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Prey naïveté and predator-prey interactions between *Pterois volitans,* Pomacentridae, and Tetraodontidae in two reefs in the Guna Yala Archipelago, Panama

Jesse Garrett-Larsen
School of International Training, Fall 2017

Abstract

The invasion of *Pterois volitans* along the Atlantic coast of the Americas is one of the top marine conservation issues of the century. Prey naïveté has been suggested as a mechanism for the success of *P. volitans,* but conclusive field observations have not been completed. This study tested for prey naïveté *in situ* by comparing time spent by Pomacentridae and Tetraodontidae in close proximity to *P. volitans* and a native predator, *Cephalopholis cruentata*. Difference in time spent by Pomacentridae and Tetraodontidae in the presence of the two predators was observed. The predators *P. volitans* and *C. cruentata* were sequentially observed for ten-minute-long periods in the morning and evening on two coral reefs near El Porvenir over the course of a week in November 2017. It was found that Pomacentridae and Tetraodontidae were naïve to *P. volitans*, spending significantly more time in their presence than *C. cruentata* (M_P = 232.48, SD_P = 177.73; M_C = 38.21, SD_C = 42.05). A new action pattern was observed in which *P. volitans* appeared to lure Tetraodontidae using their pectoral and dorsal fins. It was also found that cloud cover and presence of Serranidae did not have an observable effect on *P. volitans* predator-prey interactions (M_{Cloudy} = 57.59, SD_{Cloudy} = 93.60; M_{Clear} = 110.54, SD_{Clear} = 142.82). This information supports previous studies on prey naïveté in *P. volitans* and provides an ecological overview of feeding ecology and behavior.

<u>Acknowledgments</u>

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<u>Introduction</u>

The San Blas Archipelago is located on the Northern coast of Panama in the autonomous comarca of Guna Yala. The archipelago has been extensively studied and is known for its coral reefs. The total reef system covers an estimated area of 638 km^2 along 480 km of coastline (Andrefouet and Guzman 2005). The comarca of Guna Yala is located between Punta San Blas (9°34'N 78°58'W) to Puerto Obaldia (8°40'N 77°25'W), encompassing 320,600 ha of mainland forest and ocean, including 365 coral islands (Guzman et al. 2003). The Northern coast of Panama does not experience upwelling as the Southern coast does, leading to much larger expanses of coral reef systems. Panama experiences two distinct seasons – the rainy and the dry season. Because Panama is so close to the equator (~9°N) that seasons are not caused by the angle of the earth. Instead, they are caused by the Intertropical Convergence Zone (ICZ), a belt of low equatorial pressure where moisture-laden trade winds converge near the warmest parts of the ocean, producing a dramatic increase in rainfall (Linsley et al. 1994). The rainy season lasts from May to early December in Panama, bringing heavy rains that can result in substantial runoff into reefs near the shore (Clifton et al. 1997). The coast line is almost entirely forested in Guna Yala with the majority of the human population living on nearshore islands.

Threats to coral reefs in the region include thousands of tourists annually who pollute the ocean and break corals, island expansion, coral mining, fishing, waste disposal, and crustacean diving. The Guna governing body has passed laws to conserve the reefs and they remain productive and diverse with corals, fish, and other marine organisms. The reefs in Guna Yala support fifty-seven species of scleractinian coral, four hydrocorals, gorgonian corals, sponges, and a multitude of fish (Clifton et al. 1997). The four main reef types in Guna Yala are fringing reefs, costal patches, reef complexes, and deep reefs. Fringing reefs are physically connected with the mainland or large islands. They have flat, shallow corals with outer slopes to 10 m deep. Reef complexes are comprised of multiple reef types (Andrefouet and Guzman 2005).

Study Sites

The first week of this study was carried out near Isla Tigre in Digir and the second near El Porvenir by Punta San Blas. All reefs surveyed in this study were fringing reefs or reef complexes. See Figure 1 for maps of the study sites.

Invasive Species

The past 10,000 years on Earth have been shaped by humans. Although there is debate over the exact start, a new epoch, the Anthropocene, has been recognized by scientists, acknowledging human disturbance of our planet (Smith and Zeder 2013). Of the innumerable effects that the human population has had on the environment, the introduction of exotic species to novel environments is one of the less obvious but more ubiquitous and deleterious ones. Invasive species are non-native species, introduced by human activities, that threaten ecosystems, habitats, or species (Pejchar and Mooney 2009). These invasive species drive indirect human caused environmental change and are widely accepted as the second greatest cause of species endangerment, topped only by habitat loss (Pejchar and Mooney 2009). Non-native species affect ecosystems by altering habitats, competing with and preying on native

species, changing nutrient cycles, and energy budgets among other things (Miehls et al. 2009). Invasive species can be found in all parts of the world. Plant species such as kudzu (*Pueraria montana var. lobata*) have taken over large swaths of land in North America, covering more than 3 million ha in the eastern USA (Pejchar and Mooney 2009). Terrestrial species, including the brown tree snake (*Boiga irregularis*) in Guam have posed substantial threats to native fauna and lead to the extinction of native organisms (Browne et al. 2000).

Aquatic Invasive Species

Aquatic invasive species come in many forms. Zebra mussels (*Dreissena polymorpha*) have become a major problem in North America, Europe, and Russia, changing food web interactions and trophic structures in their invaded range (Miehls et al. 2009). In their comprehensive review of global marine invasive species, Molnar et al. (2008) assessed 329 marine invasive species. They found that, in 2008, at least one marine invasive species was found in 194 marine ecoregions out of the world's 232. The major vectors for introduction were shipping (69%), aquaculture (41%), canal construction (17%), and aquarium trade (6%). There were 38 species of invasive fish that were identified. Most invasive marine species occur in the Temperate Northern Atlantic and Pacific oceans as well as the Eastern Indo-Pacific (Molnar et al. 2008). As well as an ecological cost, invasive fish species have an economic cost as well. It was reported in 2005 that the total economic losses that can be attributed to invasive fish total between $1 billion to $5.7 billion every year (Lovell et al. 2006). One of the most well documented marine invasions that is currently occurring is the invasion of the Pacific Red Lionfish *Pterois volitans* along the Atlantic coast of the Americas.

Pterois volitans History

Pterois volitans, or Pacific Red Lionfish, are native to the western Pacific from southern Japan to western Australia and into the South Pacific (Côté et al. 2013). They are one of the eight species within the family Scorpaenidae, subfamily Pteroinae. genera *Pterois* (Kochzius et al. 2003). The first sightings of *P. volitans* were documented off the coast of Florida in 1985 off Dania Beach (Morris Jr. and Akins 2009). They have rapidly spread along the Atlantic coastline of the Americas from Rhode Island in the United States to Brazil (Hixon 2016). With the help of citizen scientists and modern technology, the scope and rate of the invasion of *P. volitans* has been exceedingly well documented. Data has been archived in public databases such as the US Geological Survey Nonindigenous Aquatic Species database and the Reef Environmental Education Foundation Volunteer Survey Project database (Côté et al. 2013). See Figure 2 for maps of *P. volitans* spatial distribution throughout time.

Lionfish have a very low genetic diversity off the Atlantic coast of the United States, indicating a strong founder effect stemming from the release of a small group of *P. volitans* or multiple releases of individuals in southern Florida (Côté et al. 2013). It has been suggested that the vector for introduction into Florida waters was the aquarium trade (Côté et al. 2013; Cure et al. 2012). After their introduction, *P. volitans* became the first introduced marine fish to become a major invasive threat in the Atlantic Ocean (Albins and Hixon 2013). Along with *P. volitans,* a sibling species, *P. miles* was introduced to the United States. *Pterois miles* was also introduced to

the Mediterranean Sea via the Suez Canal from the Red Sea in the early 1990's (Kochzius et al. 2003). Although the two species are difficult to distinguish, *P. miles* has one fewer dorsal and anal fin ray compared to *P. volitans* (Morris Jr. et al. 2008). It appears that *P. miles* is restricted to the United States mainland and has not spread like *P. volitans* (Albins and Hixton 2013). Studies have found that there may be genetic breaks in the populations of *P. volitans* in the Atlantic Ocean. Buttterfield et al. (2015) found one genetic break between the Bahamas, Turks, and Caicos versus the Caribbean. They also found low genetic variation in the invasive population in their introduced range. This is important to conservation and education efforts. If the low genetic variability is maintained, it is more likely that rare recessive alleles will be expressed, decreasing the fitness of the population as a whole. If more *P. volitans* are introduced into the Caribbean, a larger gene pool will be available, and *P. volitans* are likely to increase in fitness, avoiding genetic bottlenecks and increasing the genetic diversity in the population (Butterfield et al. 2015).

Effect of P. volitans on Coral Reefs

Red lionfish are voracious predators that feed on small fish and crustaceans on coral reefs (Mumby et al. 2011). In an experimental reef matrix in the Bahamas, a single lionfish reduced the average abundance of fish per reef by 93.7%. *Pterois volitans* have a negative effect 2.6 times stronger than a native grouper does on average fish abundance (Albins 2013). Red lionfish also have caused a 79% reduction in the recruitment of native fishes during a five week long experimental period (Albins and Hixton 2008). In their invaded range, *P. volitans* have been shown to consume 22 families of teleosts, 14 families of crustaceans, and three families of mollusk, with the majority (78% by volume) being teleosts (Eddy et al. 2016; Morris Jr. and Akins 2009). Families relevant to this study include Pomacentridae, Tetraodontidae, Labridae, and Scaridae – all families that have been reported to be consumed by *P. volitans* (Eddy et al. 2016; Morris Jr. and Akins 2009). *Pterois volitans* have the ability to expand their stomachs over 30 times in volume when consuming a large meal. This means that they can eat a large meal and withstand starvation for up to 12 weeks without dying (Morris Jr. et al 2008). Daily consumption of *P. volitans* is approximately equal to 2.5-6.0% of their body weight every day in their native range, and some studies have suggested that this rate may be higher in their invaded range (Morris Jr. et al. 2008). Some of the fish that are consumed by *P. volitans* are herbivorous, including species from the families Munididae, Portunidae, Grapsidae, Gobiidae, Scaridae, Blennidae, and Acanthuridae (Cure et al. 2013; Eddy et al. 2016). When herbivorous fish are removed, algal cover increases in coral reefs, outcompeting corals, and occasionally leading to phase shifts, where the dominant cover changes from live coral to algae (Agudo and Salas 2014; Hughes et al. 2007). Red Lionfish have ecological effects on coral reef structure much stronger than those of similarly sized native piscivores (Albins 2013). On Bahamian coral reefs, *P. volitans* consumed native fish at an average rate of 1.44 kills h^{-1} (Côté and Maljkovic 2010). The invasion has become so severe that it has been recognized as one of the world's top conservation issues (Albins and Hixton 2013).

