation to their invasion success.

Key words: lionfish, endoparasite, biogeography, invasive species, enemy release

Acknowledgments

I would like to express my deepest appreciation to the Nova Southeastern University Presidential Faculty Research and Development Grant (PFRDG) for providing funding for this research. I would like to especially thank my main advisor Dr. David Kerstetter, co-advisor and lead parasitologist Dr. Chris Blonar, and thesis committee member Dr. Bernhard Riegl. My greatest appreciation goes out to all whom were involved with the following non-profit agencies, institutions, fishing charters, and the avid recreational dive community who helped in collection: NSU Fisheries Research Laboratory, NSU Farquhar College of Arts and Sciences, Florida Keys National Marine Sanctuary, Biscayne National Park, Reef Environmental Educational Foundation (REEF), Bermuda Natural History Museum, Atlantis Charters; Beaufort, NOAA NMFS Mississippi Marine Laboratory, Flower Garden Banks National Marine Sanctuary via Permit# 2009-001, Bimini Biological Field Station Tournament, Discovery Bay Marine Lab & Field Station -University of West Indies, University of Puerto Rico & PRExtreme Dive Shop, Turks & Caicos Reef Fund, Caribbean Oceanic Restoration and Education (CORE) Foundation, Eco-Mar Belize, Panama Divers & Octopus Garden, Council on International Educational Exchange (CIEE) Research Stations Bonaire, and Barbados Blue Water Sports. It was an awe-inspiring experience to witness all the dedication and hard work of every institution, organization, and divers coming together to make a positive change in their coral reef communities.

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Introduction

Invasive species are becoming an increasingly common threat to coastal communities globally. The success of invasive species in a new ecosystem generally stems from the lack of predation and reduced ecological or biological constraints that shape the density, range, and ecological niche of the species in its native environment (Minchella & Scott, 1991; Cohen & Carlton, 1998; Ruiz *et al.*, 2000; Torchin *et al.*, 2005). Optimum prey availability coupled with low predation in ideal environmental conditions can enhance the overall fitness of the invader (Torchin *et al.*, 2003; Sax *et al.*, 2007) resulting in their ability to outcompete trophically similar native species. The expansion and establishment of lionfish complex *Pterois volitans* (Linnaeus, 1758) and *Pterois miles* (Bennett, 1828) across the Western Atlantic, Caribbean, and Gulf of Mexico has been one of the most ecologically damaging marine invasions recorded (Albins & Hixon, 2011). The lionfish invasion has had direct and indirect effects on reef ecosystems, fisheries, and the recreational dive community. Removal efforts have included derbies at recreational diver tournaments and the development of a commercial lionfish fishery. These removal efforts appear to only reduce local populations (Barbour *et al.*, 2011) and such citizen-based efforts have not been yet thoroughly evaluated for their effectiveness on population suppression (Biggs & Olden, 2011). Submersibles have observed lionfish populations below the recreational dive limit, indicating that removal efforts only target a small percentage of total lionfish populations.

One of the intriguing possible explanations for the speed of lionfish establishment is the enemy release hypothesis (ERH), which theorizes that non-indigenous species thrive in new habitats due to the scarcity of natural enemies compared to their native range (Keane & Crawley, 2002; Torchin *et al.*, 2001 and 2002; Mitchell & Power, 2003). The "enemies" in ERH are generally predators such as larger fishes and marine mammals. Parasites are often overlooked as a potential

ecological enemy even though they can clearly cause detrimental effects on their host populations. “Parasitic release” results when a non-native species experiences a competitive advantage over a native species because of a relative lack of parasitism. Several studies have found that invasive species have fewer parasites in their expanded range relative, as they leave behind their "native" parasites (Torchin & Mitchell, 2004) and are slow to be invaded by the pool of available parasites in the expanded range. Differences in host susceptibility, time of introduction, vector introduction (i.e., ballast water or aquarium trade), taxonomic isolation, and distance from native range all contribute to decreased parasite diversity and abundance in invasives (Blakeslee *et al.*, 2009). However, the advantage of parasite release is often temporary since the native parasites eventually adapt to infect the non-native species as well (e.g., see Gendron *et al.*, 2012).

Lionfish were likely initially introduced to the Caribbean and western North Atlantic via the accidental or incidental release of aquarium fish (Hare & Whitfield, 2003; Whitfield *et al.*, 2002; Courtenay, 1995; Morris *et al.*, 2009; Ruiz-Carus *et al.*, 2006). Molecular studies suggest that the present population is the result of either a “single release event” of a small group or a “multiple release” scenario of limited numbers of individuals; in either scenario, the limited number of introduced individuals has resulted in a relatively low genetic diversity within the western North Atlantic lionfish population (Hamner *et al.*, 2007; Betancur-R *et al.*, 2011). The small number of individuals released also reduced the probability of introducing native parasites along with their host. Furthermore, the source of the lionfish was the aquarium trade; such fish are frequently treated with antiparasitics, and are unlikely to be transferred with additional hosts required to complete complex parasite life cycles (Torchin *et al.*, 2003).

Parasitism is a form of symbiosis in which one partner (the *parasite*) extracts some resource from another (the *host*), thereby causing it some degree of harm. As a life-history strategy, parasitism is highly successful and has been adopted broadly across all taxonomic groups, from bacteria to vertebrates. There are two main types of

parasites: endoparasites (live/feed within host) and ectoparasites (live/feed on the outside surface of host). Common parasites found among marine organisms include nematodes, digeneans, cestodes, acanthocephalans, monogeneans, and crustaceans. The characteristic life cycles of parasites, often requiring a variety of intermediate and determinate hosts, allow these organisms to interact with hosts at multiple trophic levels.

Many processes shape the distribution and abundance of parasites, including dispersal, competition, and predation (Thomas *et al.*, 2005; Poulin, 2007). However, parasite distribution and abundance are also affected by a number of unique processes and factors due to their interactions with their host (i.e., the body of another organism) and symbiotic dependence on at least one (and often several) species of hosts, each with their own ecological requirements and niches (Thomas *et al.*, 2005). Specifically, parasite intensity varies significantly over time depending on the availability of intermediate and final hosts, which may themselves be subject to seasonal or long-term climatic changes (MacKenzie, 1987; Palm, 2004). Overall parasite populations can also be subject to environmental changes that may affect their complex life history stages and cause host populations to either increase or decrease (Sasal *et al.*, 2007).

Few studies have examined the parasite fauna of lionfishes from their native ranges in the Red Sea and central Pacific (Paperna & Overstreet, 1981; Ali *et al.*, 2001,2003; Diamant *et al.*, 2004). In the Red Sea, about one-third of the 38 species of *Sphaeromyxa* (Lom, 2004), are parasitized by the myxozoan *Sphaeromyxa zaharoni* (Diamant *et al.*, 2004) known to infect the gall bladder. *S. zaharoni* parasitizes *P. miles* and other Scorpaeniformes fishes, although this parasite species has not been documented in the southeastern United States (Diamant *et al.*, 2004). A study in the Red Sea also observed the myxozoan *Ceratomyxa elegans* (Jameson, 1929) in one gallbladder of the black scorpionfish *Scorpaena porcus*, a species within the same family as lionfish (Ali *et al.*, 2006). The earliest description of ectoparasites found in lionfish occurred in surveys of marine fishes in the Indo-Pacific region, where the

copepods *Taeniacanthus miles* (Pillai, 1963) and *Acanthochondria* sp. (Leigh-Sharpe & Oakley, 1972) were found on *P. miles* (Dojiri & Cressy, 1987) and *P. volitans* (Dojiri & Ho, 1988), respectively. A leech *Trachelobdella lubrica* (Grube, 1840) was first described on *P. volitans* (Paperna, 1976) in Japan; this was also the first ectoparasite to be found on lionfish from the invaded range (Jacksonville, Florida (USA) in Ruiz-Carus *et al.*, 2006 renamed by Bullard *et al.*, 2011). During a re-description of several cultured marine species in Japan, *Benedenia epinepheli* (Yamaguti, 1937) Meserve, 1938 (Monogenea: Capsalidae) was found in *P. volitans* (Ogawa *et al.*, 1995). Five *P. volitans* captured in the Red Sea off the coast of Sharm El-Sheikh in South Sinai, Egypt were found to host the intestinal trematode *Proneohelicometa aegyptensis* (Ozaki, 1925) (Hassanine, 2006). In 2001, *P. miles* were found to host trichinoid ciliates co-infesting with the dactylogyrid monogenean *Haliotrema* sp. (Johnson & Tiegs, 1922) on the gills (Colorni & Diamant, 2005).

