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

Kayelyn Regina Simmons
Nova Southeastern University, ksimmons011@live.com

NSUWorks Citation

Kayelyn Regina Simmons. 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*. Master's thesis. Nova Southeastern University. Retrieved from NSUWorks, Oceanographic Center. (2)
https://nsuworks.nova.edu/occ_stuetd/2.

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 acanthacephalans: *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 Blanar, 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 or 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.

Table of Contents

List of Figures

List of Tables

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 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 predatorssuch 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 *Proneohelicometra 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 comunities. 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 parasite 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 (se 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 (). The similarity matrix was based on a Bray-Curtis similarity matrix calculated from unstandardized, square-root transformed data (Blanar *et al.,* 2011).

Results

Collections

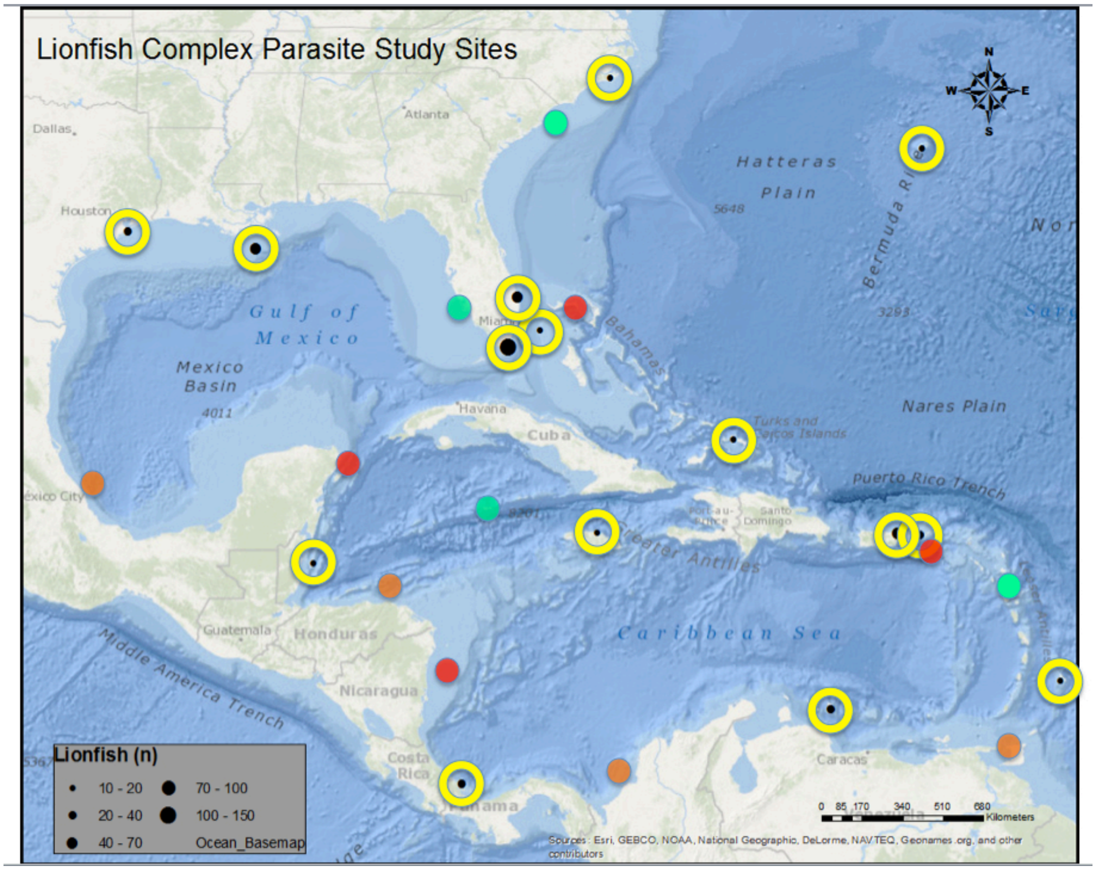
Samples from the Gulf Coast, Western Atlantic, and Caribbean were collected from participating sites as seen in Table 1. A total of 516 lionfish from the invaded range were collected with majority of lionfish caught from the Florida East Coast (USA) (n = 145) and the smallest sampled site was Bimini (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 be processed, orange dots represents 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.



Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org, and other contributors

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**
___*Contracaecum sp.___	**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%
___*Raphidascaris sp.___	**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%
___*Paracuria adunca___	**A**	0.02	-	-	-	-	-	-	-	-	-	-	-
	%	2.07%	-	-	-	-	-	-	-	-	-	-	-
___*Hysterothylaceum sp.___	**A**	-	-	0.05	-	-	-	-	-	-	-	-	-
	%	-	-	5.26%	-	-	-	-	-	-	-	-	-
Lecithochirium floridense	**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%
___*Tergestia sp.___	**A**	-	-	-	-	-	-	-	-	-	-	-	0.03
	%	-	-	-	-	-	-	-	-	-	-	-	2.50%
Unidentified sp.	**A**	-	-	-	0.07	-	-	-	-	-	-	0.08	-
	%	-	-	-	3.45%	-	-	-	-	-	-	1.32%	-
___*Nybelinia sp.___	**A**	0.03	-	0.11	-	-	-	-	0.33	-	-	-	-
	%	2.76%	-	5.26%	-	-	-	-	25.00%	-	-	-	-
___*Tentacularia sp.___	**A**	-	-	-	0.17	-	-	-	-	-	-	-	-
	%	-	-	-	10.34%	-	-	-	-	-	-	-	-

		FEC	**NCA**	**BER**	**FLJ**	**BIM**	**TCI**	**JAM**	**BEL**	**PAN**	**PRI**	**GCC**	**STT**
Serrasentis sp.	**A**	-	-	-	0.07	-	-	-	-	-	-	-	-
	%	-	-	-	6.90%	-	-	-	-	-	-	-	-
Dollfustentis sp.	**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%	-
Trachelobdella lubrica	**A**	0.01	-	-	0.10	-	-	0.05	-	-	-	0.03	-
	%	1.38%	-	-	6.90%	-	-	5.00%	-	0.-%	-	2.63%	-
Rocinela stignata	**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.