Life History

Many life history factors have been suggested for the success of *P. volitans* in its introduced habitat including high reproductive output, rapid growth, diet, and prey naïveté (Côté et al. 2013**).** For a comprehensive review of *P. volitans*, see Côté et al. (2013). An average female *P. volitans* can spawn up to 2 million eggs each year (Côté et al. 2013). During spawning events, females produce buoyant masses of eggs that can be dispersed by wind and currents. The post-spawning larval stage lasts for 20-35 days, plenty of time for dispersal to occur (Butterfield et al. 2015). High individual growth rates combined with the high reproductive rates lead to extreme population growth rates in invaded regions, reaching densities up to more than 390 fish per hectare compared to their native densities of 80 fish per hectare in the Pacific (Albins and Hixton 2013; Green and Cote 2008). Pteroines, including *P. volitans*, are gonochoristic, exhibiting ? little sexual dimorphism only during reproduction (Morris Jr. et al 2008). *Pterois volitans* physiology allows them to survive in temperatures as low as 10°C, allowing a very large invaded geographic region (Côté et al. 2013; Kimball et al. 2004). While coral reefs generally host the most lionfish, they have also been found in seagrass beds, mangroves, and artificial structures in depths up to 300m (Albins and Hixton 2013; Barbour et al. 2010; Pimiento et al. 2013). Red lionfish are crepuscular hunters, meaning they hunt during dusk and dawn when there are low levels of light (Cure et al. 2012; Harwell 2017). Red lionfish have also been shown to be significantly more active when the skies are overcast (Côté and Maljkovic 2010).

Predation of P. volitans

There have been no reports of diseases affecting *P. volitans* and very low levels of endo- and ecto-parasites (Kindinger 2014). This in conjunction with the lack of native predators due to their natural history and phenotype has led to rapid increases in abundance on many reefs (Hixton et al. 2016). These factors have made *P. volitans* extremely strong negative interactors with the potential to convert most reef-fish biomass to *P. volitans* biomass, leaving reef fish populations greatly diminished (Albins and Hixton 2013). Red lionfish have dorsal, pelvic, and anal fin spines which contain apocrine-type venom glands which produce acetylcholine and a neurotoxin that can lead to severe injuries in humans and potential predatory fish (Albins and Lyons 2012; Haddad Jr et al. 2003; Morris Jr. 2008). A possible reason for the lack of natural predators is overfishing of groupers which, at high levels, appear to be natural biocontrols of lionfish (Mumby et al. 2011). In the Exuma Cays Land and Sea Park, fishing has been banned for 20 years, resulting in the highest biomasses of groupers in the Caribbean where they are overfished regularly. In this site, it was found that the biomass of lionfish was significantly negatively correlated with the biomass of grouper, suggesting that groupers may be a natural biocontrol of *P. volitans* (Mumby et al. 2011).

Study Species

Cephalopholis cruentata, commonly known as the Graysby, belong to the Serranidae family and are common on coral reefs in Guna Yala. They are diurnal, hunting during the day close to the surface of the water and retreating to deeper caves at night. Similar to *P. volitans*, *C. cruentata* are crepuscular hunters. The diet of *C. cruentata* consists predominantly of fish (75%)

as well as crustaceans (18%) (Nagelkerken 1979). *Canthigaster rostrata*, the Atlantic sharpnose puffer, belong to the Tetraodontidae family. They are found in Guna Yala in mixed coral and rubble habitat. *Canthigaster rostrata* grow to 2-3.5 inches and are social animals. Female *C. rostrata* defend territories from other females and small males. Dominant males are haremic, patrolling their own territories which generally include one to six female territories (Sikkel 1990). *Stegastes* spp., or damselfishes, belong to the Pomacentridae family. Fish in this family are prevalent throughout the region of Guna Yala. Damselfish are fondly known as gardeners because they maintain a patch of algae and are extremely territorial, attacking anything that enters their space (Humann and Deloach 2014).

Prey Naïveté

The red queen hypothesis describes the evolutionary arms race that is always present between coexisting organisms. It says that any given gain in fitness through evolution by one individual or species is balanced by loss in fitness by others (Valen 1977). This phenomenon has led to the multitude of defensive adaptations in plants, animals, and bacteria that can be observed across the globe. Evolutionary prey naïveté occurs when there is an absence of exposure to a novel predator over evolutionary time - this can result in nonexistent or ineffective antipredator behavior in their presence (Côté et al. 2013). When a non-native predator is introduced to a new ecosystem, the new prey have not been coevolving with the non-native predator and therefore are unequipped to avoid predation. *Pterois volitans* have a few unique predation traits that are new to the Atlantic Ocean. Their cryptic coloration and slow movement create an effective form of camouflage, and their long pectoral fins are used to slowly stalk and herd small fish into corners to be consumed (Albins and Hixton 2013). In addition to these methods, sit-and-wait ambush hunting has also been observed along with a blowing behavior, where *P. volitans* produces a jet of water directed at their prey which seems to distract or confuse them, possibly making consumption easier (Cure et al. 2012). The jet of water blown at prey often results in the fish facing the *P. volitans*, increasing the probability of head-first capture and consumption (Albins and Lyons 2012).

In order for a prey to appropriately respond to predators, they need to obtain and synthesize accurate information from the predator. This can come in many different forms – scent, chemical, sound, visual cues, and possibly others that humans cannot begin to understand. When a novel predator such as *P. volitans,* is introduced into an environment, prey appear not to respond to important cues and do not have strong anti-predator responses in a lab setting (Lonnstedt and McCormick 2013). It has been suggested that prey naïveté is more common in marine systems than terrestrial because there is persistent isolation in marine environments (i.e. Pacific vs Atlantic) and less in terrestrial environments which have been homogenized over millions of years (Cox and Lima 2006).

Prey naïveté has been cited in many papers as a possible factor for *P. volitans* success (Albins 2013; Albins and Hixton 2013; Black et al. 2014; Côté et al. 2013; Cure et al. 2012; Eddy et al. 2016; Ingeman 2016; Kindinger 2014). However, there still seems to be a lack of conclusive data on prey naïveté in *P. volitans* outside of the lab (Black 2014; Kindinger 2014). Behavioral studies examining the interactions between *P. volitans* and *Stegates planifrons* and

Stegates leucostictus have suggested some form of naïveté to *P. volitans* (Black 2014; Cure et al. 2012; Kindinger 2014). Direct observational studies are necessary to better understand the phenomenon of prey naïveté to *P. volitans* to corroborate findings by previous researchers. The families Tetraodontidae and Pomacentridae were selected for this study because of their abundance in the field. Both were extensively hunted by *P. volitans* and *C. cruentata.*

Ethology

The study of ethology, or animal behavior, has existed for more than 50 years (Tinbergen, 1963). One of the primary questions that is asked by ethologists is, why is this behavior taking place? Broadly, behaviors can be explained using four categories: mechanism, adaptive value, ontogeny, and phylogeny. These can be categorized into two even broader levels: proximate and ultimate explanations. A proximate explanation for a behavior draws upon immediate factors that can generally be quantified such as temperature or location. This category includes mechanism and ontogeny. Mechanistic explanations of behavior can include physical morphology, physical mechanisms, and other underlying biological factors. Ontological explanations focus on the development of an organism throughout its lifespan, often associated with learning. Ultimate explanations look further back at evolutionary factors to explain behaviors. Ultimate explanations include adaptive value and phylogeny. Functional (adaptive value) explanations investigate the immediate fitness advantage of a behavior. Finally, phylogenetic explanations look to evolutionary factors and phylogenetic trees and what selective pressures in the past shaped the current behavior (Tinbergen, 1963).

Prey naïveté can be measured by comparing behavioral responses of prey to invasive and native predators (Black et al. 2014; Gamazo 2013; Kindinger 2014). In this experiment, time spent by small damselfish (*Stegastes spp.*) and Sharpnose Pufferfish (*C. rostrata*), within the same site as a native predator, Graysby (*C. cruentata*), was compared to time spent within the same site as *P. volitans*. Time within site was recorded during ten-minute-long observations on two reefs near El Porvenir island in the Guna Yala Archipelago.

Research Question

Is there a difference in time spent by Pomacentridae and Tetraodontidae in close proximity to *P. volitans* or Serranidae and what are the predator-prey interactions between *P. volitans*, Pomacentridae, and Tetraodontidae in two coral reefs near El Porvenir in the Guna Yala Archipelago?

Hypotheses

H$_0$: There is no difference between time spent by Pomacentridae and Tetraodontidae within the same site as *P. volitans* or Serranidae.

H$_A$: There is a difference between time spent by Pomacentridae and Tetraodontidae within the same site as *P. volitans* or Serranidae.

Objectives

1) To better understand *P. volitans* predator-prey interactions and 2) To test for prey naïveté to *P. volitans* in Pomacentridae and Tetraodontidae in the Guna Yala archipelago.