Initial comparisons of parasitism in their native range suggest that lionfish in the Western Atlantic and Caribbean have drastically different parasite communities. Several lionfish captured off the coast of Beaufort, North Carolina in 2011 were found to have adult *Lecithochirium floridense* (Manter, 1934; Crowcroft, 1946) (Digenea: Hemiuridae) parasitizing their stomachs (Bullard *et al.*, 2011). The most recent study investigating lionfish parasitism occurred in Bonaire and a single isopod *Excorallana* sp. (Stebbing, 1904) (Cymothoidae: Corallanidae) was found to parasitize the gills of a single lionfish (Poole, 2011). There have been several studies on comparing parasitism of introduced species in native versus introduced range(s) (Torchin & Mitchell, 2004; Blakeslee *et al.*, 2009); however, this type of study has not yet been conducted for the lionfish complex. The few available studies suggest that parasite diversity and abundance are low in invasive lionfishes; the resulting enemy release would be a direct advantage for them, especially given the relatively high prey availability and ideal environmental conditions (e.g., temperature, salinity) in the expanded range. In the significant absence of predators, parasite release may be

an alternative explanation for the rapid establishment of the lionfish complex within the Western North Atlantic, Gulf of Mexico, and Caribbean Sea waters.

Purpose and Objectives

This project explores the “enemy release hypothesis” and addresses whether the lack of parasitism in lionfish is an additional factor aiding in their successful establishment in the invaded range. This project fundamentally addresses the invasion on a wide geographic scale and leads to questions regarding whether international ecosystem-based strategies would effectively manage lionfish populations. There are three goals of this project: (1) to describe the endoparasite fauna of lionfish in the greater Caribbean region, (2) to compare endoparasite faunal diversity among locations in the greater Caribbean region, and (3) to use the dates of introduction and parasite community as a proxy for lionfish acclimatization rates into their invaded region.

Methods

Sample Collection

Lionfish host specimens were collected from several sources via partnering academic institutions, commercial/recreational dive shops, volunteer fishermen, and non-profit environmental organizations (Table 1). Lionfish collection methods utilized standard recreational diver spearing at depth in coral reef communities, except for a small number of individuals that were caught by hook-and-line off Fort Lauderdale. The primary source for lionfish from the South Florida area were collected from two research-only sites within the Florida Keys National Marine Sanctuary, Biscayne National Park, various recreational divers collecting lionfish throughout Monroe, Miami-Dade, Broward, and Palm Beach counties as part of lionfish removal programs fostered by local dive shops, Reef Environmental Educational Foundation (REEF), and Biscayne National Park. Recreational divers also collected lionfish opportunistically in the northern Florida Atlantic Coast (Jupiter, FL).

An email letter or message using social media networks such as Facebook were sent out to non-local (Caribbean and Gulf of Mexico) dive shops, diving charter operations, national marine parks, or government associations actively involved in lionfish removal efforts. As an incentive for participation and labor, a reward of US\$5.00 per lionfish was offered, as well as shipping costs. In some cases, coolers and freezer gel-packs were also provided. Lionfish specimens were frozen to 0°C by the participating group, then shipped overnight to ensure no further deterioration of samples. Once received, specimens were immediately processed, refrigerated (at *ca.* 4°C), or frozen to preserve any potential parasites.

For analytic purposes, each sample site was segregated into three general bioregions representing broad biological provinces: Gulf of Mexico (GOM), South Atlantic Bight (SAB), and the Caribbean (CAR).

Table 1: Lionfish collection sites and abbreviations.

Country	Collection Location	Source Institution/Organization	Abbreviation
Bahamas	Bimini	Bimini Biological Field Station Tournament	BIM
Barbados	Southern reef tract	Barbados Blue Water Sports	BAR
Belize	Belize Barrier reef	Eco-Mar Belize	BEL
Bermuda	Southern reefs	Bermuda Natural History Museum	BER
Bonaire	Southern reefs	Council on International Educational Exchange (CIEE) Research Stations Bonaire	BON
Jamaica	Southern shore	Discovery Bay Marine Lab & Field Station - University of West Indies	JAM
Turks & Caicos	Providenciales	Turks & Caicos Reef Fund	TCI
Panama	Atlantic Coast	Panama Divers & Octopus Garden	PAN=
United States	Beaufort, North Carolina	Atlantis Charters	NCA
	Palm Beach, Broward, Dade, and Monroe (Florida Keys) Counties, Florida	NSU Fisheries Research Laboratory, Florida Keys National Marine Sanctuary, Biscayne National Park, Reef Environmental Educational Foundation (REEF)	FEC
	Gulf Coast	NOAA NMFS Mississippi Marine Laboratory	GCC
	Jupiter and Fort Pierce, Florida	NOAA NMFS Mississippi Marine Laboratory, Recreational divers	FLJ
	Puerto Rico	University of Puerto Rico & PRExtreme Dive Shop	PRI
	Saint Thomas, USVI	Caribbean Oceanic Restoration and Education (CORE) Foundation	STT
	Flower Garden Bank, Texas	Flower Garden Banks National Marine Sanctuary (via NOAA permit # 2009-001)	TEX

Laboratory Processing

All lionfish were thawed, then weighed (± 0.1 g) and measured (± 1 cm) using both total and standard lengths. Dorsal and anal spine counts along with pectoral ray length (cm) and other length measurements were recorded for later morphometric analyses. The gills were removed and each gill arch was examined individually. The buccal cavity was rinsed, and the rinse examined for ectoparasites and food items. The eyes were removed, dissected (humour, retina, lens), and examined.

The body cavity was opened ventrally, and the sex of the fish recorded. The body cavity and surface of all internal organs (heart, liver, spleen, digestive tract, gonads, kidney, swim bladder) were examined individually for parasites. All internal organs (brains, dorsal musculature, stomach, intestines, etc.) were compressed between glass plates and examined for endoparasites

All helminthes (monogeneans, digeneans, cestodes, acanthocephalans) were initially removed from any encasing cyst or outer membranes and then transferred to a 95% ETOH solution. Parasites were fixed by a dehydration/rehydration process in a series of increasing ethanol solutions, then stained in acetocarmine and mounted on permanent slides for identification. Nematodes are cleared for 14 days in 70% ethanol with 5% glycerol, and were examined via temporary wet mounts or semi-permanent mounts in glycerine. Any annelid and arthropod ectoparasites were examined whole, unstained and preserved in 95% ETOH. Final identifications of all parasites were based on standard synthetic keys and primary literature from sources listed in Table 2. Key genus-specific structures (larval sheath, boring tooth, cecum tract, etc.) and parasite stages (i.e., adult vs. larval stages) were used identification.

Data Analysis

Dates of introduction for each site were derived from literature sources (Schofield, 2009; Morris *et al.*, 2009; Morris & Whitfield, 2009; Schofield, 2010), and the USGS Non-indigenous Aquatic Species Database (USGS, 2013).

Quantitative descriptor prevalence was used to analyze parasite populations

Table 2: Lionfish sample locations with the date of introduction, total lionfish sampled, length (standard) (cm), weight (grams), and sex ratio. Anecdotal dates of introduction are labeled with an asterisk (Schofield, 2009, 2010; Morris *et al.*, 2009; Morris & Whitfield, 2009; US Geological Survey, 2013). Note: collection location abbreviations are from Table 1.

