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Thesis of Abigail Ehlers Kimbrel

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

PREDATION EFFICIENCY OF LIONFISH (*PTEROIS VOLITANS* AND *P. MILES*) IN
DIFFERING LEVELS OF HABITAT COMPLEXITY

By

Abigail Ehlers Kimbrel

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

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Abstract

The invasion of the Indo-Pacific lionfish (*Pterois sp.*) into the Atlantic and Caribbean has received attention around the globe. Venomous spines, over-sized fanlike pectoral fins, slow movement, and novel feeding strategies have allowed lionfish to become effective apex-predators. Recent research has determined that lionfish use inshore mangrove habitats as foraging grounds, which are also used as nursery habitats for juvenile fish, thus reducing recruitment of native fish populations. The purpose of this study was three-fold: (1) determine the predation efficiency of lionfish in differing mangrove habitat complexities, (2) examine the influence of temperature and behavior of prey commonly found in mangroves, including Mosquitofish (*Gambusia sp.*), mummichog (*Fundulus sp.*), and grass shrimp (*Palaemonetes paludosus*) on lionfish predation efficiency, (3) compare the predation efficiency of lionfish to a native predator – lane snapper *Lutjanus synagris* – under the same parameters. We found that complexity level, complexity type, temperature, and prey significantly affects lionfish predation efficiency. However, the size of the predator, predator maneuverability within the habitat, and the amount of cover provided for prey to hide behind does not significantly affect lionfish predation efficiency. In comparison to the native lane snapper, we found that temperature, predator size and overall habitat complexity significantly affects lane snapper predation efficiency whereas complexity level and type have no significant affect.

Key words: Lionfish, Predation Efficiency, Habitat Complexity, Mangrove, Lane Snapper

Introduction

The introduction of the Indo-Pacific lionfish *Pterois* sp. into the western Atlantic Ocean and Caribbean Sea has led to the fastest invasion documented for a marine fish and one of the best documented marine invasions to date (Morris 2009, Côté and Smith 2018). Since the first documented sighting of lionfish off the coast of southeast Florida in 1985, the population has become established along the U.S. Atlantic coast, as far north as Maine seasonally, and around every island and along most of the Central and South American Atlantic coasts southward to central Brazil, as well as the Gulf of Mexico (Whitfield et al. 2002, Schofield 2009, Gonzalez et al. 2009, Schofield 2010, Ferreira et al. 2015). Lionfish have been found in nearly every natural habitat (i.e., coral reefs, seagrass beds, temperate hard bottom reefs) and man-made (i.e., artificial reefs) habitat throughout their invaded range to depths of more than 610 meters (m) (Schofield 2009, Gress et al. 2017, Côté and Smith 2018). The successful establishment of lionfish has presented a unique set of challenges to both native fauna and fisheries managers.

The rapid expansion of the lionfish population has received much attention from the scientific community. Although still largely unknown, many researchers have speculated that lionfish invasion may have catastrophic impacts on the marine ecosystem (e.g., Côté et al. 2013, Côté and Smith 2018). The diet of these predators has generated concern from scientists and the public, as they reportedly have a diet consisting of primarily crustaceans and teleost fishes. For example, in reef ecosystems, lionfish to consume 57 different species of reef fishes from at least 25 families (Jasper et al. 2018, Acero et al. 2019). Lionfish have also shown a dietary shift with increased size from primarily crustaceans to a more teleost-dominated diet (Côté et al. 2013, Jasper et al. 2018, Acero et al. 2019). Furthermore, lionfish are able to consume prey that is up to one-half of the predating lionfish's total body length, expanding their stomach up to 30 times its normal size (Fishelson, 1997). Due to their rate of population growth and associated predation, most lionfish research has focused on determining the impacts of the invasion on the reef community. For example, Albins and Hixon (2008) found that a single lionfish can reduce the abundance of small native fishes by 80% in five weeks on small patch reefs. Green et al. (2012) documented an average 65% decline in prey fish biomass in the Bahamas over two years following the lionfish invasion. Besides consuming prey fish, lionfish may compete with other predators for available prey species. In addition to the direct effects on coral reef ecosystems, the lionfish invasion may lead to potentially detrimental trophic cascades. These cascading trophic

interactions have been described by Albins and Hixon (2013) in which lionfish greatly decrease herbivorous fish biomass through predation. Consequently, macroalgae could potentially increase and overgrow corals due to the reduction in herbivory by scarid parrotfishes and labrid wrasses, thus also contributing to the structural degradation of the coral reef. As an exceptionally successful invader with significant effects on the native communities, the lionfish invasion may be one of the most damaging marine invasions to date (Sutherland et al. 2011, Albins and Lyons 2012, Albins and Hixon 2013).