Methods

Seven coral reefs in two regions of the Guna Yala archipelago were surveyed for *P. volitans* and Serranidae. Three reefs near Isla Tigre and four near El Porvenir islands were sampled. Six days were spent on Isla Tigre sampling and nine days were spent on El Porvenir sampling. Sites were visited based on input from local fishermen and proximity. See Table 1 for site names and GPS coordinates of every location surveyed.

Each site was sampled by swimming unidirectionally over the reef, haphazardly sampling lionfish and Serranidae that were encountered along the way. At each reef, a series of standardized 10-minute observations were taken in the morning (6:30-9:00) and afternoon (15:00-18:00) weather permitting. If all lionfish and Serranidae were sampled before the allotted time period was up, a second survey was completed in the same manner. A minimum distance of 3 m was kept between the observer and focal predator when possible to reduce observer influence on the interactions (Cure et al. 2012; Gamazo 2013).

Before each predator observation, data were recorded noting cloud cover Clear = 0-25%, Partly Cloudy = 25-75%, Overcast = > 75% cloud cover), region, reef, date, microhabitat, estimated predator size (Lionfish: greater or less than 10 cm to differentiate between juveniles and adults (Agudo and Salas 2014), Serranidae: total length (TL) in inches), and number of groupers visible at the start of the sample period (Cure et al. 2012).

Observations fell into two different categories: timed, and counts. Timed data were calculated by recording the length of time that predator was doing a particular action. Timed data were recorded for the time that the predators were hunting, and the amount of time that small fish were within the same site as the focal predator (Cure et al. 2012; Gamazo 2013). Timing commenced at the beginning of the observation period and ended after 10 minutes. Any timed events were ended when the observation period ended even if the event was not over. Count events were recorded for strikes, and consumptions. Count events were recorded as they occurred and did not affect proportion of time events. See Table 2 for ethogram defining action patterns.

At the end of each observation period, the depth at the final location of the predator was recorded to the nearest meter using a tape measure. After all predators were sampled, if the allotted time was not up, the reef was sampled a second time in the reverse direction.

All prey fish were identified to at least the family level using Humann and Deloach's Reef Fish Identification 4th Edition upon return to land.

Student's t-tests in Microsoft Excel 2016 were used to analyze and compare the data.

Ethics

This study complied with all ethical standards set forth by the Local Review Board and the School of International Training and was approved by the Local Review Board. No vulnerable human populations were involved in this study. No animals were harmed over the course of this study. All observations were made from at least 2 m from focal fish to minimize stress to animals when possible. All procedures were conducted to avoid any pain or suffering of animal subjects.

Results

A total of 57 observations were recorded over the course of five days (20 – 25 November 2017). Thirty-three observations were of *P. volitans* and 27 were *C. cruentata*. Of the 57 observations, 39 were carried out on Porvenir Front 1 (9º33'27.0"N 78º56'45.0"W), and 18 on Isla Aguadargana Complex (9º33'08.5"N 78º56'42.1"W). Sample locations are circled in red on Figure 1.

Prey Naïveté

There was a significant difference between time spent by Pomacentridae and Tetraodontidae within the same site as *P. volitans* ($M = 232.48$, $SD = 177.73$) and *C. cruentata* ($M = 38.21$, $SD = 42.05$) conditions; $t(112) = 7.36$, $p < 0.001$ (Figure 3). There was a significant difference in time spent by Pomacentridae within the same site as *P. volitans* ($M = 204.70$, $SD = 217.75$) and *C. cruentata* ($M = 37.67$, $SD = 50.93$) conditions; $t(55) = 3.68$, $p < 0.001$ (Figure 4). There was a significant difference in time spent by Tetraodontidae within the same site as *P. volitans* ($M = 260.27$, $SD = 127.04$) and *C. cruentata* ($M = 38.75$, $SD = 33.10$) conditions; $t(55) = 8.32$, $p < 0.001$ (Figure 5). There was a significant difference in time that *P. volitans* spent hunting Pomacentridae ($M = 122.28$, $SD = 145.08$) and Tetraodontidae ($M = 29.88$, $SD = 42.29$) conditions; $t(64) = 3.47$, $p < 0.001$ (Figure 7). *Pterois volitans* struck at Tetraodontidae more than Pomacentridae, shown in Figure 8.

Pterois volitans Predator-Prey Interactions

On average, Pomacentridae and Tetraodontidae spent the most time within the same site as *P. volitans,* shown in Figure 6 ($N = 33$). Pomacentridae were consumed once and Tetraodontidae twice by *P. volitans* during the study.

There was not a significant difference in time spent hunting by *P. volitans* in cloudy conditions ($M = 57.59$, $SD = 93.60$) and clear conditions ($M = 110.54$, $SD = 142.82$) conditions; $t(63) = 1.78$, $p = 0.081$ (Figure 9). There was no significant difference between time that *P. volitans* spent hunting with Serranidae present ($M = 99.14$, $SD = 107.30$) and absent ($M = 70.00$, $SD = 118.04$) conditions; $t(22) = 0.86$, $p = 0.401$ (Figure 10).

Pterois volitans were found on two of the seven reefs surveyed, showed in Figure 1. Both reefs were near Punta San Blas. Microhabitats where *P. volitans* were found hunting include hard coral, cave, sand, rubble, and rock. All observations were carried out in water 1-6 m deep. *Pterois volitans* were observed hunting both in groups and solitarily, shown in Figures 10 and

11. An action pattern was observed multiple times in which *P. volitans* spread their dorsal and pectoral fins, swaying their dorsal fins back and forth. Tetraodontidae would approach the dorsal and pectoral fins and occasionally bite them. The *P. volitans* would quickly turn towards the Tetraodontidae and strike, sometimes resulting in consumption.

Discussion

This study investigated prey naïveté to *P. volitans* and predator-prey interactions between Pomacentridae and Tetraodontidae and *P. volitans* in the San Blas archipelago, Panama. Pomacentridae and Tetraodontidae spent significantly more time within the same site of *P. volitans* than Serranidae, indicating that these families are naïve to *P. volitans*. The null hypothesis that there is no difference between time spent by Pomacentridae and Tetraodontidae within the same site as *P. volitans* or Serranidae is rejected. This corroborates previous findings that Pomacentridae and other small fish are naïve to *P. volitans* (Gamazo 2013; Kindinger 2014) using a different experimental design based on time spent within the same site as native and invasive predators *in situ*. This new information is valuable because it tests in the field, theories that have been developed under controlled conditions.

The phenomenon of prey naïveté in Pomacentridae and Tetraodontidae, more specifically, the lack of antipredator behavior could be due to many factors. A mechanistic explanation could be that the small fish simply do not have the physical ability (due to lack of morphological structures or neural pathways) to detect *P. volitans* so they have no reason to move away. A study on Pomacentridae response to predatory threat signals showed that Pomacentridae did not respond to any signals, olfactory, visual, or a combination of both, from *P. volitans* (Lonnstedt and McCormick 2013). This illustrates the cryptic nature of *P. volitans*. A phylogenetic explanation for the lack of response to *P. volitans* cues could include lack of historical evolutionary pressure on Pomacentridae to evolve mechanisms to process threat signals from *P. volitans*. It is possible that in the context of risk sensitive courtship in Pomacentridae, fitness is increased by ignoring *P. volitans*. It may be worth the risk of consumption for males to perform courtship behavior and have the possibility of copulation even with *P. volitans* present. This was shown in *Stegastes leucostictus* in an experiment where they exhibited anti-predator behavior when exposed to *P. volitans*, but their risk-sensitive mating behavior was unchanged (Black et al. 2014). In the current study, no Pomacentridae mating behavior was observed, suggesting that the difference in time spent within the same site as *P. volitans* is better explained by prey naïveté than a calculated fitness increase. There do not appear to be ontological explanations for prey naïveté to *P. volitans*. While it has been demonstrated that Pomacentridae have the ability to alter their behavioral response to native predators (*Cephalopholis microprion*), exhibiting stronger antipredator behavior after being conditioned to learn *C. microprion* cues, the same effect was not present when tested with *P. volitans* (Lonnstedt and McCormick 2013).

Much less research on interactions between *P. volitans* and Tetraodontidae has been published. In the current study, *Canthigaster rostrata,* the Atlantic sharpnose puffer, appears to have been the preferred target for *P. volitans* to strike at, but were hunted, for significantly less time than Pomacentridae. This could be explained by the type of hunting that was used by *P.*

volitans. When hunting Pomacentridae, *P. volitans* displayed the characteristic behavior described by Cure et al. (2012), fanning out its pectoral fins, appearing to concentrate on one fish, and slowly moving towards the prey. This process was time consuming and did not result in any consumptions during the observation periods. A previously undescribed hunting action pattern was observed in which *C. rostrata* approached *P. volitans* from behind, appearing to be lured by the dorsal and pectoral fins of the *P. volitans*. When the *C. rostrata* was close to the fins, the *P. volitans* would quickly turn towards the puffer and strike. It was observed on occasion that the *C. rostrata* would bite the dorsal or pectoral fin of the *P. volitans*, resulting in the same turn and strike motion. This behavior was also observed in *P. volitans* by Harwell (2017). A similar behavioral pattern was described in the Scorpionfish *Iracundus signifer,* where, prior to feeding, *I. signifer* raised its dorsal fin and used it to lure and distract small fish, leading to consumption (Shallenberger and Madden 1973). It is compelling that a fish of the same family displays the same class of behavioral pattern. It is possible that the biting behavior exhibited by *C. rostrata* is territorial in nature, as Sikkel (1990) did not specify if territorial aggression was solely directed towards conspecifics.