Location	Year of First Sighting	n	Length Range (cm)	Weight Range (g)	Sex Ratio (F:M)
FEC	*1985, 1992	145	4.5-30.2	2.0-1009.4	14:15
NCA	2000	12	13.3-25.6	77.1-700.0	5:1
BER	2000	19	16.3-34.5	121.5-1400.0	1:12
FLJ	2001	50	12.4-31.0	49.3-800.0	1:1
BIM	2004	10	10.4-22.3	30.5-361.7	3:1
TCI	*2006, 2007	13	8.8-30.5	16.3-800.0	1:2
JAM	2008	20	12.2-26.7	41.0-700.0	14:5
BEL	2009	12	12.5-26.5	45.3-745.0	4:7
BON	2009	32	7.4-17.0	12.9-167.9	6:5
PAN	2009	21	8.8-25.1	19.0-573.2	3:4
PRI	2009	44	4.0-18.0	1.2-164.0	1:1
GCC	2010	55	9.5-29.0	17.1-470.0	1:1
STT	2010	40	12.7-27.7	59.9-800.0	1:2
BAR	2011	18	8.2 – 17.6	13.6-187.4	3:1
TEX	2012	25	11-23.6	36.9-583.2	13:6

according to ecological equations in Bush *et al.* (1997). Prevalence is calculated as the number of host infected with individuals of particular parasites taxa/species divided by the number host sampled and is commonly expressed as a percentage. Mean abundance is the total number of individuals of particular parasite taxa/species in a sample of an individual host divided by the total number of hosts sampled. Mean abundance is used instead of mean intensity because this method includes both infected and non-infected hosts.

Due to the low occurrence of parasites in the data set, “0” (null) values were a significant consideration in analyzing the population and community level data (see below). Due to the continuous reef tract, South Florida (i.e., the east coast of Florida from the Florida Keys through Palm Beach County) was considered a single sample site. SPSS univariate analysis was used to observe standard length (cm) and weight (g) distribution among sex at each sample site. Parasite infracommunity (all parasites of a given species within an individual host) composition was assessed using PRIMER-E (Clarke & Warwick, 2001). A graphical representation of infracommunity differences among lionfish from each site was generated by non-metric multidimensional scaling (NMDS) in PRIMER 6.1.13). The similarity matrix allowed for comparisons to be made between sites because each site was represented by a single point; distance among points was inversely proportional to infracommunity similarity, and the relative strength and direction of influence of most abundance parasite species was represented by vector (\cdot). The similarity matrix was based on a Bray-Curtis similarity matrix calculated from unstandardized, square-root transformed data (Blanar *et al.*, 2011).

Results

Collections

Samples from the Gulf Coast, Western Atlantic, and Caribbean were collected from participating sites as seen in Table 1. A total of 516 lionfish from the invaded range were collected with majority of lionfish caught from the Florida East Coast (USA) (n = 145) and the smallest sampled site was Bimini (Bahamas) (n = 10) (Figure 1). The most parasites found were from lionfish captured the Florida East Coast (n = 270) while the least parasites were found in lionfish from Texas (USA), Bonaire, and Barbados (n = 0). Table 3 shows host data for each site: date of first sighting, sample size, standard length range, weight range, and sex ratio.

As seen in the map as Figure 1, Florida East Coast lionfish possessed the largest sample size. Figure 2 shows the standard length (cm) distribution by each sample site, displaying outliers. Mean standard length is 16.95 cm. Florida East Coast lionfish represented size classes found amongst all sites. Bermuda had relatively large lionfish while Puerto Rico had relatively smaller lionfish. As fish length can also depend on sex and maturity. Even though size (length) at maturity is estimated for males at 10.0 cm TL and females at 17.5 cm TL (Morris, 2009; Barbour *et al.*, 2011), this study did not possess enough physiological data necessary to conduct a comprehensive adult versus juvenile analysis. Detectability of lionfish has been found to be dependent on size class, habitat complexity, and their cryptic behavior (Kulbicki *et al.*, 2012; Green *et al.*, 2013) influencing the efficiency of diver-based removal tactics (Ruttenberg *et al.*, 2012).

Parasites

Nematodes consisted of 51% of all the parasites found followed by Digenea of 26% (Figure 3). Other taxa observed were at lower compositions. The visceral cavity was the prime location of parasitism with nematodes being found in the muscular lining of the intestine, liver, and stomach, while digeneans were more localized in the

Figure 1: Lionfish sample sites. Graduated symbols indicate sample size (n). Green dots represent sites that are still to be processed, orange dots represent sites that are currently in collection, and red dots represent new target sites. Note that the large symbol in south Florida (USA) includes lionfish from the Florida Keys through Palm Beach County; similarly, the medium symbol off Louisiana (USA) includes Gulf of Mexico lionfish from Louisiana through Alabama.

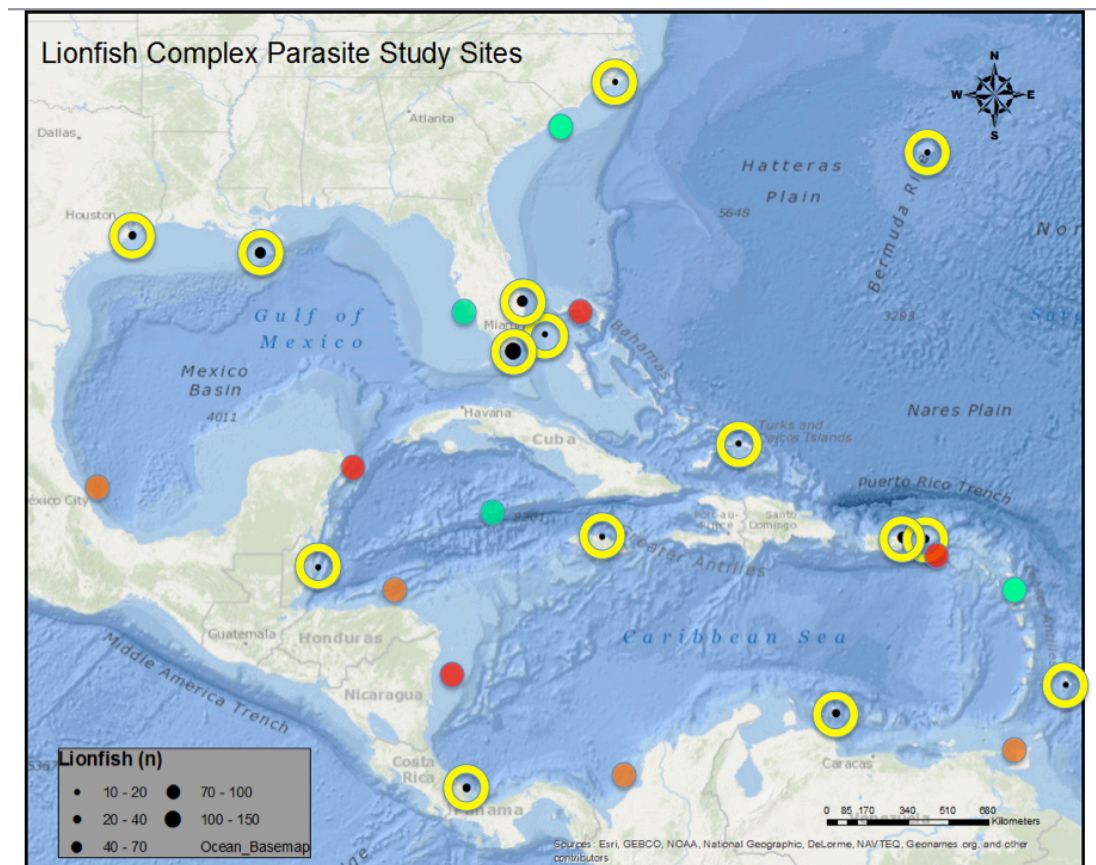


Table 3: Prevalence (%) and abundance data for each species/taxon at each site. New host descriptions are indicated with an asterisk. Note: collection location abbreviations are from Table 1.