The overall success of the lionfish invasion is often attributed to a variety of morphological, behavioral, and physiological characteristics that allow lionfish to be highly effective predators as well as providing protection from native predators in their invaded range (Albins and Hixon 2011, Albins and Lyons 2012). The first line of defense against potential native predators are 18 venomous spines located in the pelvic, dorsal, and anal fins (Morris 2009, Morris and Whitfield 2009, Albins and Lyons 2012). Furthermore, elongated fin rays, camouflaged coloration, and slow movement reduces their detectability by both predators and prey (Albins and Hixon 2011, Pimiento et al. 2015). Over-sized fanlike pectoral fins not only help lionfish stabilize themselves in the water column but are also used to corral and corner smaller prey (Allen and Eschmeyer 1973, Fishelson 1997, Albins and Lyons 2012). While approaching potential prey, lionfish are also able to produce jets of water directed towards their prey which may distract or confuse them. Regardless of approach tactic, the prey fish faces the attacking lionfish, increasing the likelihood of head-first capture and easy swallowing (Albins and Lyons 2012). This predatory strategy, unique to the lionfish, contributes to a higher degree of predation efficiency.

Although most of the lionfish research has speculated the impacts of the lionfish invasion on coral reef ecosystems, as habitat generalists, lionfish have been found in other critical non-reef ecosystems. Barbour et al. (2010) discovered lionfish colonizing in mangrove habitats in the Bahamas with further studies even suggesting that mangroves could serve as lionfish nurseries. One hypothesis is that lionfish preferentially settle in shallow habitats, like mangroves, before moving to deeper reefs as they grow larger (Claydon et al. 2012). Jud and Layman (2012) found that juvenile and young adult lionfish exhibited exceptionally high site fidelity in estuarine habitats over extended periods of time. In addition to being able to invade multiple types of habitats, lionfish are able to tolerate broad salinity and temperature regimes. In 2014, lionfish

were found in estuarine habitats near Jupiter, Florida, as far inland as 6.6 km from the ocean, demonstrating that lionfish are able to tolerate brief exposures to salinities as low as 1 part per thousand (ppt) (Jud et al. 2014). Kimball et al. (2004) and Barker et al. (2018) reported that lionfish have a broad thermal range between 10 and 38°C. Furthermore, mangrove visual census surveys conducted by Florida Fish and Wildlife (FWC) now report lionfish utilizing mangroves and inshore estuarine systems in southeast Florida (Claydon et al. 2012, Biggs and Olden 2011, Beal and Dark 2014, Pimiento et al. 2015, Andradi-Brown 2019). The ability of lionfish to tolerate broad temperature and salinity regimes and invade multiple habitats combined with their voracious appetite for small-bodied fishes could prove detrimental to reef biodiversity.

Mangroves are critical habitats that significantly influence the ecological and economic health of coastal communities in Florida (Adams et al. 2006, Nagelkerken et al. 2001, Mumby et al. 2004, Kathiresan and Bingham 2001, Kathiresan 2012, Verge 2017). Mangroves help to protect the shoreline and prevent erosion from damaging storm and hurricane force winds, waves, and flooding (Kathiresan 2012, Verge 2017). The mangroves' intricate root systems also help to prevent erosion by decreasing wave energy and stabilizing sediments (Kathiresan 2012, Verge 2017). Mangroves also help to maintain water quality and clarity by filtering pollutants and trapping sediments out of the water column which prevents them from reaching open-water environments. However, the ability of mangroves to filter out pollutant is dependent on salinity, which fluctuates with freshwater inputs and tidal period (Tam and Wong 1999, Verge 2017). Salinity in south Florida mangroves fluctuate between 18 and 30 parts per thousand (Gilmore and Snedaker 1993).

Perhaps most importantly, mangroves serve as important nursery habitats for numerous reef-associated fishes (Nagelkerken et al. 2000). In addition to the high abundance of food resources (Lee et al. 2014) found in this ecosystem, the shallow-water microhabitats, high turbidity, and reduced visibility created by the mangrove ecosystem also help to facilitate lower predation pressure. The highly complex prop root system also helps to reduce predator-prey interactions by providing protection for small fishes and invertebrates (Lee et al. 2014). Because mangroves provide a nursery habitat for juvenile reef fishes, they also attract predatory fishes in search of easy prey, such as great barracuda *Sphyraena barracuda* (Nagelkerken et al. 2000, Nagelkerken et al. 2001, Verweiji et al. 2006). The utilization of mangroves by lionfish – in addition to the current native predators – may have detrimental effects on the recruitment to reef

habitats by means of reducing the survival of juvenile reef fishes through predation and competition (Barbour et al. 2010).