The comparatively low amount of time spent by *P. volitans* actively hunting Tetraodontidae and high number of strikes could be associated with behavioral syndromes. Behavioral syndromes are defined as a suite of correlated behaviors reflecting consistency in one individual in behavior across two or more situations (Sih et al. 2004). Humans with similar phenotypic characteristics may have different personalities. Some are more bold, others more aggressive, and others more calm. Generally, these personality characteristics are present in more than one situation. An entire population shifts their aggression levels depending on the situation, but some remain consistently more aggressive than others across different situations. These individuals may do well in competitive contexts, but less well in parental care or situations requiring caution (Sih et al. 2004). It was observed previously that *P. volitans* travel different distances from their dens when hunting (Harwell 2017). It is possible that there is an activity level behavioral syndrome that links activity levels, distance traveled to hunt, and type of hunting employed in *P. volitans.* For example, some *P. volitans* may be more likely to hunt Tetraodontidae using the luring action pattern if they stayed closer to their dens and had lower activity levels (low activity behavioral type).

Pterois volitans also showed substantial phenotypic plasticity in scale patterns. Many were an even mix of dark and light coloration, but some were substantially lighter or darker. While all *P. volitans* observed were > 10 cm in length, they varied between 6 and 12" TL.

It is possible that *P. volitans* are actively hunting both Pomacentridae and Tetraodontidae when their fins are flared and appear to be concentrating on Pomacentridae. Their dorsal and pectoral fins appear to serve multiple functions including herding small focal fish and luring other small fish. These actions are not mutually exclusive, in fact, if the pectoral and dorsal fins do lure small fish, it would be impossible to herd fish and not attract other fish. It is possible that the higher strike frequency at Tetraodontidae is the result of the luring properties of *P. volitans* fins being more effective at attracting fish than the herding properties.

A comparison of the feeding ecology of *P. volitans* and *C. cruentata* may reflect the different feeding strategies used by the two species. Both fish are piscivores, feeding on small reef fish (Cote and Maljkovic 2010; Nagelkerken 1979). *Pterois volitans* utilize techniques including sit-and-wait, stalking, and the observed luring behavioral pattern. Red lionfish do not travel far from their dens to hunt and generally are slow-moving predators (Harwell 2017). *Cephalopholis cruentata* employ sit-and-wait as well as rapid hunting techniques, rapidly swimming through hard coral beds, sticking their heads in crevices, appearing to look for prey. This could be one reason that Pomacentridae and Tetraodontidae spent significantly less time in the presence of *C. cruentata*. This does not explain why Pomacentridae and Tetraodontidae spent so much time within the same site as *P. volitans*.

Predator-prey interactions between *P. volitans* and their prey have been studied before. It was found in a previous study that activity level and time spent hunting were significantly higher when there were overcast skies with greater than 70% cloud cover (Cote and Maljkovic 2010). In this study, no evidence was found that overcast conditions lead to higher activity levels and hunting time. This may be due to the small sample size of the study.

It has been suggested that groupers (Serranidae) may be able to counter the negative effects of *P. volitans* on small reef fish (Ellis and Faletti 2016; Mumby et al. 2011). This study found no significant effect of Serranidae on average time spent by *P. volitans* hunting small reef fish. The Guna people's diet relies heavily on seafood, leading to overfishing in many parts of the Guna Yala archipelago as is evident by the lack of large fish on all reefs sampled. For Serranidae to have a negative effect on *P. volitans*, extremely high density of Serranidae must be present (Mumby et al. 2011). No Serranidae over the size of 12" TL were observed on any of the reefs surveyed. There was not a high enough density of Serranidae to affect the feeding ecology of *P. volitans,* and the *C. cruentata* that were present were not large enough to compete with *P. volitans*.

Ecological repercussions of prey naïveté to *P. volitans* have been well documented. The abundance of small native fish on coral reefs was reduced significantly when *P. volitans* were introduced, causing a loss of around five species on experimental reefs. A native grouper reduced the abundance of these fish by 35%, while *P. volitans* reduced the abundance by 90% (Albins 2013). Net recruitment of reef dwelling fish was reduced by an average of 79% on experimental reefs exposed to *P. volitans* (Albins and Hixton 2008). Red lionfish consume herbivores such as parrotfish and damselfish (Morris Jr. and Akins 2009). These herbivores graze on macroalgae on the reefs. Herbivory by these species is an area-specific rate, so that, if sudden changes in area of grazable substrate occur, grazing intensity will be strongly impacted (Mumby and Steneck 2008). In 1983, an unidentified pathogen reduced the population of *Diadema antillarum* by more than 93% in the Caribbean, resulting in a phase shift in which local reef community dominance shifted from live coral cover to macroalgal cover (Lessios 2004). The rapid die off of algal consuming organisms increases the availability of macroalgae for the remaining organisms, overwhelming their appetite, and providing opportunities for macroalgae to escape predation once predators are satiated (Mumby and Steneck 2008). When macroalgae becomes the dominant cover in a reef habitat, large number of corals die, disrupting the food web interactions,

effecting the tourism industry and fisheries (Hughes et al. 2007). The loss of *D. antillarum* has already lead to phase shifts in some regions (Lessios 2004). Herbivorous fish such as parrotfish still control macroalgae on some reefs, but the decreased pressure on macroalgae on reefs with high lionfish densities, consuming herbivores, could lead to more phase shifts and loss of healthy coral reef habitat.

Humans have contributed to the invasion of *P. volitans* in a plethora of ways. The transportation of exotic fish around the world through the aquarium trade, the original introduction to Atlantic waters in the 1980's, and overfishing of possible natural enemies of introduced exotic species are all causes of the current invasion.

The aquarium trade has been recognized as a vector for non-native marine fish introductions (Padilla and Williams 2004; Semmens et al. 2004). The aquarium trade is an unregulated, highly lucrative, industry, making it possible for any person to order aquatic invasive species to own (Padilla and Williams 2004). Ornamental exotic fish have been found in high densities off the coast of Florida, where it was concluded that they were introduced from aquaria (Semmens et al. 2004). *Pterois volitans* are thought to have been one of these introductions as they are popular fish in the aquarium trade and during the time of their introduction, non-native fish were being found by divers along the coast of Florida at a disproportionally high rate (Cote et al. 2013; Semmens et al. 2004).

Fishing is ubiquitous in Guna Yala, providing food for tourists and local towns. In areas with food webs that are already strained from overfishing of top predators, such as groupers, smaller predators, called mesopredators, increase in abundance. This increase adds pressure to small fish including herbivores in a phenomenon called mesopredator release (Prugh et al. 2009). This release often destabilizes communities and can lead to local extinctions. Mesopredator release may have been a factor in reefs that were sampled in this study. No large Serranidae were observed, but smaller *C. cruentata* were abundant. If this effect is amplified by even more pressure from fishermen, there is a large population of *P. volitans*, and native herbivores such as *D. antillarum* are depleted, there is a serious danger of loss of reef habitat.

Unfortunately, *P. volitans* appear to have no natural enemies in the Guna Yala archipelago. The only way to remove *P. volitans* is to do so manually. Studies have been completed, assessing the functionality of manually hunting *P. volitans* to reduce their impact on coral reef ecosystems (Frazer et al. 2012; Leon et al. 2013). By removing *P. volitans* on reefs in the Cayman Islands monthly, it was possible to reduce the density and shift the size frequency distribution of the remaining red lionfish to smaller sizes (Frazer et al. 2012). It was found separately that in locations where lionfish were removed, there was a 2.76 - 4.14 fold reduction in *P. volitans* biomass (Leon et al. 2013). The Reef Environmental Education Foundation (REEF) and similar organizations have held fishing events that led to the capture of more than 10,000 *P. volitans* and *P. miles* in the Bahamas and Florida (Aguilar-Perera 2012). The "Eat Lionfish" campaign has been endorsed by many scientists as well as the National Oceanic and Atmospheric Administration of the United States. While this is an attractive short-term solution, it is imperative that there is a plan to support a market for *P. volitans* if consumers develop a

taste for the fish. The movement could become counterproductive if red lionfish become valuable enough to farm or take from their native regions (Aguilar-Perera 2012).

Alternative uses for *P. volitans* lie in cancer research. The venom from *P. volitans* reduced the number of tumors in lab mice in controlled studies and it is thought that a medium sized dose of venom could be optimum to treat cancer cells (Balashubashini et al. 2006). These studies all promote the use of *P. volitans* and incentivize collection.

Only two out of the seven sites sampled in this study had populations of *P. volitans*. This means that the invasion has not reached every reef in Guna Yala. One way that *P. volitans* spreads is through egg dispersal. Sites where *P. volitans* were present appeared to have stronger currents and were more exposed to deeper ocean than those where they were not found. This supports the idea that the eggs of *P. volitans* are dispersed through oceanic currents to new locations (Cote et al. 2013; Freshwater et al. 2009). With the combination of removal by humans, management of coral fish populations, and reduced fishing pressure, it is possible that the negative effects of *P. volitans* on coral communities can be combatted. Marine protected areas have already started to appear in Guna Yala. Local communities have started creating marine protected areas around their islands. In Digir, one of these small protected areas was surveyed and no *P. volitans* were found. Local level monitoring of these areas is important to ensure that *P. volitans* remain absent. Ultimately, these protected areas could be key to combatting the lionfish invasion. If large native apex predators return to these areas, the combination of competition, consumption, and human removal of *P. volitans* may be able to control the invasion (Mumby et al. 2011).

A possible source of error could have come from observer bias as blinding was not possible. As this was an observational study *in situ*, the observer always knew which sample was being recorded. There was a relatively small sample size even though a two-week long period was allotted to collect data for this study. The first week was spent on Isla Tigre, where no *P. volitans* were found. The second week was spent on El Porvenir where two days of sampling were needed to locate *P. volitans*. A total of only five days were spent collecting data on *P. volitans*. This significantly reduces the power of the data. Steps were taken to reduce effects of the observer on the behavior of *P. volitans* and prey. It is possible that the fish were aware of the observer's presence, leading to a change in behavior. Difficulties in observing *P. volitans* at depths greater than 3m arose as the breath of the observer could not be held for a full 10 minutes. As much time as possible was spent observing from 3 meters, but occasionally, the observational distance was further. For this reason, all samples were taken in water < 10 m deep. Many of these problems could be solved by recording video of *P. volitans* trials with a digital camera with a zoom to analyze in the lab. SCUBA gear would also be invaluable for collecting more complete data on the overall density of *P. volitans* on coral reefs.