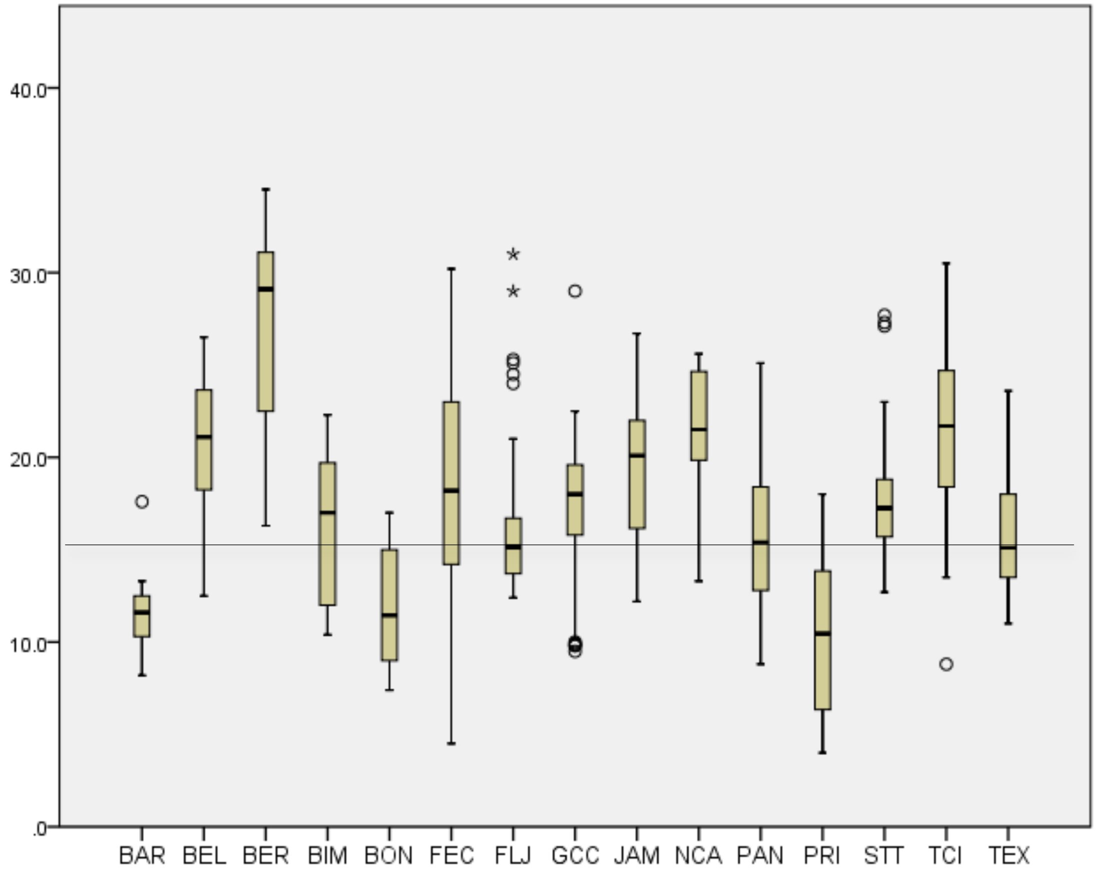


Figure 3: Lionfish complex total parasite fauna distribution, all sampled individuals combined, segregated according to taxonomic phylum. All lionfish collected from the wild from the western North Atlantic, Gulf of Mexico, and Caribbean Sea.

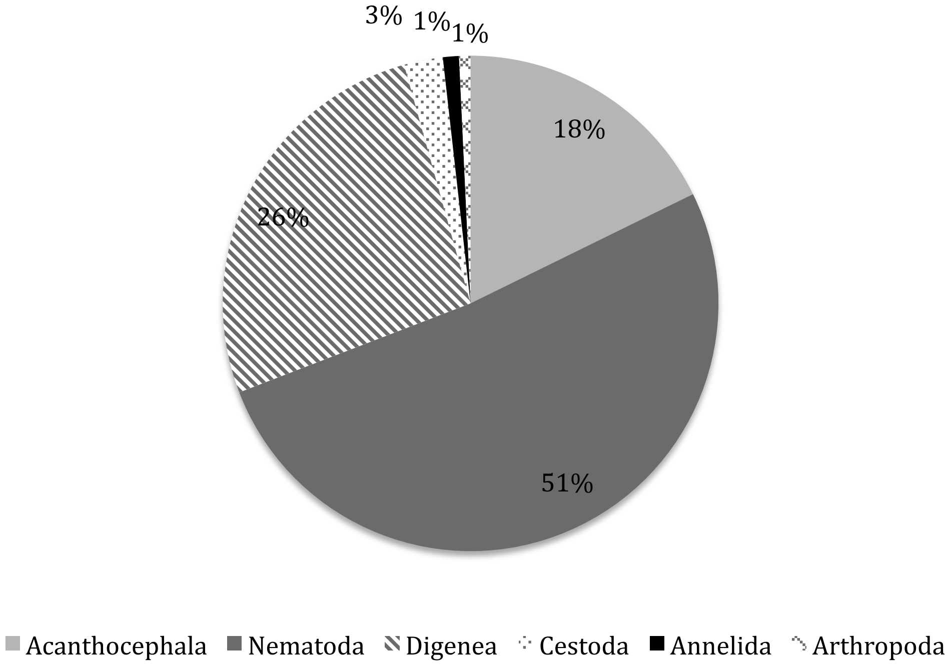


Figure 4: Lionfish parasite community distribution by taxa at each sample site. No parasites were found in any of the lionfish from BON, BAR, or TEX. Note: collection location abbreviations are from Table 1.

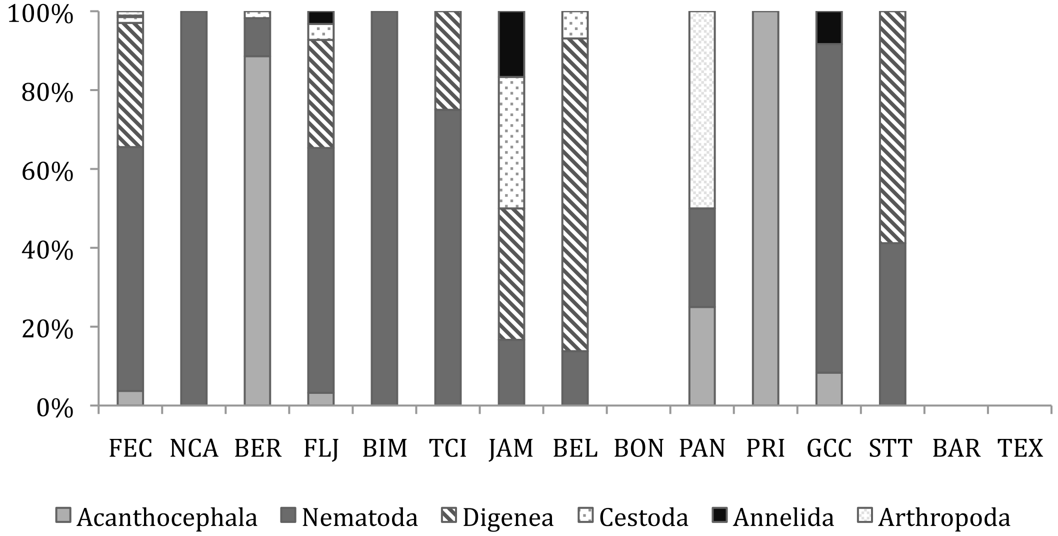


Table 4: Reference table for previously described parasite fauna in the invasive Indo-Pacific lionfish complex *P. volitans* and *P. miles* in both the native and invaded ranges.