		FEC	NCA	BER	FLJ	BIM	TCI	JAM	BEL	PAN	PCI	GCC	STT
<i>*Contracaecum sp.</i>	A	0.43	1.92	0.53	0.79	0.90	0.08	0.05	0.67	0.05	-	0.42	0.13
	%	13.10%	41.67%	10.53%	31.03%	40.00%	7.69%	5.00%	41.67%	4.76%	-	14.47%	7.50%
<i>*Raphidascaris sp.</i>	A	0.70	1.83	-	0.90	0.60	0.15	0.00	0.00	-	-	0.08	0.05
	%	13.79%	25.00%	-	27.59%	10.00%	7.69%	0.00%	0.00%	-	-	5.26%	5.00%
<i>*Paracuria adunca</i>	A	0.02	-	-	-	-	-	-	-	-	-	-	-
	%	2.07%	-	-	-	-	-	-	-	-	-	-	-
<i>*Hysterothylaceum sp.</i>	A	-	-	0.05	-	-	-	-	-	-	-	-	-
	%	-	-	5.26%	-	-	-	-	-	-	-	-	-
<i>Lecithochirium floridense</i>	A	0.59	-	-	0.90	-	0.08	0.10	3.83	-	-	-	0.25
	%	13.79%	-	-	31.03%	-	7.69%	5.00%	41.67%	-	-	-	10.00%
<i>*Tergestia sp.</i>	A	-	-	-	-	-	-	-	-	-	-	-	0.03
	%	-	-	-	-	-	-	-	-	-	-	-	2.50%
Unidentified sp.	A	-	-	-	0.07	-	-	-	-	-	-	0.08	-
	%	-	-	-	3.45%	-	-	-	-	-	-	1.32%	-
<i>*Nybelinia sp.</i>	A	0.03	-	0.11	-	-	-	-	0.33	-	-	-	-
	%	2.76%	-	5.26%	-	-	-	-	25.00%	-	-	-	-
<i>*Tentacularia sp.</i>	A	-	-	-	0.17	-	-	-	-	-	-	-	-
	%	-	-	-	10.34%	-	-	-	-	-	-	-	-

		FEC	NCA	BER	FLJ	BIM	TCI	JAM	BEL	PAN	PRI	GCC	STT
<i>Serrasentis sp.</i>	A	-	-	-	0.07	-	-	-	-	-	-	-	-
	%	-	-	-	6.90%	-	-	-	-	-	-	-	-
<i>Dollfustentis sp.</i>	A	0.07	-	4.42	-	-	-	-	-	-	0.05	-	-
	%	4.14%	-	26.32%	-	-	-	-	-	-	4.55%	-	-
Acanth 2 Illiosentis?	A	-	-	-	0.07	-	-	-	-	0.05	-	-	-
	%	-	-	-	6.90%	-	-	-	-	4.76%	-	-	-
Acanth 3 pointed	A	-	-	0.89	-	-	-	-	-	-	-	0.01	-
	%	-	-	10.53%	-	-	-	-	-	-	-	1.32%	-
<i>Trachelobdella lubrica</i>	A	0.01	-	-	0.10	-	-	0.05	-	-	-	0.03	-
	%	1.38%	-	-	6.90%	-	-	5.00%	-	0.-%	-	2.63%	-
<i>Rocinela stignata</i>	A	0.02	-	-	-	-	-	-	-	0.10	-	-	-
	%	1.38%	-	-	-	-	-	-	-	9.52%	-	-	-

Figure 2: Lionfish standard length (cm) distribution across all sample sites; length indicated by the y axis. Mean standard length for all lionfish in this study combined was 16.95 cm (indicated by the solid horizontal line). Note: collection location abbreviations are from Table 1.

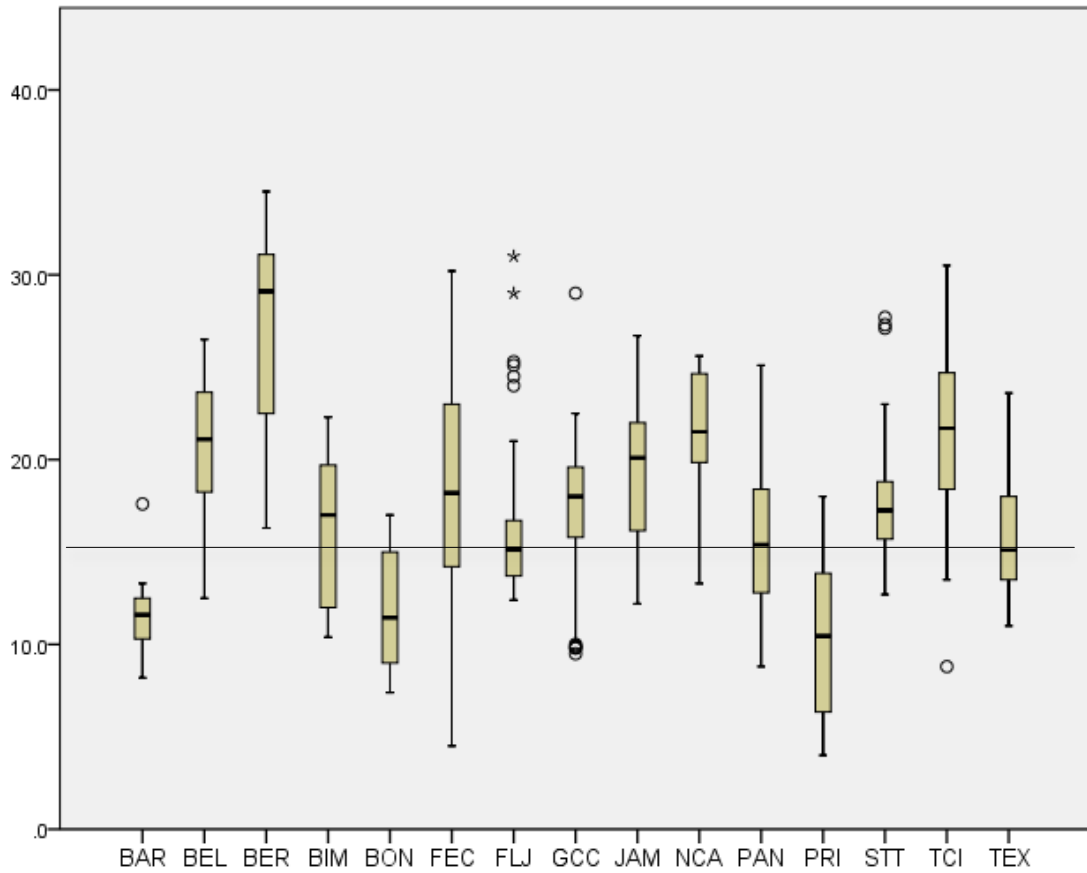


Figure 3: Lionfish complex total parasite fauna distribution, all sampled individuals combined, segregated according to taxonomic phylum. All lionfish collected from the wild from the western North Atlantic, Gulf of Mexico, and Caribbean Sea.

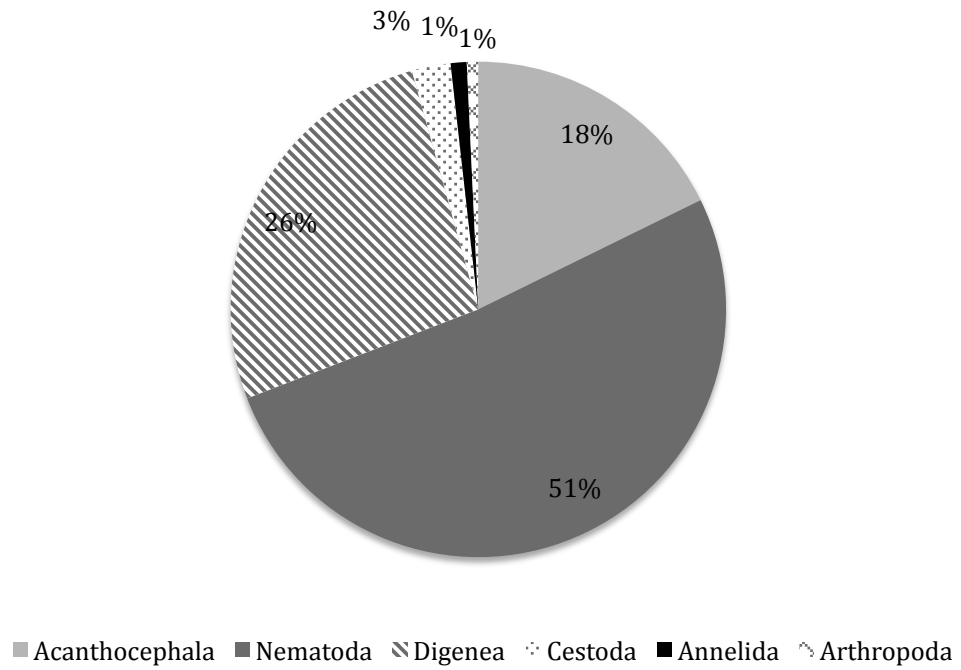


Figure 4: Lionfish parasite community distribution by taxa at each sample site. No parasites were found in any of the lionfish from BON, BAR, or TEX. Note: collection location abbreviations are from Table 1.