Conclusions and Future Studies

This study provides evidence, from *in situ* observation, of prey naïveté behavior in Pomacentridae and Tetraodontidae in the presence of *P. volitans* in the Guna Yala archipelago. Results show that these two families spent significantly more time within the same site as the

invasive *P. volitans* than native species *C. cruentata.* Thus the null hypothesis that there is no difference between time spent by Pomacentridae and Tetraodontidae within the same site as *P. volitans* or Serranidae was rejected. A new *P. volitans* action pattern was described for the first time. This action pattern was specifically found in the interaction of Tetraodontidae individuals that appeared to be lured toward the pectoral and dorsal fins of *P. volitans* before being struck at. *Pterois volitans* were found on two reefs in the Punta San Blas region and were absent from two reefs in the Punta San Blas region and three in the Digir region. Cloud cover and the presence of Serranidae did not have a significant effect on *P. volitans* predator-prey interactions.

Future studies could compare percent macroalgae cover on reefs with varying densities of *P. volitans* as well as the effects of mesopredator release on coral reefs in Guna Yala. The possible luring properties of *P. volitans* dorsal and pectoral fins, and the biting behavior observed by *C. rostrata* should be studied further. Studies trying to identify behavioral syndromes in *P. volitans* could compare distance traveled from den to activity levels and hunting strategies of individuals. Phenotypic plasticity in coloration could also be compared with hunting times, depth, and prey type.

Pterois volitans have taken over coral reefs throughout the west coast of the Atlantic Ocean, causing massive damage to these ecosystems. Many factors have been suggested as causes for the rapid growth. This study has confirmed that prey naïveté is an important factor with Pomacentridae and Tetraodontidae spending more time in the presence of *P. volitans* than a native predator.

Appendix A

Table 1. Survey locations. Locations in bold indicate sites where *P. volitans* were observed.

Region	Site	GPS
Digir	Isla Tigre Trench	9°26'8.82"N 78°31'31.21"W
Digir	Isla Tigre Shelf	9°26'1.76"N 78°31'13.26"W
Digir	Isla Buga	9°28'42.12"N 78°30'52.30"W
Punta San Blas	**Porvenir Front 1**	**9º33'27.0"N 78º56'45.0"W**
Punta San Blas	**Isla Aguadargana Complex**	**9º33'08.5"N 78º56'42.1"W**
Punta San Blas	House Reef	9°33'09.9"N 78°57'14.2"W
Punta San Blas	Isla Aguadargana Side Reef	9°33'07.7"N 78°56'57.5"W

Appendix B

Table 2. Ethogram describing Timed (FH, WS) and Count (S, C) events.

|	
Fish Hunting (FH) *Timed*	Lionfish pectoral fins flared, focusing on one fish (Cure et al. 2012). Time starts at first fin flare and lasts until fins are unflared, prey escapes, or prey is consumed. Only one fish can be hunted at a time. Serranidae focus directly on one fish. Includes time spent striking.
Within Site (WS) *Timed*	Fish is within the same site as the focal predator. Site is defined by geographic features at the beginning of each sample period. If no defining geographic features are present, site is a circle 1 m in diameter around the focal predator (Gamazo 2013). Time starts when predator and prey enter same site and end when the prey is consumed or either predator or prey exits the site without the other. If both change site together, it is still counted as same site.
Strike (S) *Count*	Successful and unsuccessful attacks on potential prey are both counted as one strike (Cure et al. 2013). Strikes do not result in consumption of the prey.
Consumption (C) *Count*	Successful capture of prey resulting in the prey being consumed by the predator (Cure et al. 2013).

Appendix C

Figure 1. Study sites from top left to bottom right: Panama, San Blas Archipelago, Porvenir region, Digir region. Thumb tacks mark study sites. In the bottom left map, red circles mark sites with *P. volitans* (N = 7).