Taxa	**Family/Order**	**Parasite**	**Region**	**Host(s)**	**Publication(s)**
Annelida: Hirudinea	Piscicolidae	*Trachelobdella lubrica* (Grube, 1840)	Japan	*P. volitans*	Paperna, 1976
Arthropoda: Copepoda	Chondracanthidae	*Acanthochondria* sp. (Leigh-Sharpe & Oakley, 1972)	Japan	*P. volitans*	Dojiri & Ho, 1988
Arthropoda: Copepoda	Poecilostomatoida	*Taeniacanthus miles* (Pillai, 1963)	India	*P. miles*	Dojiri & Cressy, 1987; Tang et al., 2013
Monogenoids	Capsiladae	*Benedenia epinepheli* (Yamaguti, 1937)	Japan	*P. volitans*	Ogawa et al., 1995
Platyhelminthes: Monogenea	Dactylogyridean	*Haliotrema* sp. (Johnson & Tiegs, 1922)	Eilat, Israel	*P. miles*	Paperna, 1972;Colorni & Diamant, 2005
Protozoa: Ciliophora	Trichodinidae	Trichodinid ciliates	Eilat, Israel	*P. miles*	Paperna, 1972;Colorni & Diamant, 2006
Myxozoa	Spheromyxidae	*Sphaeromyxa zaharoni* (Diamant et al., 2004)	Red Sea	*P. miles*	Diamant et al., 2004
Trematoda	Opecolidae	*Proneohelicometra aegyptensis* (Ozaki, 1925)	Red Sea	*P. volitans*	Nagaty & Aal, 1962; Hassanine, 2006
Annelida: Hirudinea	Piscicolidae	*Trachelobdella lubrica* (Grube, 1840)	Jacksonville, Florida (USA)	*P. volitans*	Ruiz-Carus et al., 2006; Celik & Aydin, 2006
Digenea	Hemiruidae	*Lecithochirium floridense* (Manter, 1934)	Beaufort, North Carolina (USA)	*P.* c.f. *volitans*	Bullard et al., 2011
Arthropoda	Cymothoidae	*Excorallana* sp. *(Stebbing, 1904)*	Bonaire	*P. volitans & P. miles*	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 stignata* (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 PERMANONVA/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 *Dollfustentis* 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	*_Contracaecum sp._ (Railliet & Henry, 1912)	BER, NCA, JFL, FPH, ALA, FEC BIM, TCI, JAM, STT, BEL, PAN	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	*_Raphidascaris_ sp. (Railliet & Henry, 1912)	NCA, JFL, FPH, FEC, BIM, TCI, STT	freshwater and marine teleosts	Worldwide	Moravec & Justine, 2012; Smith, 1984; Reger _et al.,_ 1983; Rego _et al.,_ 1983; Bicudo _et al.,_ 2005; Tavares & Luque, 2006
Nematoda	Anisakidae	*_Hysterothylaceum_ sp. (Ward & Magath, 1917	BER	freshwater and marine teleosts	Gulf of Mexico, Brazil, Kuwait, Japan, North America, Mediterranean	Eiras & Rego, 1987; Petter & Sey, 1997; Yoshinaga _et al.,_ 1989; Moser & Hsieh, 1992
Nematoda	Acuarioidae	*_Paracuria adunca_ (Creplin, 1846)	FEC	piscivorous birds	Worldwide	Diaz _et al.,_ 2004
Digenea	Hemiuridae	_Leithochirium floridense_ (Manter, 1934)	JFL, FEC, TCI, JAM, STT, BEL	marine teleosts	Worldwide	Cribb _et al.,_ 2002; Moravec _et al.,_ 1997; Yeo & Spierler, 1980; Klimpel _et al.,_ 2001; Salgado-Maldonado & Kennedy, 1997; Salgado-Maldonado _et al.,_ 1997; Vidal-Martínez _et al.,_ 2001; Parukhin, 1989; Bullard _et al.,_ 2011
Digenea	Fellodistomidae	*_Tergestia_ sp. (Stossich, 1887)	JFL, STT	marine teleosts	North Atlantic, Mediterranean	Bartoli _et al.,_ 2003; Bray & Gibson, 1980; MacKenzie et al., 2008
Acanthocephala	Rhadinorhynchidae	*_Serrasentis_ sp. (Van Cleave, 1923)	JFL	crustaceans, marine teleosts, elasmobranchs	Brazil, Arabian Sea, Persian Gulf	Maghami _et al._ 2008; Fatima & Khan, 2005
Acanthocephala	Illiosentidae	_Dollfustentis sp._ (Golvan, 1969)	FEC,BER, PRI	Marine and estuarine teleosts, crustaceans	Subtropics of Atlantic Ocean	Amin, 1998
Cestoda	Trypanorhyncha	*_Nybelinia_ sp. (Poche, 1926)	BER, FEC, BEL	elasmobranchs	Worldwide	Palm _et al.,_ 1997
Cestoda	Trypanorhyncha	*_Tentacularia_ sp. (Bosc, 1797)	JFL	elasmobranchs	Worldwide	Bray, 2013; Palm _et al.,_ 2009
Annelida: Hirudinea	Piscicolidae	_Trachelobdella lubrica_ (Grube, 1840)	JFL, FPH, ALA, FEC, JAM	marine teleost	circumtropical, Mediterranean, Europe, North Atlantic	van der Land (2001); Hayward & Rylan (1990); MEDIN (2011); Worms (2013)
Arthopoda: Isopod	Cymothoidae	*_Rocinela stignata_ (Schioedte & Meinert,,1879)	FEC PAN	marine teleost	Gulf of Mexico, Caribbean, Yucatan, eastern Pacific, West Indies	Kensley & Schotte, 1989; Schotte _et al.,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.

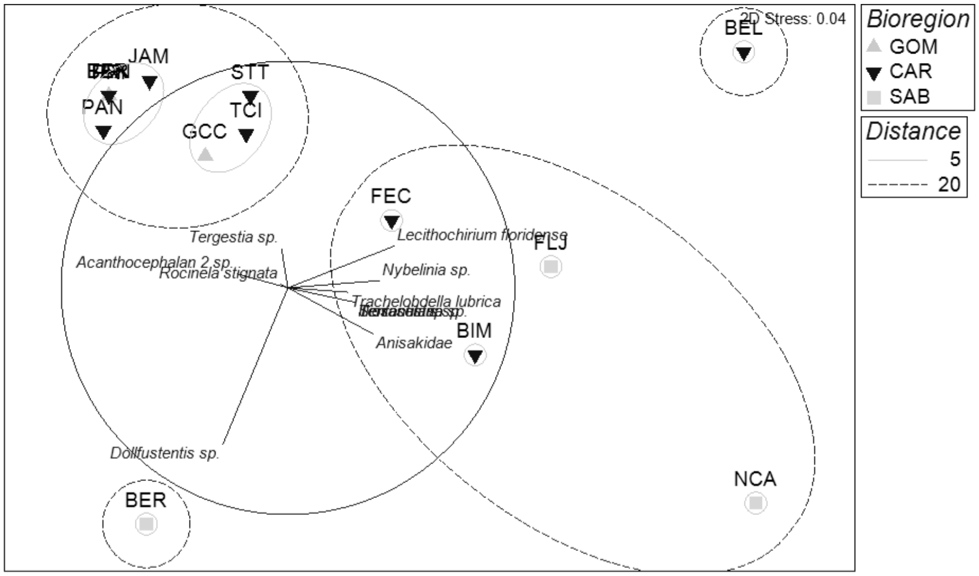
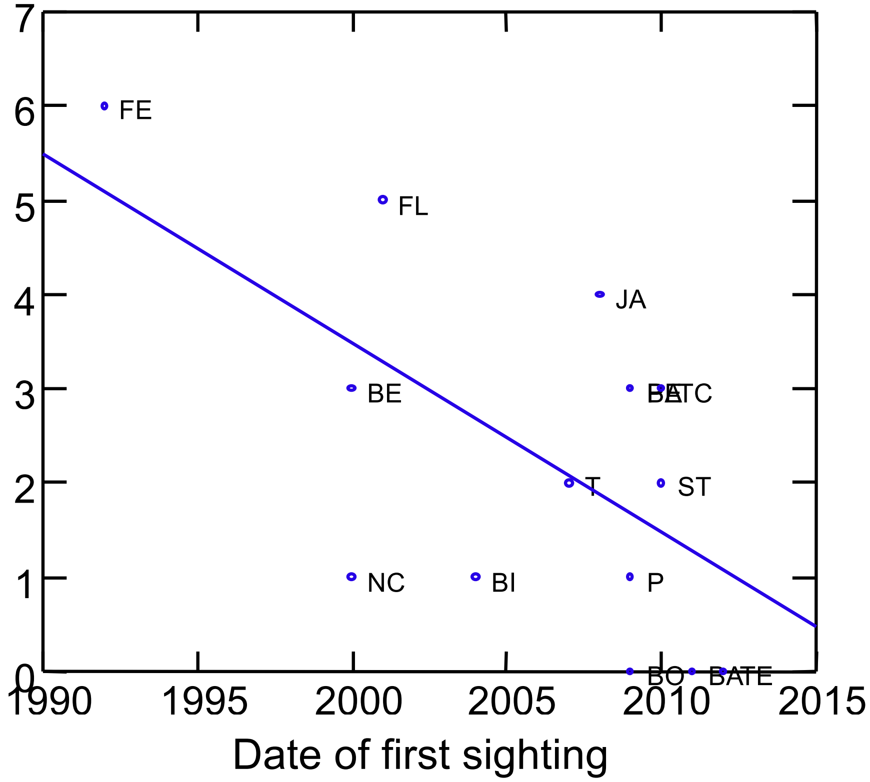


Figure 6: Linear regression model showing the correlation between the year of first sighting and parasite taxonomic diversity. $r^2 = 0.368$,DF = 1, F = 7.57, p = 0.017. Note: collection location abbreviations are from Table 1.