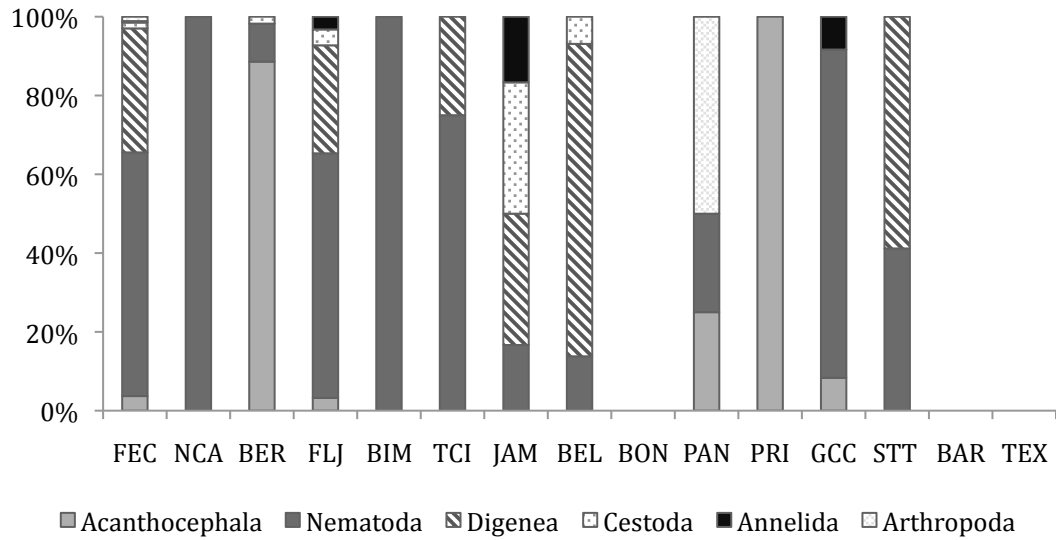


Table 4: Reference table for previously described parasite fauna in the invasive Indo-Pacific lionfish complex *P. volitans* and *P. miles* in both the native and invaded ranges.

Taxa	Family/Order	Parasite	Region	Host(s)	Publication(s)
Annelida: Hirudinea	Piscicolidae	<i>Trachelobdella lubrica</i> (Grube, 1840)	Japan	<i>P. volitans</i>	Paperna, 1976
Arthropoda: Copepoda	Chondracanthidae	<i>Acanthochondria</i> sp. (Leigh-Sharpe & Oakley, 1972)	Japan	<i>P. volitans</i>	Dojiri & Ho, 1988
Arthropoda: Copepoda	Poecilostomatoidea	<i>Taeniacanthus miles</i> (Pillai, 1963)	India	<i>P. miles</i>	Dojiri & Cressy, 1987; Tang et al., 2013
Monogenoids	Capsiladae	<i>Benedenia epinepheli</i> (Yamaguti, 1937)	Japan	<i>P. volitans</i>	Ogawa et al., 1995
Platyhelminthes: Monogenea	Dactylogyridean	<i>Haliotrema</i> sp. (Johnson & Tiegs, 1922)	Eilat, Israel	<i>P. miles</i>	Paperna, 1972; Colorni & Diamant, 2005
Protozoa: Ciliophora	Trichodinidae	Trichodinid ciliates	Eilat, Israel	<i>P. miles</i>	Paperna, 1972; Colorni & Diamant, 2006
Myxozoa	Spheromyxidae	<i>Sphaeromyxa zaharoni</i> (Diamant et al., 2004)	Red Sea	<i>P. miles</i>	Diamant et al., 2004
Trematoda	Opecolidae	<i>Proneohelicometra aegyptensis</i> (Ozaki, 1925)	Red Sea	<i>P. volitans</i>	Nagaty & Aal, 1962; Hassanine, 2006
Annelida: Hirudinea	Piscicolidae	<i>Trachelobdella lubrica</i> (Grube, 1840)	Jacksonville, Florida (USA)	<i>P. volitans</i>	Ruiz-Carus et al., 2006; Celik & Aydin, 2006
Digenea	Hemiruidae	<i>Lecithochirium floridense</i> (Manter, 1934)	Beaufort, North Carolina (USA)	<i>P. c.f. volitans</i>	Bullard et al., 2011
Arthropoda	Cymothoidae	<i>Excorallana</i> sp. (Stebbing, 1904)	Bonaire	<i>P. volitans & P. miles</i>	Poole, 2011

mucus of the stomach and intestinal fluids. Lionfish parasite distribution varied across sites geographically. Only two ectoparasites were observed in this study, both inhabiting the gills: the Cymothid isopod *Rocinela stagnata* (Schioedte & Meinert, 1879) and the marine leech previously described, *Trachelobdella lubrica* (Paperna, 1972 & 1976; Ruiz-Carus *et al.*, 2006, Bullard *et al.*, 2011). The lack of ectoparasites may be a consequence of shipping, freezing, or handling practices after capture.

Table 5 summarizes previously described parasites found in lionfish from the native and invaded range. Taxonomic and geographic distribution information for each newly described parasites found in this study is summarized in Table 4.

Parasite Community Analysis

The PERMANOVA/distances and centroids/ANOSIM analyses were used to indicate differences among community structure per site. A dummy variable was included to account for the high occurrence of significant zeros in the data set. The nonmetric multidimensional scaling (NMDS) plot in Figure 5 shows community similarities and their parasite species vectors. This test analyzes the variation within the data using distance matrices. Ellipses indicate site clustering at 5% and 20% distance (using CLUSTER groupings in PRIMER-E). Vectors indicated the relative contribution of individual parasite taxa to overall community similarity. The stress value of 0.04 indicated that differences in community structure was being adequately represented in two dimensions. The Caribbean sites related to both the SAB and GOM lionfish; however, the lionfish located closer in geography such to FEC formed a distinct group. Belize was another outlier driven by the dominance of *L. floridense* over Anisakids, and the high prevalence of *Dollfusentis* sp. caused Bermuda to be an outlier as well.

The ANOSIM analysis to test for significant differences across among all sites resulted in a Global-R 0.048 (relatively low) and $p = 0.967$ proving there was no significant difference in community structure among sites. Grouping the sites into bioregions and testing for regional differences resulted in a Global-R 0.069 and $p =$

0.014 indicating there were weak but significant differences on a regional scale. This value may have resulted from similarities among sites from which no parasites were collected. A distance matrix was generated using approximate GPS site coordinates in Geographic Distance Matrix Generator v1.2.3. The results give a Rho = 0.16, $p = 0.142$ showing there was no significant relationship between distance and parasite community structure. A linear regression model was used to show the influence of date of first sighting on the parasite taxa diversity (Figure 6). The results gave an $r^2 = 0.368$, $df = 1$, $F = 7.57$, and $p = 0.017$ indicating there was a significant positive relationship between time since first lionfish sighting and parasite diversity.

Table 5: Lionfish complex parasite fauna and geographic information. An asterisk marks new host descriptions derived from this study. Note: collection location abbreviations are from Table 1.