Appendix D
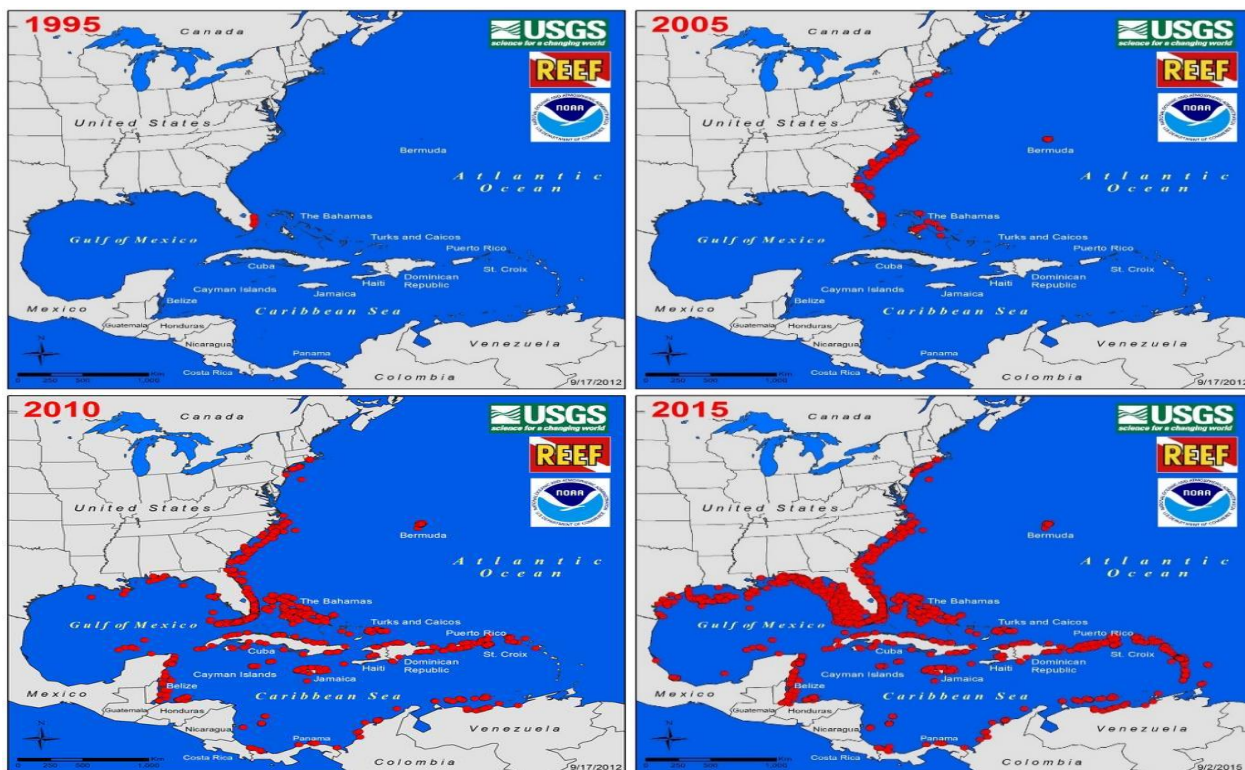
Figure 2. *Pteroios volitans* spatial distribution in 1995, 2005, 2010, and 2015 (top left to bottom right). Data are from the REEF, USGS, and NOAA databases. Images courtesy of usgs.gov.
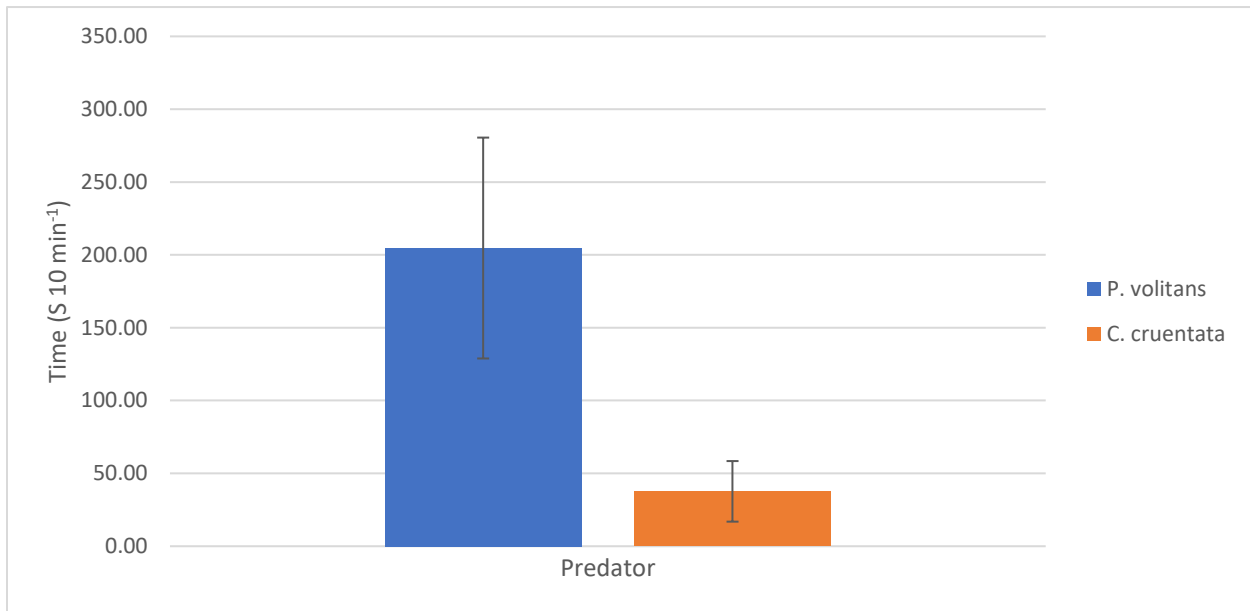
Appendix E
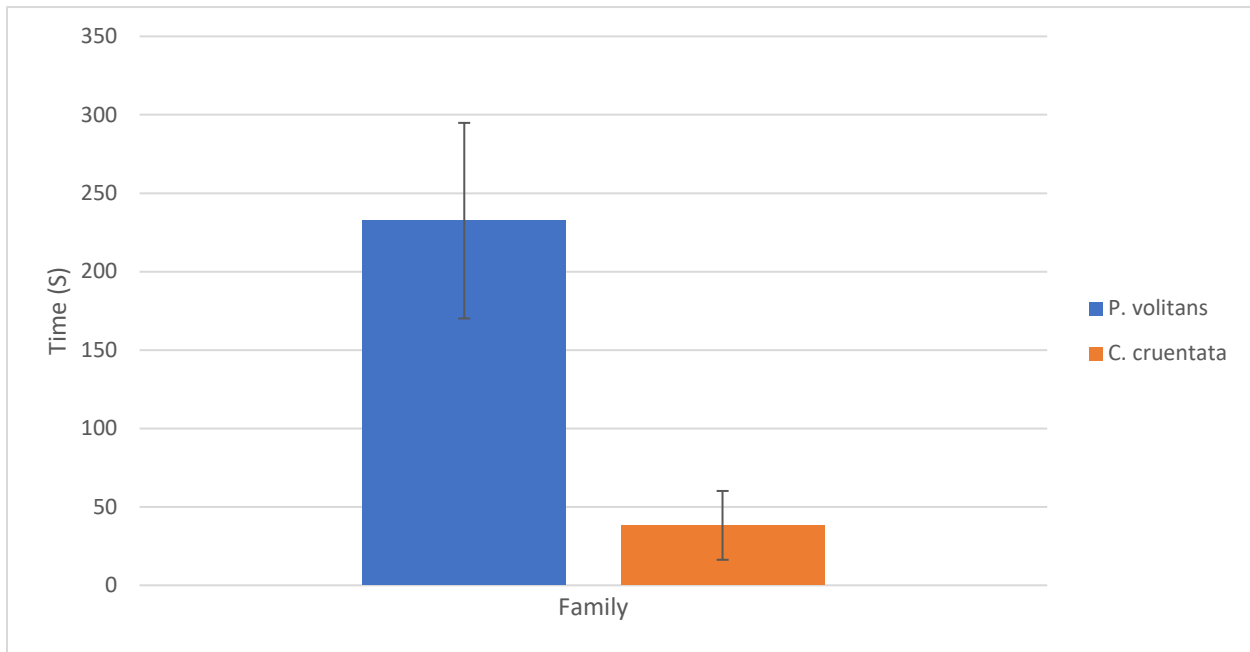
Figure 3. Average time spent by Pomacentridae and Tetraodontidae within the same site as *P. volitans* and *C. cruentata* during 600 second observations ($N_{P.\ volitans} = 33$, $N_{C.\ cruentata} = 24$).
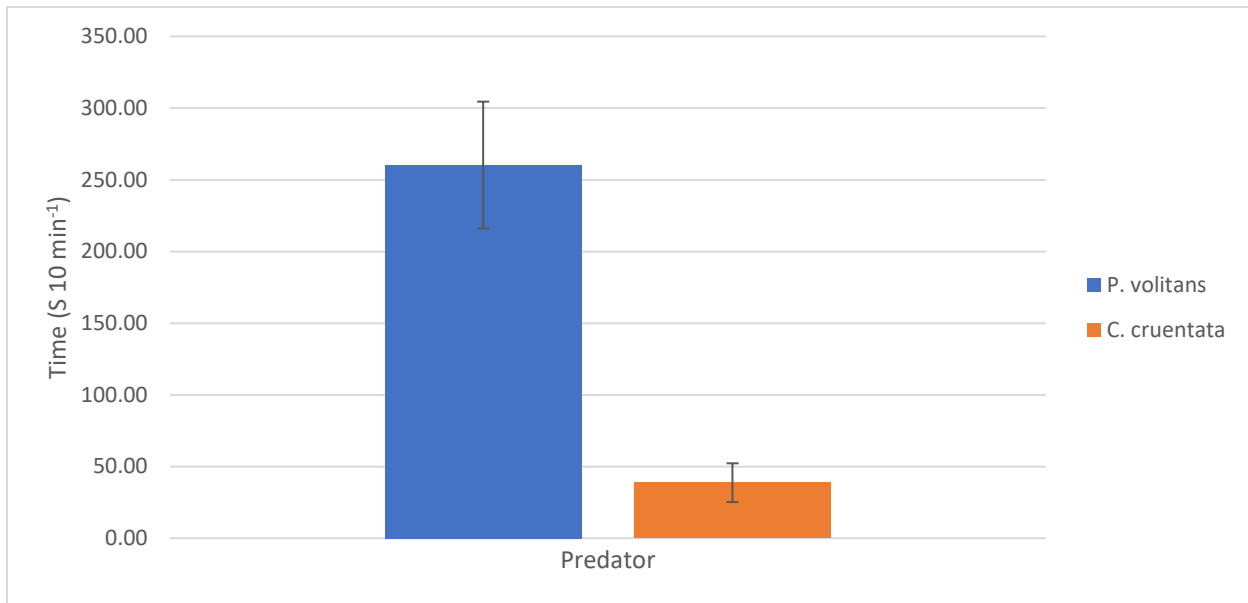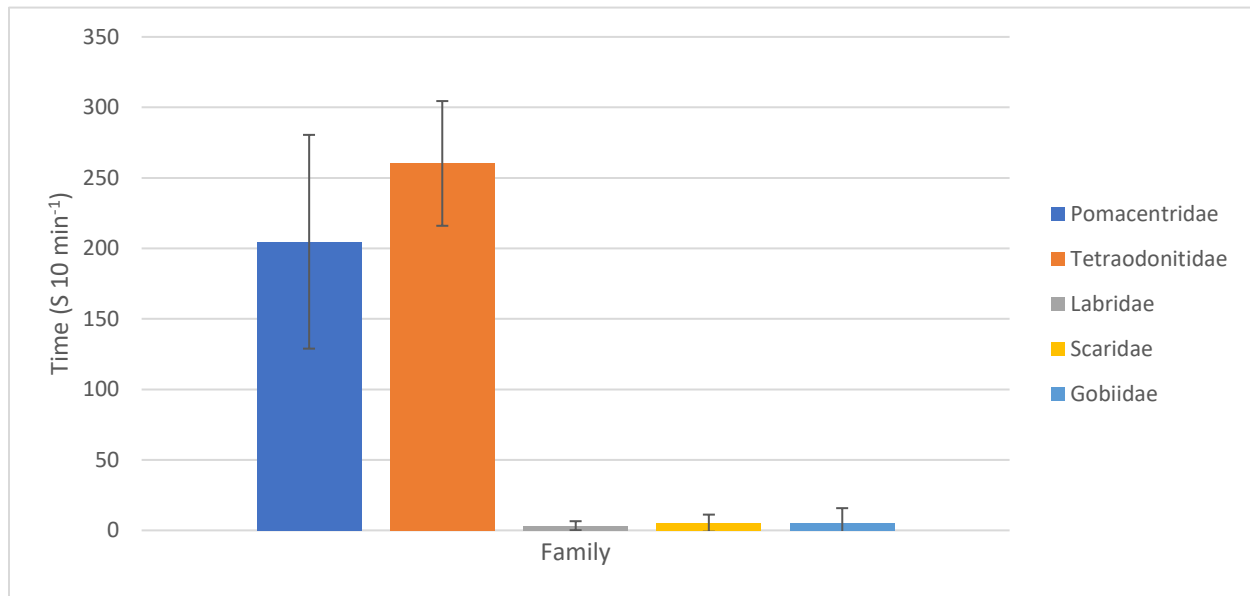
Appendix F

Figure 4. Average time spent by Pomacentridae spp. within the same site as *P. volitans* and *C. cruentata* during 600 second observation periods ($N_{P.\ volitans} = 33$, $N_{C.\ cruentata} = 24$). Error bars represent 95% CI.
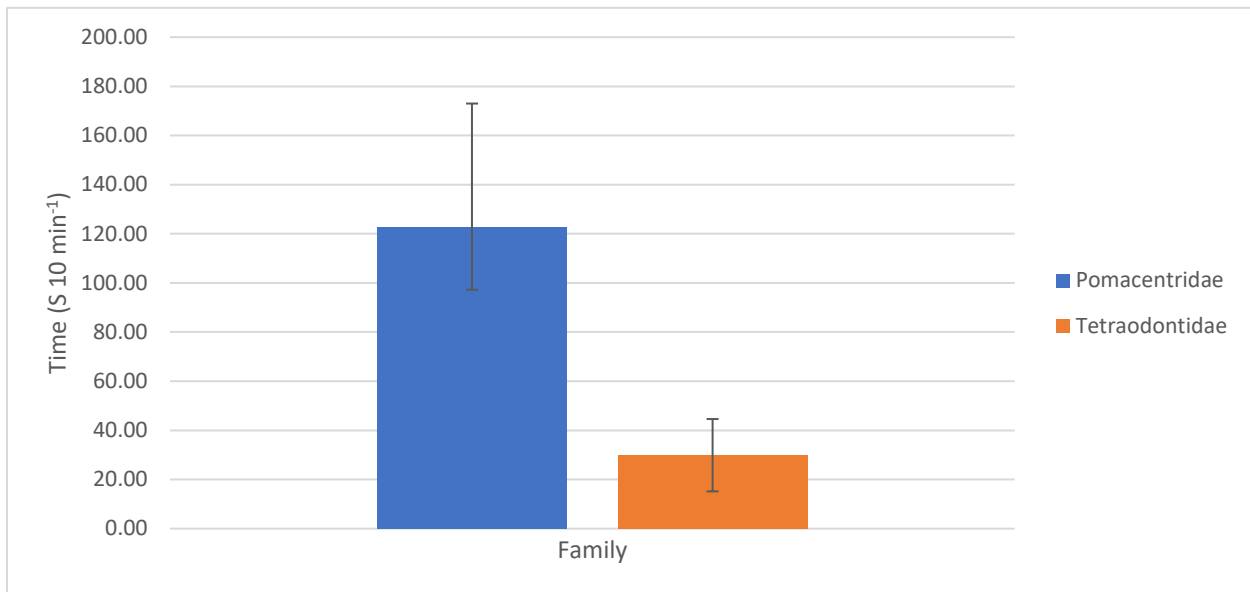
Appendix G