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 (Ruitenberg *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 *Contracaeum* sp. life cycle has not be completely described, although adult stages are known 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 *Raphidscaris* is known to infect the intestinal tract of marine fishes (Moravec & Justine, 2012). *Hysterothylaceum* 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 inhabitant 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 paratentic 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 anticycloinic 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 the combat the lionfish invasion.

References

Albins, M.A. & Hixon, M.A. (2011). Worst-case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes,* 96:1151-1157.

Ali M. A., Hasan A., & Abdel-Aziz, A. M. (2001). *Sphaerospora undulata* sp. n. (Myxozoa: Myxosporea) infecting the kidney of haffara seabream *Rhabdosargus haffara* (Teleostei: Sparidae) from the Red Sea, light and transmission electron microscopy. *Journal of Egyptian Academic Society for Environmental Development*,. (A - Aquaculture) 1: 89-100.

Ali M., Abdel-Baki A. S., Sakran T., Entzeroth R., Abdel-Ghaffar A. (2003). Light and electron microscopic of *Myxobolus stomum* sp. n. (Myxosporea: Myxobolidae) infecting the blackspotted grunt *Plectorhynicus gaterinus* (Forsskall, 1775) in the Red Sea, Egypt. *Parasitology Research,* 91: 390-397

Ali, M., Abdel-Baki, A., & Sakran, T. (2006). *Myxidium elmatboulii* n. sp. and *Ceratomyxa ghaffari* n. sp. (Myxozoa: Myxosporea) Parasitic in the Gallbladder of the Red Sea Houndfish *Tylosurus choram* (Rüppell, 1837) (Teleostei: Belonidae) from the Red Sea, Egypt. *Acta Zoologica*, 45:97-103.

Amin, O.M. (1998). NOAA Technical Report NMFS 135: Marine Flora and Fauna of the Eastern United States: Acanthocephala.

Amin, O.M., Nahhas, F.M., Al-Yamani, F. & Abu-Hakima, R. (1984). On three acanthocephalan species from the some Arabian Gulf fishes off the coast of Kuwait. *Journal of Parasitology,* 70:168-170.

Anderson, R. C. (1992). *Nematode parasites of vertebrates: their development and transmission*. CAB International, Oxford

Anderson, R.C. (2000). *Nematode Parasites of Vertebrates, Their Development and Transmission*. 2nd ed. CABI Publishing, London, 650 p.

Audicana, M.T. & Kennedy, M.W. (2008). *Anisakis simplex:* form obscure infectious worm to inducer of immune hypersensitivity. *Clinical Microbiology Reviews,* 21:360-379.

Barbour, A.B., Allen, M.S., Frazer, T.K., & Sherman, K.D. (2011). Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PlosOne,* 6:e19666

Bartoli, P., Bray, R.A., & Gibson, D.I. (2003). *Lecithostaphylus retroflexus* (Molin, 1859) (Zoogonidae) and *Tergestia acanthocephala* (Stossich, 1887) (Fellodistomidae) (Digenea) from the epipelagic teleost *Belone belone* (L.) in the western Mediterranean. *Systematic Parasitology*, 54:131-143.

Beaver, P.C., Jung, R.O.C., Cup, E.W. (2008). Curstacea, Linguatulid, Millipedes, Centipedes, Scorpions, Spiders, Ticks and Mites. *Clinical Parasitology*, Lea & Febiger, Philadelphia.

Bellay, S., Lima, D.P.Jr., Takemoto, R.M., & Luque, J.L. (2011). A host-endoparasite network of Neotropical marine fish: are there organizational patterns? *Parasitology*, 138:1945-1952.

Betancur-R., R., Hines, A., Acero, A.P., Orti, G., Wilbur, A.E., & Freshwater, D.W. (2011). Reconstructing the lionfish invasion: Insights into Greater Caribbean iogeography. *Journal of Biogeography,* 38:1281-1293.

Beverley-Burton, M. (1978). Population genetics of *Anisakis simplex* (Nematoda: Ascaridoidea) in Atlantic Salmon (*Salmo salar*)and their use as biological indicatiors of host stocks. *Environmental Biology of Fishes,* 3:369-377.

Bicudo, A.J.A., Tavares, L.E.D., & Luque, J.L. (2005). Larvas de Anisakidae (Nematoda: Ascaridoidea) parasitas da cabrinha *Prionotus punctatus* (Bloch, 1793) (Osteichthyes: Triglidae) do Litoral do Estado do Rio de Janeiro, Brasil. *Brazilian Journal of Veterinary Parasitology*,14:109-118.

Blakselee, A.M.H., Fowler, A.E., & Keogh, C.L. (2013). Marine Invasions and Parasite Escape: Updates and New Perspectives. *Advances in Marine Biology,* 66:87-161.

Blakeslee, A.M.H., Keogh, C.L., Byers, J.A., Kuris, A.M., Lafferty, K.D., & Torchin, M.A. (2009). Differential escape from parasites by two competing introduced crabs. *Marine Ecology Progress Series,* 393:83-96.

Biggs, C.R. & Olden, J.D. (2011). Multi-scale habitat occupancy of invasive lionfish (*Pterois volitans*) in coral reef environments of Roatan, Honduras. *Aquatic Invasions,* 6:347-353.

Bray, R.A & Gibson, D.I. (1980). The Fellodistomidae (Digenea) of fishes from the northeast Atlantic. *Bulletin of British Museum (Natural History): Zoology,* 37:199-293.

Bray, R. (2013). *Tentacularia* Bosc, 1797. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=105081 on 2013-12-1

Briggs, J.C. (1995). *Global Biogeography*. Elsevie, Amsterdam.

Bullard, S.A., Barse, A.M., Curran, S.S., & Morris, Jr., J.A. (2011). First record of digenean from invasive lionfish, *Pterois* CF. *volitans,* (Scorpaeniformes: Scorpaenidae) in the Northwestern Atlantic Ocean. *Journal of Parasitology,* 97:833-837.

Bush, A.O., Lafferty, K.D., Lotz, J.M., & Shostak, A.W. (1997). Parasitology meets ecology on its own terms: Margolis *et al. Journal of Parasitology,* 83:575-583.

Catalano, S.R., Whittington, I.D., Donnellan, S.C., & Gillanders, B.M. (2013). Parasites as biological tags to assess host population structure: Guidelines, recent genetic advances and comments on a holistic approach. *International Journal of Parasitology: Parasites and Wildlife* *http://dx.doi.org/10.1016/j.ijppaw.2013.11.001*

Celik, E. S., & Aydin, S. 2006. Effect of *Trachobdella lubrica* (Hirudinea: Piscicolidae) on biochemical and haematological characteristics of black scorpion fish (*Scorpaena porcus*, Linnaeus 1758). *Fish Physiology and Biochemistry.* 32: 255–260.