Taxa	Family	Parasite	Lionfish Location	Common Host	Geographic Distribution	Reference
Nematoda	Anisakidae	* <i>Contracaecum</i> sp. (Railliet & Henry, 1912)	BER, NCA, JFL, FPH, ALA, FEC BIM, TCI, JAM, STT, BEL, PAN, NCA, JFL, FPH,	invertebrates, freshwater and marine teleosts, seals, sea birds, dolphins	Worldwide	Semenova, 1979; Esinbarth, 2009; Kanarek & Bohdanowicz, 2009; Whitfield & Hegg, 1977; Anderson, 1992; Yamaguti, 1961
Nematoda	Anisakidae	* <i>Raphidascaris</i> sp. (Railliet & Henry, 1912)	FEC, BIM, TCI, STT	freshwater and marine teleosts	Worldwide Gulf of Mexico, Brazil, Kuwait, Japan, North America, Mediterranean	Moravec & Justine, 2012; Smith, 1984; Reger <i>et al.</i> , 1983; Rego <i>et al.</i> , 1983; Bicudo <i>et al.</i> , 2005; Tavares & Luque, 2006
Nematoda	Anisakidae	* <i>Hysterothylacium</i> sp. (Ward & Magath, 1917)	BER	freshwater and marine teleosts	North America, Mediterranean	Eiras & Rego, 1987; Petter & Sey, 1997; Yoshinaga <i>et al.</i> , 1989; Moser & Hsieh, 1992
Nematoda	Acuarioidae	* <i>Paracuria adunca</i> (Creplin, 1846)	FEC	piscivorous birds	Worldwide	Diaz <i>et al.</i> , 2004
Digenea	Hemiuridae	<i>Leithochirium floridense</i> (Manter, 1934)	JFL, FEC, TCI, JAM, STT, BEL	marine teleosts	Worldwide	Cribb <i>et al.</i> , 2002; Moravec <i>et al.</i> , 1997; Yeo & Spierler, 1980; Klimpel <i>et al.</i> , 2001; Salgado-Maldonado & Kennedy, 1997; Salgado-Maldonado <i>et al.</i> , 1997; Vidal-Martinez <i>et al.</i> , 2001; Parukhin, 1989; Bullard <i>et al.</i> , 2011
Digenea	Fellodistomidae	* <i>Tergestia</i> sp. (Stossich, 1887)	JFL, STT	marine teleosts	North Atlantic, Mediterranean	Bartoli <i>et al.</i> , 2003; Bray & Gibson, 1980; MacKenzie <i>et al.</i> , 2008
Acanthocephala	Rhadinorhynchidae	* <i>Serrasentis</i> sp. (Van Cleave, 1923)	JFL	crustaceans, marine teleosts, elasmobranchs	Brazil, Arabian Sea, Persian Gulf	Maghami <i>et al.</i> 2008; Fatima & Khan, 2005
Acanthocephala	Illiosentidae	<i>Dollfustentis</i> sp. (Golvan, 1969)	FEC, BER, PRI	teleosts, crustaceans	Subtropics of Atlantic Ocean	Amin, 1998
Cestoda	Trypanorhyncha	* <i>Nybelinia</i> sp. (Poche, 1926)	BER, FEC, BEL	elasmobranchs	Worldwide	Palm <i>et al.</i> , 1997
Cestoda	Trypanorhyncha	* <i>Tentacularia</i> sp. (Bosc, 1797)	JFL	elasmobranchs	Worldwide	Bray, 2013; Palm <i>et al.</i> , 2009
Annelida: Hirudinea	Piscicolidae	<i>Trachelobdella lubrica</i> (Grube, 1840)	JFL, FPH, ALA, FEC, JAM	marine teleost	circumtropical, Mediterranean, Europe, North Atlantic, Gulf of Mexico, Caribbean, Yucatan, eastern Pacific, West Indies	van der Land (2001); Hayward & Rylan (1990); MEDIN (2011); Worms (2013)
Arthropoda: Isopod	Cymothoidae	* <i>Rocinela stignata</i> (Schioedte & Meinert., 1879)	FEC PAN	marine teleost	Indies	Kensley & Schotte, 1989; Schotte <i>et al.</i> , 1995; 2009

Figure 5: Lionfish parasite community similarity matrix using nonmetric multidimensional scaling (NMDS) plot of sample sites. Individual sites are labeled as per Table 1 with a symbol indicating each site's bioregion. Note: collection location abbreviations are from Table 1.

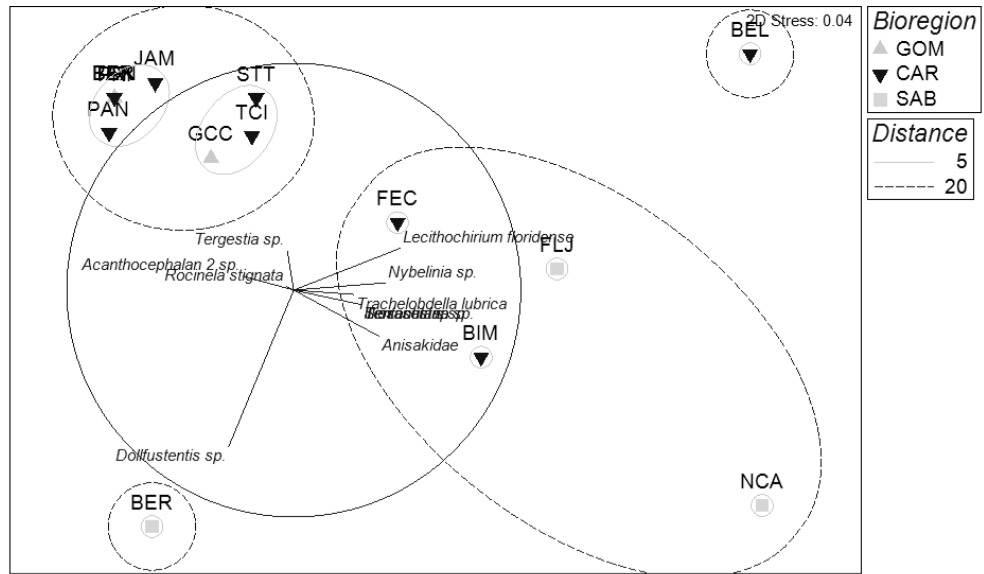
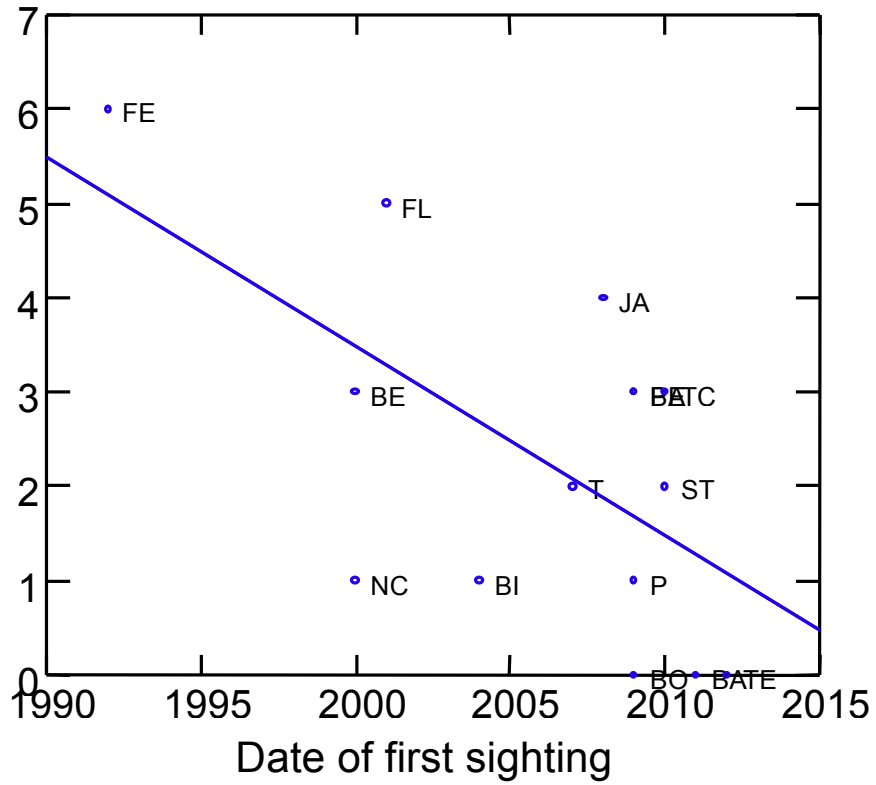


Figure 6: Linear regression model showing the correlation between the year of first sighting and parasite taxonomic diversity. $r^2 = 0.368$, $DF = 1$, $F = 7.57$, $p = 0.017$. Note: collection location abbreviations are from Table 1.