Figure 5. Average time spent by Tetraodontidae within the same site as *P. volitans* and Serranidae during 600 second observation periods ($N_{P.\ volitans} = 33$, $N_{C.\ cruentata} = 24$). Error bars represent 95% CI.
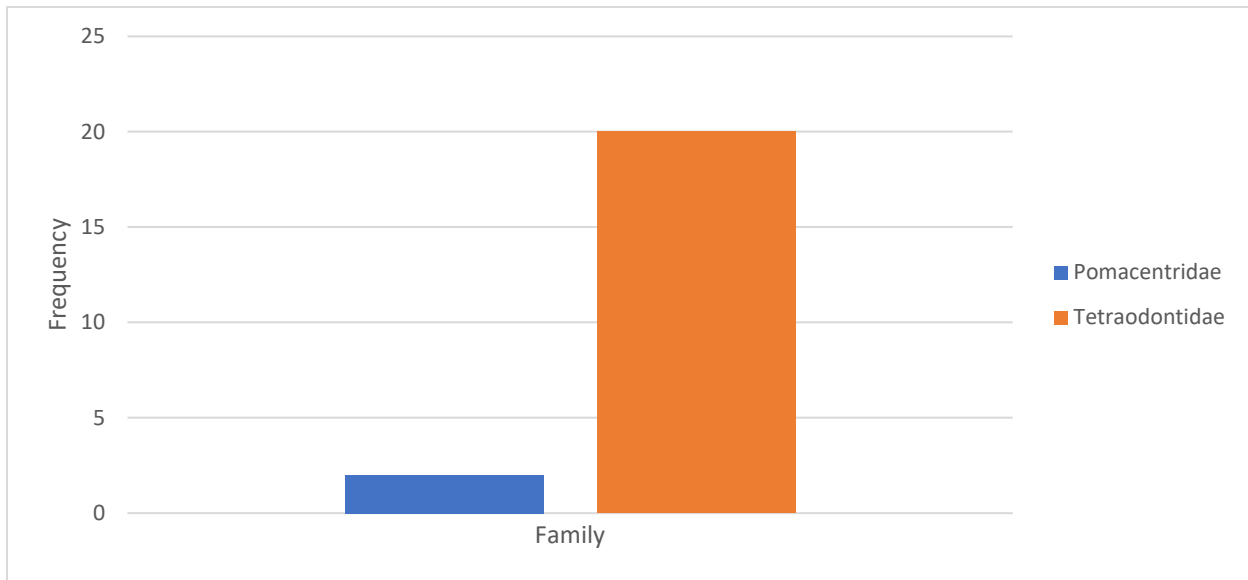
Appendix H

Figure 6. Average time spent by different teleost families within the same site as *P. volitans* during thirty-three, 600 second observation periods. Error bars represent 95% CI.
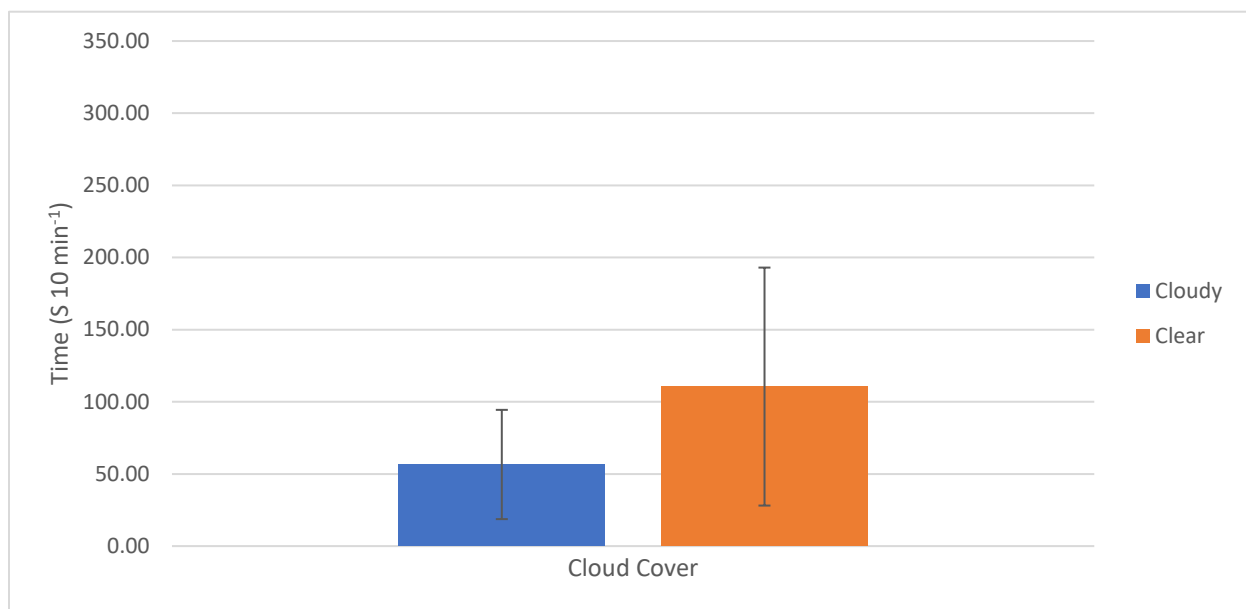
Appendix I

Figure 7. Average time spent by *P. volitans* hunting Pomacentridae and Tetraodontidae during thirty-three, 600 second observation periods. Error bars represent 95% CI.
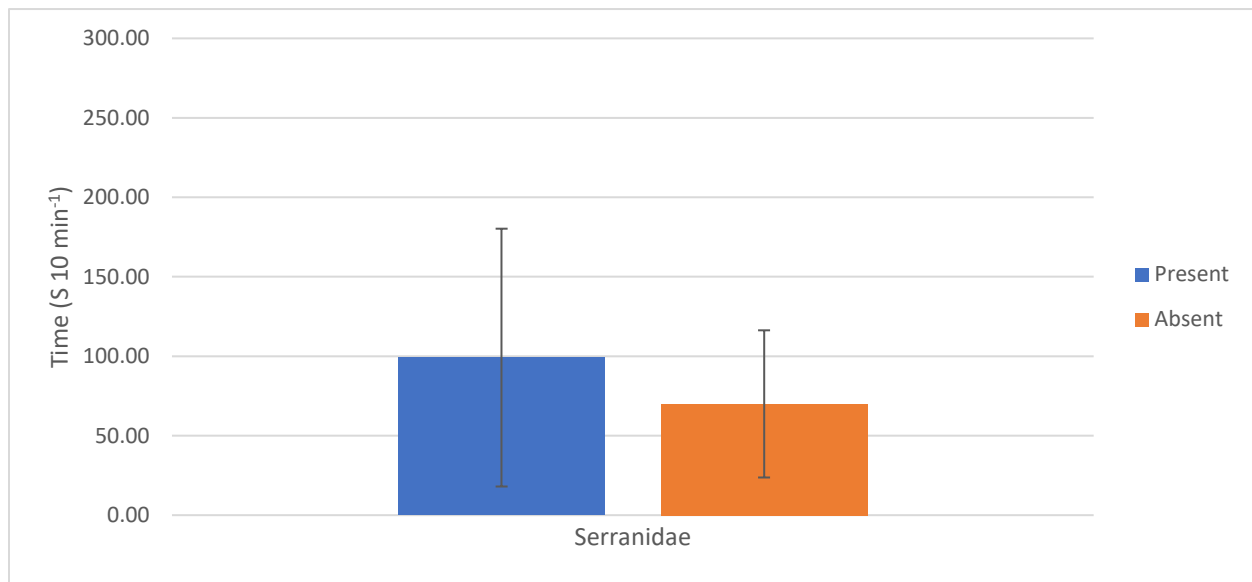
Appendix J

Figure 8. Number of strikes at Pomacentridae and Tetraodontidae by *P. volitans* over all 33 observation periods ($N_P = 2$, $N_T = 20$).

Appendix K

Figure 9. Average amount of time spent by *P. volitans* hunting under cloudy (>75% cloud cover) and clear (<75% cloud cover) conditions during thirty-three, 600 second observation periods ($N_{Cloudy} = 21$, $N_{Clear} = 12$). Error bars represent 95% CI.

Appendix L

 Figure 10. Average time spent by *P. volitans* hunting with *C. cruentata* present and absent during 600 second observation periods ($p_p = 7$, $p_a = 26$). Error bars represent 95% CI.

Appendix M

Figure 11. Two *P. volitans* hunting together on Isla Aguadargana Complex (9º33'08.5"N 78º56'42.1"W).

Appendix N

Figure 12. One *P. volitans* hunting alone on Porvenir Front 1 (9º33'27.0"N 78º56'45.0"W).

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References:

Agudo E. A., Salas, E. K. (2014). Lionfish abundance, size structure and spatial distribution along the Venezuelan coast (*Pterois volitans*, Pteroinae: Scorpaenidae). *Rev Biol Trop, 62,* 151-158.

Aguilar-Perera, A. (2012). Eating lionfish: An effective solution to control its invasion? *Proceedings of the 65th Gulf and Caribbean Fisheries Institute,* Santa Marta, Colombia, November 5-9, 2012.

Albins, M. A. (2013). Effects of invasive Pacific red lionfish *Pterois volitans* vs. a native predator on Bahamian coral-reef fish communities. *Biological Invasions, 15* (1), 29-43.

Albins, M. A., Hixton, M. A. (2008). Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser, 367*, 233-238.