Chérubin, L.M. & Richardson, P.L. (2007). Caribbean current variability and the influence of Amazon and Orinoco freshwater plumes. *Deep Sea Research I,* 54:1451-1473.

Clarke, KR, Gorley, RN, (2006). PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIssac, H.J. (2004). Is invasion success explained by the enemy release hyphothesis? *Ecology Letters*, 7:721-733.

Cohen, A.N., & Carlton, J.T. (1998). Accelerating invasion rate in a highly invaded estuary. *Science,* 279:555-558.

Colorni, A. & Diamant, A. (2005). Hyperparasitism of trichodinid ciliates on monogenean gill flukes of two marine fish. *Diseases of Aquatic Organisms*, 65:177-180.

Cortés, J. & Jiménez, C.E. (2003). Past, present and future of the coral reefs of the Caribbean coast of Costa Rica: 223–239. In: Cortés, J. (ed) *Latin American coral reefs*. Elsevier Science B.V., Amsterdam.

Cowen, R.K., Paris, C.B., & Srinivasan, A. (2006). Scaling of connectivity inmarine populations. *Science*, 311:522–527.

Cribb, T.H., Bray, R.A., Wright, T., & Pichelin, S. (2002). The trematodes of groupers (Serranidae: Epinephelinae): Knowledge, nature and evolution. *Parasitology*, 124:S23-S42.

Criscione, C.D., Poulin, R., & Blouin, M.S. (2005). Molecular ecology of parasites: elucidating ecological and microevolutionary processes. *Molecular Ecology,* 14:2247-2257.

Criscione, C.D., Cooper, B., & Blouin, M.S. (2006). Parasite genotypes identify source populations of migratory fish more accurately than fish genotypes. *Ecology,* 87:823-828.

D'Alessandro, E., Sponaugle, S., & Lee, T. (2007). Patterns and process of larval fish supply to coral reefs of the upper Florida Keys. *Marine Ecology Progress Series,* 331:85-100.

Diamant, A., Whipps, C.M., & Kent, M.L. (2004). A new spcecies of *Sphaeromyxa* (Myxosporea:Sphaeromyxina: Shaeromyxidae) in Devil Firefish, *Pterois miles* (Scorpaenidae), from the northern Red Sea: Morpholoy, ultrastucture, and phylogeny. *Journal of Parasitology*, 90:1434-1442.

Diaz, J.I., Cremonte, F., & Navone, G.T. (2004). First record of the Acuarioid Nematode *Paracuria adunca* from South America, with new morphological details and discussion of cordons. *Comparative Parasitology*, 71:238-242.

Dojiri, M. & Cressey, R.F. (1987). Revision of the Taeniacanthidae (Copepoda: Poecilostomatoida) parasitic on fishes and sea urchins. *Smithsonian Contributions to Zoology* 447: 1-250, figs. 1-166.

Dojiri, M. & Ho, J.S. (1988). Two Species of *Acanthochondria* Copepoda Poecilostomatoida parasitic on fishes of Japan." *Report of the Sado Marine Biological Station*, Niigata University 18:47-56.

Drake, J.M. & Lodge,D.M. (2006). Allee effects, propagule pressures and the probability of establishment: risk analysis for biological invasions. *Biological Invasions,* 8:365:375.

Eiras, J.C.. & Reggo, A.A. (1987). The histopathology of *Scomber japonicas* infection by *Nematobothrium scombri* (Trematoda: Didymozoidae) and of larval anisakid nematode infections in the liver of *Pagrus pagrus. Memórias do Institute Oswaldo Cruz, 82:155-159.*

Eisenbarth, A. (2009). Occurrence of Intestinal Fish Parasites in Australia: Identification of Anisakid Nematodes in Commerically Available Fish Species from South Australian Water. *Diplomica Verlag GmbH,* Hamburg, Germany 88.

Fatima, M.B. & Khan, A. (2005). Two New Helminth Parasites from Pakistan, with Redescription of the Acanthocephalan *Centrorhynchus fasciatum* (Westrumb, 1821). *Pakiston Journal of Zoology,* 37:257-263.

Fleurant, C., Wilson, D., Johns, W., Garzoli, S., & Smith, R. (1999). CTD/O2, LADCP and XBT Measurements Collected aboard the R/V SEWARD JOHNSON, November–December 1998: North Brazil Current Rings Experiment Cruise 1(NBC-1), NOAADROARAOML35; PB2000102446, 268p.

Fonseca, A.C., Salas, E., & Cortés, J. (2006). Monitoreo del arrecife coralino Meager Shoal, Parque Nacional Cahuita, Costa Rica (sitio CARICOMP). *Revista de Biología Tropical*, 54:755–763.

Frazer, T.K., Jacoby, C.A., Edwards, M.A., Barry, S.C., & Manfrino, C.M. (2012). Coping with the lionfish invasion: Can targeted removals yield beneficial effects? *Reviews in Fisheries Science*, 20:185-191.

Freshewater, D.W., Hines, A., Parham, S., Wilbur, A., Sabaoun, M., Woodhead, J., Akins, L., Purdy, B., Whitfield, P.E., Paris, C.B. (2009). Mitochondrial contral region sequence analyses indicate dispersal from the US East Coast as the source of the invasive Indo-Pacific lionfish *Pterois volitans* in the Bahamas. *Marine Biology,* 156:1213-1221.

Gendron, A.D., Marcogliese, D.J., & Thomas, M. (2012). Invasive species are less parasitized than native competitors, but for how long? The case of the round goby in the Great Lakes-St. Lawrence Basin. *Biological Invasions,* 14:367-384.

Glikson, D.A., Fratantoni, D.M., Wooding, C.M., & Richardson, P.L. (2000). North Brazil Current ring experiment: surface drifter data report November 1998–June 2000. Technical Report, July 2000, WHOI-2000-10, 121p

Gotelli, N.J. & Rohde, K. (2002). Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecology Letters,* 5:86-94.

Green, S.J., Tamburello, N., Miller, S.E., Akins, J.L., and Côté, I.M. (2013). Habitat complexity and fish size effect the detection of Indo-Pacific lionfish on invaded coral reefs. *Coral Reefs,* 32:413-421.

Grevar, F.S. (1999). Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biological Invasions,* 1:313-323.

Grosholz, E.D. (2005). Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences,* 102:1088-1091.

Hamner, W.M. & Hauri, I.R. (1981). Effects of island mass: Water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. *Limnology & Oceanography,* 26:1084-1102.

Hamner, R. M., Freshwater, D. W., & Whitfield, P. E. (2007). Mitochondrial cytochrome b analysis reveals two invasive lionfish species with strong founder effects in the western Atlantic. *Journal of Fish Biology, 71*(sb), 214-222.

Hare, J. A. and P.E. Whitfield. 2003. An integrated assessment of the introduction of lionfish (Pterois volitans/miles complex) to the Western Atlantic Ocean. NOAA Technical Memorandum NOS NCCOS. p 21.

Hassanine, S., Seehagen, A., Palm, H.W., & Rosenthal, H. (2001). Deep-water metazoan fish parasites of the world. *Logos Verlag*, Berlin, Germany, 317 p.

Hassanine, R.M.E. (2006). Trematodes from Red Sea fishes: *Proneohelicometra aegyptensis* gen. nov., sp. nov. (Opecoelidae Ozaki, 1925) and *Neohypocreadium gibsoni* sp.nov. (Lepocreadiidae Odhner 1905). *Acta Parasitologica*, 51:249-254.