Discussion

Marine invasions have become a threat to coastal ecosystems globally by altering biodiversity, organism interactions, and community structure (Prenter *et al.*, 2004; Blakeslee *et al.*, 2013). Parasite host interactions in relation to non-indigenous species such as the lionfish may have indirect or direct effects on invasions success and competitive or predatory interactions with native species (Prenter *et al.*, 2004). This study shows that “parasite release” may have promoted rapid establishment of the lionfish complex in the Western Atlantic, Gulf of Mexico, and Caribbean. Past studies of lionfish parasitism in their native ranges are scarce and parasite faunal description is a research topic generally limited to their invaded range (Diamant *et al.*, 2004; Hassanine, 2006; Ruiz-Carus, 2006; Bullard *et al.*, 2011). Studies on the trophic ecology and feeding habits of lionfish in the native range are rare as well, possibly because native populations are stable and therefore non problematic. It is important to understand how lionfish are trophically interacting with other reef-associated species in all reef environments in order to understand their establishment across large spatial and temporal scales. Invasion success resulting from parasite release relates to the vector strength such as mode of introduction (i.e., live aquarium trade, canals, aquaculture, etc.), frequency, and specific host life stages (Ruiz *et al.*, 2000, Blakeslee *et al.*, 2013). Both host life stage and parasite life stage (i.e., propagules) are important in determining invasion success (Colautti *et al.*, 2006; Drake & Lodge, 2006; Grevar, 1999; Hopper & Roush, 1993; Kolar & Lodge, 2001; Miller *et al.*, 2007) because parasites tend to have an aggregated distribution causing some host to not be infected (Shaw *et al.*, 1998).

The family Anisakidae consists of intestinal roundworms that have complex life stages and is known to cause zoonosis in humans as a result of consumption of raw fish (Ruitenbergh *et al.*, 1979; Beaver *et al.*, 1984; Ishikura *et al.*, 1993; Yoshimura, 1998; McCarthy & Moore, 2000; Audicana & Kennedy, 2008; Kanarek & Bohdanowicz, 2009). Anisakid nematodes are cosmopolitan and generally use

teleosts as paratenic, intermediate, or definitive host (Anderson, 2000). The *Contracaecum* sp. life cycle has not been completely described, although adult stages are known to inhabit the digestive tract of definitive hosts such as pinnipeds, porpoises, piscivorous sea birds (Whitfield & Hegg, 1977; Eisenbarth, 2009; Kanarek & Bohdanowicz, 2009). First intermediate hosts include a broad range of marine invertebrates (Semenova, 1979; Eisenbarth, 2009; Kanarek & Bohdanowicz, 2009) and second intermediate (or paratenic) hosts continue the life cycle once the invertebrate or another infected fish host is ingested (Salati *et al.*, 2013). Similarly, the genus *Raphidiscaris* is known to infect the intestinal tract of marine fishes (Moravec & Justine, 2012). *Hysterothylacium* sp. are also well known generalists and the genera has been found in Brazil (Eiras & Rego, 1987), Kuwait (Petter & Sey, 1997), Japan (Yoshinaga *et al.*, 1989), and the United States (Moser & Hsieh, 1992). Other generalist species found include the Hemiurid digeneans that are known to infect the visceral cavity of marine teleost fishes (Cribb *et al.*, 2002; Moravec *et al.*, 1997; Yeo & Spieler, 1980; Klimpel *et al.*, 2001; Salgado-Maldonado & Kennedy, 1997; Salgado-Maldonado *et al.*, 1997; Vidal-Martínez *et al.*, 2001) including Scorpaeniformes that inhabit both geographic ranges (Parukhin, 1989; Bullard *et al.*, 2011). As *L. floridense* has been previously found in lionfish in North Carolina (Bullard *et al.*, 2011), *L. floridense* was found in regions that are spatially distant from the SAB region such as Belize, Turks & Caicos, Jamaica, and St. Thomas (USVI). It is very likely that *L. floridense* has adapted to lionfish being a host within its life history stage. The genus *Tergestia* sp. has eight described species within teleost hosts in the northeast Atlantic (Bray & Gibson, 1980; MacKenzie *et al.*, 2008) and is commonly found Mediterranean species (Bartoli *et al.*, 2003).

Some parasites are generalists during their larval stages, infecting mainly invertebrates, while the later stages of maturity may only be found in higher trophic level organisms. *Nybelinia* sp. and *Tentacularia* sp. were both found in the adult stage and are known to have intermediate fish hosts and a definitive elasmobranch host (Palm *et al.*, 2009). *P. adunca* was found in the larval stage and is known to have

seabirds as the definitive host (Diaz *et al.*, 2004), thereby demonstrating that parasites are transmitted via ingestion. Each parasite stage found within an organism reflects its position in the trophic web. The ecological niche lionfish have in the invaded range has allowed them to at high trophic levels. As a host that has a diet similar to higher trophic level predators, lionfish could alternatively be considered a “reservoir host,” i.e., a host in which the parasite can survive and reproduce, but the species is not the normal host (Criscione *et al.*, 2005).

The majority of the endoparasites found in the lionfish were in their larval stages demonstrating that lionfish are acting as mesopredators and intermediate vectors in parasite transmission. As generalist feeders, lionfish could be considered a paratenic host and vector for generalist or host-specific parasites. The ontogenetic shift in diet (invertebrates to primarily teleost) may alter parasite-host interactions relating to the low abundance of parasites and the presence of larval stage endoparasites. Acanthocephalans have a complex life cycle in which the primary and intermediate arthropod (Maghami *et al.*, 2008) host ingests eggs, which are then transferred to a definitive host by predator ingestion. Acanthocephalans have a vertebrate definitive host, and for some species, the use of a paratenic host is required for a complete life cycle (Amin *et al.*, 1984; Nikishin, 2001; Santos *et al.*, 2005). The paratenic host acts as a facultative vector that can be interpolated into the parasite life cycle through the food web (Kennedy, 2012). The acanthocephalan genus *Serracentis* is distinct because of its truncated comb-like spines (Yamaguti, 1963), and its presence in Jupiter, FL may indicate that lionfish are capable of being both a paratenic host and intermediate host in complex parasite life stages. Furthermore, endoparasite life cycles can be indicators of trophic webs within in an ecosystem depending on host diversity (intermediate or definitive) (Bellay *et al.*, 2011).

The presence of ectoparasites inhabiting lionfish was extremely low compared to other marine teleosts. *T. lubrica*, which has been previously described in lionfish both in the invaded and native ranges, was present in the specimens from the Florida East Coast, the Gulf Coast region, and Jamaica. This parasite species is known to

inhabit warm, tropical seas (Sağlam *et al.*, 2003) and commonly found parasitizing the gills, fins, and body of Serranids, Priacanthids, Perciformes, and other tropical marine families (Sawyer, 1986; Williams *et al.*, 1994). These fishes are highly abundant in coral reef habitats and are potential prey items for lionfish. *R. stignata* is also found in nearshore, subtropical waters in the western Atlantic (Kensley & Schotte, 1989; Schotte *et al.*, 2009) and has been recorded in marine teleosts from the Pacific region (Schotte *et al.*, 1995). The previously found Cymothoid isopod *Excorallana* sp. is also known to inhabit subtropical, coastal waters in the Caribbean and Pacific region (Stebbing, 1904; Schotte *et al.*, 1995). These findings indicate that ectoparasite transmission has a more direct relationship heavily dependent on habitat and environmental preferences exhibited by both the host and parasite. Although the presence of ectoparasites was rare in lionfish, they are clearly still susceptible to infection. It should be noted that the present study focused on endoparasites, as the method of capture and subsequent handling of collected fishes may have resulted in the loss of skin and gill ectoparasites. Thus our data on ectoparasite diversity and infection rates probably underestimate actual infection levels.

The lionfish parasite community appears to be dominated by generalist taxa (i.e., nematodes), which disagrees with stomach content analyses suggesting that lionfish are top predators. The parasite life cycle from invertebrate primary host to large ecological species such as birds and marine mammals shows that lionfish are intersecting in the normal vectors typically associated with native parasite-host interactions. The varying larval and adult stages of the observed endoparasites of lionfish show that lionfish are more likely filling an ecological niche as mid- to low level trophic predators. As stomach content and stable isotope analyses have become the standard methods for studying trophic interactions within food webs, studying endoparasites may provide similar or additional insight into these predator-prey interactions. However, the size variances in the sampled lionfish may not mirror the complete lionfish food web due to ecological, geographical, or even depth at capture differences that may influence lionfish size; especially since many of the lionfish in

smaller size classes were not prone to endoparasitism. Combining all trophic interactions (i.e., stomach content, stable isotope, endoparasitism) together could be a more all-inclusive approach in studying predator-prey interactions.