Albins, M. A., Hixon, M. A. (2013). Worst case scenario: potential long-term effects of intensive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean costal-reef communities. *Environ Biol Fishes*, *96*, 1151-1157.

Albins, M. A., Lyons, P. J. (2012). Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. *Mar Ecol Prog Ser, 448*, 1-5.

Andrefouet, S., Guzman, H. M. (2005). Coral reef distribution, status and geomorphology-biodiversity relationship in Kuna Yala (San Blas) archipelago, Caribbean Panama. *Coral Reefs, 24,* 31-42.

Balasubashini, M. S., Karthigayan, S., Somasundaram, S. T., Balasubramanian, T., Viswanathan, V., Raveendran, P, Menon, V. P. (2006). Fish venom (*Pterois volitans*) peptide reduces tumor burden and ameliorates oxidative stress in Ehrlich's ascites carcinoma xenografted mice. *Bioorganic & Medical Chemistry Letters, 16 (24),* 6219-6225.

Barbour, A. B., Montgomery, M. L., Adamson, A. A., Díaz-Ferguson, E., Silliman, B. R. (2010). Mangrove use by the invasive lionfish *Pterois volitans, 401*, 291-294.

Black, A., Weimann, S. R., Imhoff, V. E., Richter, M. L., Itzkowitz, M. (2014). A differential prey response to invasive lionfish, Pterois volitans: Prey naïveté and risk-sensitive courtship. *Journal of Experimental Marine Biology and Ecology, 460,* 1-7.

Buterfield, J. S. S., Díaz-Ferguson, E., Silliman, B. R., Saunders, J. W., Buddo, D., Mignucci-Giannoni, A. A., Searle, L., Allen, A. C., Hunter, M. E. (2015). Wide-ranging phylogeographic structure of invasive red lionfish in the Western Atlantic and Greater Caribbean. *Marine Biology*, *162* (4),1-8.

Clifton, K. E., Kim, K., Wulff, J. L. (1997). A field guide to the reefs of Caribbean Panama with an emphasis on Western San Blas. *Proc 8th Coral Reef Sym, 1,* 167-184.

Côté, I. M., Green, S. J., Hixton, M. A. (2013). Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biological Conservation, 164,* 50-61.

Côté, I. M., Maljkovic, A. (2010). Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser, 404*, 219-225.

Cox, J. G., Lima, S. L. (2006). Naïveté and an aquatic-terrestrial dichotomoy in the effects of introduced predators. *TRENDS in Ecology and Evolution, 21* (12), 674-680.

Cure, K., Benkwitt, C. E., Kindinger, T. L., Pickering, E. A., Pusack, T. J., McIlwain, J. L., Hixon, M. A. (2012). Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. *Mar Ecol Prog Ser, 467*, 181-192.

Eddy, C., Pitt, J., Morris Jr, J. A., Smith, S., Goodbody-Gringley, G., Bernal, D. (2016). Diet of invasive lionfish (*Pterois volitans* and *P. miles*) in Bermuda. *Mar Ecol Prog Ser, 588,* 193-206.

Ellis, R. D., Faletti, M. E. (2016). Native grouper indirectly ameliorates the negative effects of invasive lionfish. *Mar Ecol Prog Ser, 558*, 267-279.

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.

Freshwater, W. D., Hines, A., Parham, S., Wilbur, A., Sabaoun, M., Woodhead, J., Akins, L., Purdy, B., Whitfield, P. E., Paris, C. B. (2009). Mitochondrial control region sequence analyses indicate dispersal from the US East Coast as the source of the invasive Indo-Pacific lionfish *Pterois volitans* in the Bahamas. *Mar Biol, 155* (6), 2123-1221.

Gamazo, A. A. (2013). *Ecology and evolution of the lionfish invasion of Caribbean coral reefs: resistance, adaption, and impacts* (master's thesis). University of North Carolina at Chapel Hill, Chapel Hill, United States.

Green, S. J., Cote, I. M. (2008). Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs, 28* (1), 107.

Guzman, H. M., Guevara, C., Castillo, A. (2003). Natural disturbances and mining of Panamanian coral reefs by indigenous people. *Conservation Biology, 17* (5), 1396-1401.

Haddad Jr, V., Martins, L. A., Makyama, H. M. (2003). Injuries caused by scorpionfishes (*Scorpaena plumieri* Bloch, 1789 and *Scorpaena brasiliensis* Cuvier, 1829) in the Southwest Atlantic Ocean (Brazilian coast): epidemiologic, clinic and therapeutic aspects of 23 stings in humans. *Toxicon, 42* (1), 79-83.

Harwell, A. (2017). Into the lion's den: Feeding behavior and territorial range of Pterois volitans on 3 reefs near El Porvenir, Guna Yala. *Independent Study Project (ISP) Collection.* 2561.

Hixon, M. A., Green, S. J., Albins, M. A., Akins, J. L., Morris Jr, J. A. (2016). Lionfish: a major marine invasion. *Mar Ecol Prog Ser, 558,* 161-165.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology, 17*, 360-365.

Humann, P., Deloach, N. (2014). Reef fish identification: Florida Caribbean Bahamas 4th edition. Jacksonville, Florida: New World Publications, Inc.

Ingeman, K. E. (2016). Lionfish cause increased mortality rates and drive local extirpation of native prey. *Mar Ecol Prog Ser, 558,* 235-245.

Kimball, M. E., Miller, J. M., Whitfield, P. E., Hare, J. A. (2004). Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Mar Ecol Prog Ser, 283*, 269-278.

Kindinger, T. L. (2014). Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). *Environ Biol Fish*, *98* (2), 487-498.

Kochzius, M., Soller, R., Khalaf, M. A., Blohm, D. (2003). Molecular phylogeny of the lionfish genera *Dendrochirus* and *Pterois* (Scorpaenidae, Pteroinae) based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution, 28* (3), 396-403.

Leon, D. R., Vane, K., Bertuol, P., Chamberland, V. C., Simal, F., Imms, E., Vermeji, M. J. A. (2013). Effectiveness of lionfish removal efforts in the southern Caribbean. *Endang Species Res, 22,* 175-182.

Lessios, H. A. (2004). *Diadema antillarum* populations in Panama twenty years following mass mortality. *Coral Reefs, 24*, 125-127.

Linsley, B. K., Dunbar, R. B., Wellingon, G. M., Mucciarone, D. A. (1994). A coral-based reconstruction of intertropical convergence zone variability over Central America since 1707. *Journal of Geophysical Research, 99* (C5), 9977-9994.

Lionfish Distribution, 1995. (2016, July 21). Retrieved from https://www.usgs.gov/media/images/lionfish-distribution-1995

Lonnstedt, O. M., McCormick, M. I. (2013). Ultimate predators: Lionfish have evolved to circumvent prey risk assessment abilities. *PLoS ONE, 8* (10), 1-8.

Lovell, S. J., Stone, S. F., Fernandez, L. (2006). The economic impacts of aquatic invasive species: A review of the literature. *Agricultural and Resource Economics Review, 35* (1), 195-208.

Miehls, A. L. J., Mason, D. M., Frank, K. A., Krause, A. E., Peacor, S. D., Taylor, W. W. (2009). Invasive species impacts on ecosystem structure and function: A comparison of Oneida Lake, New York, USA before and after zebra mussel invasion. *Ecological Modelling, 220*, 3194-3209.

Morris Jr., J. A., Akins, J. L. (2009). Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamain archipelago. *Environ Biol Fish, 86*, 389-398.

Morris Jr. J. A., Akins, J. L., Barse, A., Cerino, D., Freshwater, D. W., Green, S. J., Munoz, R. C., Paris, C., Whitfield, P. E. (2008). Biology and ecology of the invasive Lionfishes, *Pterois miles* and *Pteroois volitans. Proceedings of the 61st Gulf and Caribbean Fisheries Institute*, Gosier, Goudeloupe, French West Indies, November 10-14, 2008.

Mumby, P. J., Harborne, A. R., Brumbaugh D. R. (2011). Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE, 9* (6), 1-4.

Mumby, P. J., Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology and Evolution, 23* (10), 555-563.

Nagelkerken, W. P. (1979). Biology of the Graysby, *Epinephelus cruentatus*, of the coral reef of Curacao. *Studies on the Fauna of Curacao and other Caribbean Islands, 60* (1), 1-118.

Padilla, D. K., Williams, S. L. (2004). Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Front Ecol Environ*, *2* (3), 131-138.

Pejchar, L., Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution 24 (9),* 497-504.

Pimiento, C., Nifong, J. C., Hunter, M. E., Monaco, E., Silliman, B. R. (2013). Habitat use patterns of the invasive red lionfish *Pterois volitans*: a comparison between mangrove and reef systems in San Salvador, Bahamas. *Marine Ecology, 36* (1), 28-37.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., Brashares, J. S. (2009). The rise of the Mesopredator. *BioScience, 59* (9), 779-791.

Shallenberger, R. J., Madden, W. D. (1973). Luring behavior in the Scorpionfish, *Iracundus signifer*. *Behavior, 47* (1), 33-47.

Sih, A., Bell, A., Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *TRENDS in Ecology and Evolution, 19* (7), 372-378.

Sikkel, P. C. (1990). Social organization and spawning in the Atlantic sharpnose puffer, *Canthigaster rostrata* (Tetraodontidae). *Environmental Biology of Fishes, 27,* 243-254.

Semmens, B. X., Buhle, E. R., Salomon, A. K., Pattengill-Semmens, C. V. (2004). A hotspot of non-native marine fishes: evidence for the aquarium trade as an invasion pathway. *Mar Ecol Prog Ser, 266,* 239-244.

Smith, B. D., Zeder, M. A. (2013) The onset of the Anthropocene. *Anthropocene, 4*, 1-6.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift fur Tierpsychologie, 20,* 410-433.

Valen, L. V. (1977). The Red Queen. *The American Naturalist, 111* (980), 809-810.