Hayward, P.J. & Ryland, J.S. (Ed.) (1990). *The marine fauna of the British Isles and North-West Europe: 1. Introduction and protozoans to arthropods*. Clarendon Press: Oxford, UK. ISBN 0-19-857356-1. 627 pp.

Hopper, K.R. & Roush, R.T. (1993). Mate finding, dispersal, numbers released, and the success of biological control introductions. *Ecological Entomology,* 18:321-331.

Ishikura, H., Kikuchi, K., Nagasawa, K., Ooiwa, T., Takamiya, H., Sato, N., Sugane, K. (1993). Anisakidae and anisakidosis. *Progress in Clinical Parasitology*, 2:43-102. Springer-Verlag, New York, NY.

Johnston, M.W. & Purkis, S.J. (2011). Spatial analysis of the invasion of lionfish in the western Atlantic and Caribbean. *Marine Pollution Bulletin,* 62:1218-1226.

Kanarek, G. & Bohdanowicz, J. (2009). Larval *contracaecum sp.* (Nematoda: Anisakidae) in the Great Cormorant [*Phalacrocorax carbo* (L., 1758)] form north-eastern Poland: A morphological and morphometric analysis. *Veterinary Parasitology,* 166:90-97.

Keane, R. & M.J. Crawley (2002). Exotic Plant Invasisons and the Enemy Release Hypothesis. *Trends in Ecological Evolution , 17*, 164-170.

Kennedy, C.R. (2006). *Ecology of the Acanthocephala.* Cambridge University Press.

Kensley, B., & Schotte,M. (1989). Guide to the Marine Isopod Crustaceans of the Caribbean. *Smithsonian Institution Press*. Washington, D.C. and London. 308 pp.

Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecological Evolution,* 16:199-204

Kuo, C., Corby-Harris, V., Promislow, D.E.L. (2008). The unavoidable costs and unexpected benefits of parasitism: Population and metapopulation models of parasite-mediated competition. *Journal of Theoretical Biology*, 250:244-256.

Kvach, Y. & Stepien, C.A. (2008). Metazoan parasites of introduced round and tubenose gobies in the Great Lakes: The support for the enemy release hypothesis. *Journal of Great Lakes Research,* 34:23-35.

Lee, T.N., Clarke, M.E., Williams, E., Szamnt, A.F., & Berger, T. (1994). Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bulletin of Marine Science,* 54:621-646.

Lee, T.N., Rooth, C., Williams, E., McGowan,M., Szmant, A.F. & Clarke, M.E. (1992). Influence of Florida Current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. *Continental Shelf Research,* 12:971-1002.

Lee, T.N. & Williams, E. (1999). Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *Bulletin of Marine Science,* 64:35-56.

Lester, R. J. G. (1990). Reappraisal of the use of parasites for fish stock identification. *Australian Journal of Marine & Freshwater Research,*. 41:855–864.

León, R., Vane, K., Vermeji, M., Bertuol, P., & Simal, F. (2011). Overfishing works: A comparison of the effectiveness of lionfish control efforts between Bonaire and Curaçao. *Proceedings of the 64th Gulf and Caribbean Fisheries Institute.*

MacKenzie, K. & Abaunza, P.(1998). Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. *Fisheries Research*, 38:45-56.

MacKenzie, K. Campbell, N., Matticucci, S., Ramos, P., Pinto, A.L., & Abaunza, P. (2008). Parasites as biological tags for stock identification of Atlantic horse mackerel *Trachurus trachurus* L. *Fisheries Research,* 89:136-145.

Maghami, S.S.G. ,Khanmohammadi, M., & Kerdeghari,M.(2008). *Serrasentis Sagittifer* (Acanthocephala: Rhadinorhynchidae) from the Japanese Thread Fin Bream, *Nemipterus japonicus*, in Bushehr Waters of Persian Gulf. *Journal of Animal and Veterinary Advances, 7: 1430-1433.*

Manel, S., Berthier, P., & Luikart, G. (2002). Detecting wildlife poaching: identifying the origin of individulas with Bayesian assignment tests and multilocus genotypes. *Conservation Biology*, 16:650-659.

MEDIN (2011). UK checklist of marine species derived from the applications Marine Recorder and UNICORN, version 1.0.

McCarthy, J., Moore, T.A. (2000). Emerging helminth zoonoses. *International Journal of Parasitology*, 30:1351-1361.

Miller, A.W., Ruiz, G.M., Minton, M.S., Ambrose, R.F. (2007). Differentiating successful and failed molluscan invaders in the estuarine ecosystem. *Marine Ecology Progress Series,* 332:41-51.

Minchella, D.J., & Scott, M.E. (1991). Parasitism: a cryptic determinant of animal community structure. *Trends in Ecology and Evolution,* 6:250-254.

Mitchell, C. E. & Power, A.G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature , 421*, 625-627.

Morris, J.A., Akins, J.L., Barse, A., Cerino, D., Freshwater, D.W., Green, S.J., Munoz, R.C., Pairs, C., & Whitfield, P.E. (2009). Biology and Ecology of Invasive Lionfishes, *Pterois miles* and *Pterois volitans, Gulf and Caribbean Fisheries Institute*, 61:409-413

Morris, J.A., and Whitfield, P.E. (2009). Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment. *NOAA Technical Memorandum*, 99: 57 pp.

Morris, J.A.Jr., Thomas, A., Rhyne, A.L., Breen, N., Akin, L., & Nash, B. (2011). Nutritional properties of the invasive lionfish: a delicious and nutritious approach for controlling the invasion. *AACL BioFlux,* 4:21-26.

Moravec, F. & Justine, J.L. (2012). *Raphidascaris (Icthyascaris) etelidids* n. sp. (Nematoda, Anisakidae), a new ascaridoid nematode from lutjanid fishes off New Caledonia. *Zoosystema,* 34:113-121.

Moser, M. (1991). Parasites as biological tags. *Acta Parasitologica,* 7:182-185.

Mosquera, J. & Gómez-Gesteira, M. de Castro. (2003). Parasites as biological tags of fish populations: Advantages and limitations. *Comments on Theoretical Biology,* 8:69-91.

Nikishin, V.P. (2001). The structure and formation of embryonic envelopes of acanthocephalans. *The Biological Bulletin,* 28:40-53.

Ogawa, K., Bondad-Reantaso, M.G., & Wakabayashi,H. (1995). Redescription of *Benedenia epinepheli* (Yamaguti, 1937) Meserve, 1938 (Monogenea: Capsalidae) from cultured and aquarium marine fishes of Japan. *Canadian*

Journal of Fisheries and Aquatic Sciences. (52):62-70.

Palm, H.W. (1999). Ecology of *Pseudoterranova decipiens* (Krabbe, 1878) (Nematoda: Anisakidae) from Antarctic waters. *Parasitology Research*, 85:638-643.

Palm, H.W. (2004). The Trypanorhyncha Diesing, 1863. PKSPL-IPB ,Press, Bogor, 109pp.

Palm, H.W. & Caira, J.N. (2008). Host specificity of adult versus larval cestodes of the elasmobranch tapeworm order Trypanorhyncha. *International Journal of Parasitology*, 38:381-388.

Palm, H.W., Walter, T., Schwerdtfeger,G., & Reimer, L.W. (1997). *Nybelinia* Poche 1926 (Cestoda: Trypanorhyncha) from the Moçambique coast, with description of *N. beveridgei sp. nov.* and systematic consideration of the genus. *South African Journal of Marine Science,* 18:273-285.