Inferences from known *P. volitans* and *P. miles* parasites (Table 3) and the new host descriptions derived from this study (Table 4) would indicate that lionfish are being parasitized by generalist parasites in the invaded range, similar to their parasite community in their native range. Their parasite community depends on the local parasite fauna and their ecological interactions with other marine organisms. Latitudinal variances across the invaded range indicate that geography, habitat and prey interactions effect parasite-host interactions. Geographical distances influencing population connectivity, in addition to changes in lionfish predator-prey interactions (e.g., otogenetic diet shifts), can structure parasite community assemblages (Timi *et al.*, 2010). For example, the Caribbean islands and Panama yielded the least amount of parasites and this may be heavily dependent on topographic structures (low reef complexity, barrier chains, patch reefs, etc.) and low habitat diversity in this region (Phillips & Pérez-Cruet, 1984; Fonseca *et al.*, 2006) that reduce population connectivity (Salas *et al.*, 2010).

The spatial scale of this study supports the hypothesis that host life history traits, geography, and time of introduction can influence parasite release (Blakeslee *et al.*, 2013), and the lionfish complex is the ideal species to study the complete effects of an invasion on a regional scale. Determining the biological markers, such as parasites, of marine populations in relation to neighboring populations of the same species is vital for understanding the biology, dynamics, and ecological interactions of populations (MacKenzie & Abaunaza, 1998). The geographic range of the invasive lionfish parasite community could potentially relate to host diet, feeding behavior, movement and ranges, stock connectivity, and recruitment patterns of juveniles and phylogenies (Snidermann, 1961; Moser, 1991; Williams *et al.*, 1992; Criscione *et al.*, 2006). The differences in parasite diversity pertaining to generalist versus host species-specific parasites may link to different colonization stages or solely be habitat

based. Although models and genetic studies have been previously used to explain the growth and population connectivity of the lionfish population of the western North Atlantic, this is the first study to use parasite fauna for that same purpose.

Although larval transport studies indicate that there is low population connectivity between Florida and the Bahamas (Briggs, 1995; Paris *et al.*, 2005), Bimini and Jamaica lionfish were more closely related to the Florida east coast lionfish through their common dominant nematodes *Contracaecum sp.* and *Rhapidascaris sp.* (Table 3 & Figure 5). As “crossing events” may be limited within the current system (Freshwater *et al.*, 2009), the numerous gyre systems in the Caribbean Sea may be an important factor in lionfish recruitment and retention. Typically, eddies and gyre systems are not included in lionfish expansion models, although they have been shown to be highly significant in larval transport (D’Alessandro *et al.*, 2007) and retention (Sale, 1970; Hamner & Hauri, 1981; Lee *et al.*, 1994) for other tropical species, thus encouraging rapid colonization in overlapping current-driven influential regions (Johnston & Purkis, 2011). Regions that may be highly subjective to local retention are the Florida Keys (Lee *et al.*, 1992, 1994; Lee & Williams, 1999) and the Lesser Antilles (Sponaugle & Cowen, 1996), all areas that are currently colonized by lionfish. These areas would be ideal for studying parasite occurrences that link distant populations.

Compared to colonization stages proposed by Johnston & Purkis (2011) that used abiotic factors (currents, temperature, salinity, and depth) combined with first sighting data from public sources to explain an invasion cycle, this study suggests that the connectivity between populations may be the result of source populations created from eddies and gyre systems. In the Caribbean, there are four regions that are highly subjective to population isolation based on coupled bio-physical modeling of oceanic data, habitat availability, and larval behavior of coral reef fishes: East Caribbean, West Caribbean, Bahamas-Turks & Caicos Islands, and the periphery of Panama-Colombia Gyre (Cowen *et al.*, 2006). In the eastern Caribbean, the islands of the Lesser Antilles periodically experience fluxes of salinity from riverine plumes that

develop from the North Brazil Current Rings and instigate larval entrainment (Fleurant *et al.*, 1999; Glikson *et al.*, 2000; Paris *et al.*, 2002). Variations in salinity from freshwater influx also creates anticyclonic flows on the continental shelf of the Greater Antilles and Virgin Islands, propagating both westward and eastward (Chérubin & Richardson, 2007). The Mesoamerican Barrier Reef System (MBRS) is a reef system extending about 1000 km from Yucatán Peninsula to Honduras. The MBRS is highly influenced by the northwestern flow of the Caribbean Current (Sheng & Tang, 2004; Tang *et al.*, 2006), but has highly variable flow patterns developing from Caribbean eddies that generate strong south or westerly currents depending on eddy trends (Ezer *et al.*, 2005). Similar conditions are seen in the coastal region from Costa Rica to Panama where near-shore currents flow from the northwest to the southeast creating small eddies opposite of the major Caribbean Current flow (Cortés & Jiménez, 2003). These gyre systems and rings are capable of both isolating lionfish in the Caribbean Sea islands and recruiting lionfish larvae to “upstream” reef systems.

Aside from the geographic constraints within the lionfish complex parasite community, the low genetic diversity across the two invasive species also plays a role in community structure. Limits on host genetic diversity make the population more susceptible to parasitism specifically when there is definite subdivision in parasite species among the host population (Criscione *et al.*, 2005; Criscione *et al.*, 2006). It has also been suggested that parasite species can accumulate in the host over time, such that the oldest hosts would be more likely to be infected than younger hosts (Criscione *et al.*, 2006). Demonstrated in linear regression model (Figure 6) time of introduction proves to be an influential vector for parasitism in lionfish. Infection rates can directly relate to time and the occurrence of parasite-host interactions, providing insight into identifying the initial release point for the invasion. The large abundance and diversity of taxa recognized in lionfish from the Florida East Coast supports the genetic findings of the invasion originating from the south Floridian coast (Betancur-R *et al.*, 2011). Newly invaded areas such as Texas, Bonaire, and

Barbados may require additional generations for the local lionfish populations to acclimate to their environment enough that parasite-host interactions are apparent. In a recent Great Lakes study of the invasive Eurasian round goby *Neogobius menalostomus* (Pallas, 1814), the initial parasite prevalence was very low compared to native species and only generalist taxa commonly found in the St. Lawrence River were observed (Gendron *et al.*, 2012; Kvach & Stepien, 2008). Parasite infection on an invasive species host may take several years or decades to occur (Gendron *et al.*, 2012) and usually results in parasite community structure consisting of universal generalist. However, there is still is no evidence to indicate that lionfish parasites currently have or will have detrimental effects sufficient to suppress populations.

Future lionfish research that incorporates genetics and parasitism may be able to discriminate between the two species *P. volitans* and *P. miles*. In a biogeographic genetic study, the two species are dominating various regions of the invaded range with *P. miles* generally inhabiting in the northern locations (i.e., Bermuda and eastern United States) and *P. volitans* being more universal and abundant in the Caribbean (Betancur-R. *et al.*, 2011). As seen in the Figure 4, Bermuda was dominated by acanthocephalans, which did not occur at any other sampled sites, this finding may relate to the dominant *Pterois* sp. found in the local area. Through generational life history stages, parasites in a local area exposed to a species with bottleneck genetic diversity could promote host-specific interactions (Betancur-R. *et al.*, 2011; Poole, 2011). Long-term parasite community structure research on the lionfish complex may discover patterns that aid in identifying *Pterois* sp. susceptibility to host-specific parasites in their range especially in geographically isolated areas.

It is essential for coastal management and conservationist to take a holistic approach to mitigating lionfish populations because their ecological disturbance can lead to subsequent invasions (Grosholz, 2005; Simberloff, 2006; Simberloff & von Holle, 1999). Lionfish abundance has increased rapidly since establishment and the invasion has made an impact environmentally and economically. Lionfish derbies have been known to reduce the size distribution of lionfish (Frazer *et al.*, 2012), but

total population removal has only been shown to be effective in localized areas over continuous timescales (Barbour *et al.*, 2011; Morris *et al.*, 2011, León *et al.*, 2011). Other strategies that are emerging are promoting the consumption of lionfish (Morris & Whitfield, 2009; Morris *et al.*, 2011), including the development of local commercial fisheries. This study highlights the ecological niche lionfish have as predators in coastal communities and how they interact across all trophic levels. Overall, the lionfish invasion may be the perfect example of the enemy release hypothesis and its direct benefit in invasion succession. Geographical inferences from observing the parasite community across the invaded range indicate that lionfish population connectivity occurs spatially. The broader impacts of this study suggest that invasive species management should use strategies that consider ecological and regional connectivity patterns to combat the lionfish invasion.

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