Palm, H.W., Waeschenbach, A., Olson, P.D., Littlewood, D.T.J. (2009). Molecular phylogeny and evolution of Trypanorhyncha Diesing, 1863 (Platyhelminthes: Cestoda). *Molecular Phylogenetics and Evolution,* 52:351-367.

Paperna, I. (1972). Monogenea of Red Sea fishes. III. Dactylogyridae from littoral and reef fishes. *Journal of Helminthology,* 46:47.

Paperna, I. (1976). Parasitological survey of fishes of the Red Sea and Indian Ocean. Pages 82. in: Z. Reiss and I. Paperna: *Fifth report of the H. Steinitz Marine Biology Laboratory*, Elat 1975-1976.

Paperna, I. & Overstreet, R. M., 1981. Parasites and diseases of mullets (Mugilidae). In: *Aquaculture of grey mullets*. Ed. by O. H. Oren. Cambridge Univ. Press, Cambridge, 411–493.

Paris, C.B., Cowen, R.K., Claro, R., & Linderman, K.C. (2005). Larval transport pathways from Cuban snapper (*Lutjanidae*) spawning aggregations based on biophysical modeling. *Marine Ecology Progress Series,* 269:93-106

Paris, C.B., Cowen, R.K., Lwiza, K.M.M., Wang, D., & Olson, D.B. (2002). Multivariate objectives analysis of the coastal circulation of Barbados, West Indies: implication for larval transport. *Deep Sea Research I,* 49:1363-1386.

Parukhin, A.M. (1989). Parasitic worms of bottom fishes of the southern seas. *Naukova Dumka,* Kiev, Ukraine, 156p.

Petter, J.A. & Sey, O. (1997). Nematode parasites of marine fishes of Kuwait, with a description of *Cucullanus trachinoti n. sp.* from *Trachniotus blochi*. *Zoosystema,* 19:35-59.

Phillips, P.C., Pérez-Cruet, M.J. (1984). A comparative survey of reef fishes in Caribbean and Pacific Costa Rica. *Revista de Biología Tropical* ,32:95–102.

Pillai, N.K.. (1963). Copepods of the Family Taeniacanthidae parasitic on South Indian fishes. *Crustaceana*, Leiden 6(2):110-128, figs. 1-8. (19-ix-1963)

Poole, T. (2011). The sensitivity of the invasive lionfish, *Pterois volitans*, to parasitism in Bonaire, Dutch Caribbean. *Physis: Journal of Marine Science,* 9:44-49.

Poulin, R. (1992). Determinants of host specificity in parasites of freshwater fishes. *International Journal of Parasitology*, 22:753-758.

Prenter, J., MacNeil, C., Dick, J.T.A., & Dunn, A.M. (2004) Roles of parasites in animal invasions. *Trends in Ecology and Evolution*, 19:385-390.

Rego, A.A., Vicente, J.J., Santos, C.P. & Wekid, R.M. (1983). Parasitas de anchovas, *Pomatomus saltatrix* (L.) do Rio de Janeiro. *Ciência e Cultura*, 35:1329-1386.

Ruitenberg, E.J., van Knapen, F., Weiss, J.W. (1979). Food-borne parasitic infections-old stories and new facts. *Tijdschr Diergeneeskd,* 104:5-13.

Ruttenberg, B.I., Schofield, P.J., Akins, J.L., Acosta, A., Feeley, M.W., Blondeau, J., Smith, S.G., & Ault, J.S. (2012). Rapid invasion of Indo-Pacific Lionfishes (*Pterois volitans* and *Pterois miles*) in the Florida Keys, USA: Evidence from multiple pre- and post-invasion data sets. *Bulletin of Marine Science,* 88:1051-1059

Ruiz-Carus, R., Matheson, R.E.Jr., Roberts, D.E. Jr., & Whitfield, P.E. (2006). The western Pacific red lionfish, *Pterios volitans* (Scorpaenidae), in Florida: Evidence for reproduction and parasitism in the first exotic marine fish established in state waters. *Biological Conservation*, 128:384-390.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J., & Hines, A.H. (2000). Invasion of coastal marine communities in North America: apparent patterns, process, and biases. *Annual Review of Ecology, Evolution, and Systematics,* 31:481-531.

Sağlam, N., Oguz M. C., Celik E. S., Doyuk, S.A., & Usta, A.(2003). Pontobdella muricata and Trachelobdella lubrica (Hirudinea: Piscicolidae) on some marine fish in the Dardanelles, Turkey. *Journal of Marine Biology Association of the United Kingdom*, 83:1315–1316.

Sale, P.J. (1970). Distribution of larval Acanthuridae off Hawaii. *Copeia,* 1970:765-766.

Salas, E., Molina-Ureña,H., Walter, R.P., & Heath, D.D. (2010). Local and regional genetic connectivity in a Caribbean coral reef fish. *Marine Biology,* 157:437-445.

Salati, F., Meloni, M., Cau, M., & Angelucci, G. (2013). Presence of *Contracaecum spp.* in teleosts cultured and fished in Sardinia. *Veterinary Parasitology,* 196:382-387.

Salgado-Maldonado, G & Kennedy, C.R. (1997). Richness and similarity of helminth communities in the tropical cichlid fish *Cichlasoma urophthalmus* from the Yucatan Peninsula, Mexico. *Parasitology*, 114:581-590.

Salgado-Maldonado, G., Vidal-Martínez, & Kennedy, C.R. (1997). A checklist of metazoan parasites of cichlid fish from Mexico. *Journal of the Helminthological Society of Washington*, 64:195-207.

Santos, R.S., Martins, M.L., Marengoni, N.G., Francisco, C.J., Piazza, R.S., Takashi, H.K., & Onaka, E.M. (2005). *Neoechinorhynchus curemai* (Acanthocephala: Neoechinorhynchidae) in *Prochilodus lineatus* (Osteichthyes:Prochilodontidae) from Paraná River, Brazil. *Veterinary Parasitology,* 134:111-115.

Sasal, P., Mouillet, D., Fichez, R., Chifflet, S., & Kulbicki, M. (2007). The use of fish parasites as biological indicators of anthropogenic influences in coral reef lagoons: A case study of Apogonidae parasites in New Caledonia. *Marine Pollution Bulletin*, 54:1697-1706.

Sax, D.F.,, Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hasings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I. & Rice, W.R. (2007).Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution,* 22:465–471

Schioedte, J. C. & Meinert, F. W. (1879). Symbolae ad Monographiam Cymothoarum Crustaceorum Isopodum Familiae 1. Aegidae. *Naturhistorisk Tidsskrift* , 12: 321-414.

Schmidt, Gerald D. and Nickol, Brent B., "Development and Life Cycles: [Chapter 8 in Biology of the Acanthocephala]" (1985). *Faculty Publications from the Harold W. Manter Laboratory of Parasitology*. Paper 504.

Schofield, P.J. (2009). 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. *Aquatic Invasions,* 4:3.

Schofield, P.J. (2010). Update on geographic spread of invasive lionfish's (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic Ocean, Caribbean Sea, and Gulf of Mexico. *Aquatic Invasions*, 5:117-122.

Schotte, M., Markham, J.C., & Wilson, G.D.F. 2009. Isopoda (Crustacea) of the Gulf of Mexico, Pp. 973–986 in Felder, D.L. and D.K. Camp (eds.), *Gulf of Mexico–Origins, Waters, and Biota. Biodiversity*. Texas A&M Press, College Station, Texas.

Schotte, M., B. F. Kensley, and S. Shilling. (1995). World list of Marine, Freshwater and Terrestrial Crustacea Isopoda. National Museum of Natural History Smithsonian Institution: Washington D.C., USA. http://invertebrates.si.edu/isopod/ Accessed: 01/06/2014

Semenova, M.K. (1979). The role of copepods in the life-cycle of *Contracaecum micropapillatum* (Ascaridata, Anisakidae) (In Russian). Trudy Gel' mintologicheskoi Laboratorii (Gel’minty ĥivotnykhi I rastenii), 29:126-129.

Shaw, D.J., Grenfell, B.T., & Dobson, A.P. (1998). Patterns of macroparasite aggregation in wildlife host populations. *Parasitology,* 117:597-610.

Sheldon, B.C., & Verhulst, S. (1996). Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution*, 11:317-321.

Sheng, J. & Tang, L. (2004) A two-way nested ocean-circulation model for the Meso-American barrier reef system. *Ocean Dynamics* ,54:232–242.

Simberloff, D. (2006). Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor or both? *Ecology Letters,* 9:912-919.

Simberloff, D. & Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 1:21-32.

Smith, J.D. (1984). Development of *Raphidascaris acus* (Nematoda, Anisakidae) in paratenic, intermediate, and definitive hosts. *Canadian Journal of Zoology*, 62:1378-1386.

Snidermann, C.J. (1961). Parasite tags for marine fish. *Journal of Wildlife Management*, 25:41-47.

Sponaugle, S. & Cowen, R.K. (1996). Nearshore patterns of larval supply to Barbados, West Indies. *Marine Ecology Progress Series,* 133:13-28

Stebbing, T. R. 1904. Marine crustaceans. XII. Isopoda, with description of a new genus.—*In:* J. S. Gardiner, ed., *Fauna and geography of the Maldive and Laccadive Archipelagoes,* 2: 699-721.

Tang, L., Sheng, J., Hatcher, B.G., & Sale, P.F. (2006) Numerical study of circulation, dispersion and connectivity of surface waters of the Belize shelf. *Journal of Geophysical Research,* 111:1–18.

Tang, D. & Walter, T. C.(2013). *Taeniacanthus miles* (Pillai, 1963). In: Walter, T.C. & Boxshall, G. (2013). World of Copepods database. Accessed through: Walter, T.C. & Boxshall, G. (2013). World of Copepods database at http://www.marinespecies.org/copepoda/aphia.php?p=taxdetails&id=356006 Accessed 12/19/2013.

Tavares, L.E.R. & Luque, J.L. (2006). Sistemática, biologia e importância em saúde coletiva de larvas de Anisakidae (Nematoda: Ascaridoidea) parasitas de peixes ósseos marinhos do Estado do Rio de Janeiro, Brasil. In: Silva-Souza AT. *Sanidade de Organismos Aquáticos no Brasil*. ABRAPOA, Maringá, 387 pp.

Tello, J. S., Stevens, R. D. & Dick, C.W. (2008). Patterns of species cooccurrence and density compensation: a test for interspecific competition in bat ectoparasite infracommunities. *Oikos* 117:693–702.

Timi, J.T., Luque, J.L., & Poulin, R. (2010). Host otogeny and the temporal decay of similarity in parasite communities of marine fish. *International Journal of Parasitology,* 40:963-968.

Timi, J.T., Lanfranchi, A.L., and Luque, J. (2010). Similarity in parasite communities of the teleost fish *Pinguipes brasilianus* in the southwestern Atlantic: Infracommunities as a tool to detect geographical patterns. *International Journal of Parasitology*, 40:243-254.

Thomas, F., Renaud, F., & Guégan, J.F .(2005). *Parasitism and Ecosystems*. Oxford University Press, pp. 219.

Torchin, M. L., Lafferty, K.D., & Kuris, A.M. (2002). Parasites and Marine Invasions. *Parasitiology , 124*, S137-S151.

Torchin, M. L. (2001). Release from Parasites as Natural Enemies: Increased Performance of a Globally Introduced Marine Crab. *Biological Invasisions , 3*, 333-345.

Torchin, M.E., & Mitchell, C.E. (2004). Parasites, pathogens, and invasions by plants and animals. *Frontiers in Ecology and the Environment*, 2:183-190.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., & Kuris, A.M. (2003). Introduced species and their missing parasites. *Letters to Nature,* 42: 628-630.

Torchin, M.E., Byers, J.E., & Huspeni, T.C. (2005). Differential parasitism of native and introduced snails: replacement of a parasite fauna. *Biological Invasions*, 7:885-894.

U.S. Geological Survey. [2013]. Nonindigenous Aquatic Species Database. Gainesville, Florida. Accessed [12/12/2013].

UNESCO-IOC Register of Marine Organisms. Accessed [01/03/2014].

Van der Land, J. (2001). Hirudinea, ***in***: Costello, M.J. *et al.* (Ed.) (2001). European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification, *Collection Patrimoines Naturels,* 50:234-235.

Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116:1120-1127.

Vázquez, D.P., Poulin, R., Krasnov, B.R., & Shenbrot, G.I. (2005). Species abundance and the distriubuiton of specialization in host-parasite interaction networks. *Journal of Animal Ecology,* 74:946-955.

Vidal-Martínez, V.M., Aguirre-Macedo, M.L., Scholz, T., González-Solís, & Mendoza-Franco, E.F. (2001). Atlas of the helminth parasites of cichlid fish of Mexico. *Academy of Sciences of the Czech Republic,* Ceské Budejovice, Czech Repulic, 165p.

Whitfield, A.K. & Heeg, J. (1977). On the life cycles of the cestode *Ptychobothrium belones* and nematodes of the genus *Contracaecum* from Lake St. Lucia, Zululand.*South African Journal of Science*, 73:121–122.

Whitfield, P.E., Gardner, T., Vives, S.P., Gilligan, M.R., Courtenay, W.R., Ray, G.C., & Hare, J.A. (2002). Biological invasion of the Indo-Pacific lionfish Pterois volitans along the Atlantic coast of North America. *Marine Ecology Progress Series*, 235:289-297.

Williams, H.H., MacKenzie, K., & McCarthy, A.M. (1992). Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish. *Reviews in Fish Biology and Fisheries,* 2:144-176.

WoRMS (2013). *Trachelobdella lubrica* (Grube, 1840). Accessed through: World Register of Marine Species. http://marinespecies.org/aphia.php?p=taxdetails&id=116991 [01/03/2014].

Yamaguti, S. (1961). *Systema Helminthum. Vol.III. The nematodes of vertebrates. Part I & II*. Interscience Publishers, New York

Yamaguti, S.(1963). *Synopsis of digenetic trematodes of vertebrates*. Keigaku Publishing Co. Tokyo, Japan, pp.1073.

Yeo, S.E. & Spieler, R.E. (1980). Habitat effects on the occurrence of parasites inhabiting the sergeant major, *Abudefduf saxatilis* (Linneaus), with a list of parasites of Caribbean damselfish. *Bulletin of Marine Science,* 30:313-324.

Yoshimura, K. (1998). *Angiostrongylus (Parastrongylus)* and less common nematodes. In: Cox, E.G., Kreier, J.P., Wakelin, D. (Eds.), Topley & Wilson's Microbiology and Microbial Infections, 5:635-659. Arnold, London.

Yoshinaga, T., Ogawa, K. & Wakabayashi, W. (1989). Life cycle of *Hysterothylacium haze* (Nematoda: Anisakidae: Raphidascaridinae). *Journal of Parasitology*, 75(5): 756-763.

Zerofsky, M., Harel, E., Silverman, N., & Tatar, M., (2005). Aging of the innate immune response in *Drosophila melanogaster*. *Aging Cell 4*, 103–108.

Zuk, M. & Stoehr, A.M. (2002). Immune defense and host life history. *The American Naturalist*, 160, S9–S22