The highly complex prop root system helps to reduce predator-prey interactions by providing protection for small fishes and invertebrates, furthermore, predatory success declines as habitat complexity increases (Savino and Stein 1982). For example, largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* demonstrate a reduction in the number of prey consumed and foraging success with increasing habitat complexity (Savino and Stein 1982), a finding similar to a study of predation of brown shrimp *Farfantepenaeus aztecus* by estuarine fishes in *Spartina* sp. saltmarshes (Minello and Zimmerman 1983). Both studies focused on predators that are primarily pursuit hunters and the decrease in predatory success was attributed to the increase in visual barriers between the predator and prey. However, little work has been conducted to determine the effect that habitat complexity has on the predatory success of ambush predators, like the lionfish (Fishelson 1975, James and Heck 1994, Flynn and Ritz 1999, Scheffell 2017).

Using the invasive lionfish and a native mid-level predator (lane snapper *Lutjanus synagris*) commonly found in the southeast Florida mangroves, this study aimed to quantify the effect of habitat complexity on predation efficiency within mangrove habitats. As highly efficient predators with few native predators in the Atlantic, lionfish appear to have a significant predatory advantage, their morphology may potentially limit their predatory ability in highly complex habitats. Lionfish utilize their expansive pectoral fins to both stabilize themselves in the water column and corraling smaller prey, restricting the natural expansion of the pectoral fins may impact predation efficiency. In contrast, native generalist foragers like the mangrove snapper and blue-striped grunt are visual predators that rely on visual cues to locate prey and exhibit a roving behavior while searching (Savino and Stein 1982, Scheffell et al. 2017). Stomach-content analyses suggests larger snappers may venture out to adjacent areas to feed while smaller mangrove snappers utilize mangrove prop roots for both foraging and refuge from predators (Thayer et al. 1987). Although these smaller individual snapper still have to combat reduced visibility from complex prop root systems, their short pectoral fins and moderately compressed bodies likely facilitate more maneuverability in complex habitats when compared to the invasive lionfish. We hypothesized that the relationship between predation efficiency and

habitat complexity would decrease with increasing habitat complexity for the invasive lionfish, but the native snapper species.

The purpose of this study is three-fold: (1) determine the predation efficiency of lionfish in differing mangrove habitat complexities, (2) examine the influence of temperature and prey behavior on lionfish predation efficiency in mangrove habitats, (3) compare the predation efficiency of lionfish to a native predator – lane snapper – under the same parameters. Findings from this study will help to provide valuable information that can be used to manage for lionfish in mangrove habitats and minimize ecological impacts.

Materials and Methods

IACUC approval

Collection of predator study specimens and prey and subsequent live animal experimentation was performed with approval by Nova Southeastern University Institutional Animal Use and Care (IACUC) Committee (protocol 2018.03.DK5 to D. Kerstetter, renewed in 2019 and 2020).

Specimen acquisition

Live lionfish study specimens ranging in length from 80 mm to 250 mm were acquired by a commercial fisherman from Broward and Miami-Dade counties. Lane snapper study specimens ranging in length from 120 mm to 185 mm were collected in Broward County waterways using recreational hook-and-line fishing gear. Collected lane snapper were measured and released alive if not within the required total length slot between 75 mm and 250 mm.

Three different prey species, commonly found in the mangrove prop root environments were used in the experimental trials, mosquitofish *Gambusia* sp., mummichog *Fundulus* sp., and grass shrimp *Palaemonetes paludosus*, . These species were selected as prey because they are commonly found in mangrove prop root environments, abundant, and have differing morphologies and behaviors (Anderson 1985, Thayer et al. 1987, Banikas and Thompson 2012, Hall-Scharf and Stallings 2014). Although two different species of prey fish were used in trials, it is not expected to affect the results as both mosquitofish and mummichog have similar individual sizes and similar schooling tendencies. Prey specimens were either obtained from local pet stores or collected using cast nets and minnow traps in the surrounding mangrove

forests around the Oceanographic Center campus (a Florida Fish and Wildlife Conservation Commission (FWC) permit is not needed for baitfish collection with a state recreational fishing license). Collected prey species were transported to the Nova Southeastern University Oceanographic Center campus in aerated buckets, then individually measured for total length (TL) and placed in 10-gallon holding tanks. Individual lengths ranged from 20.2 to 39.0 mm for mosquitofish, 25.4 to 62.8 mm for mummichog, and 9.5 to 28.0 mm for grass shrimp.

All animals were kept in recirculating holding tanks for approximately 14 days to allow for acclimation before use in trials. The holding tanks for all predator and prey species was kept at one of the following four temperature regimes, 15°C, 20°C, 25°C, and 30°C, while salinity was maintained at 20 ppt to mimic estuarine conditions. Lionfish holding tanks were made up of three plastic water tanks containing approximately 60 gallons of saltwater, which housed up to 8 lionfish per tank at a time. Lane snappers were held in 100-gallon divider aquariums with one fish per section.

Lionfish and lane snapper study specimens were either tagged with a T-bar anchor tag inserted into the muscle approximately 3 cm behind the pectoral fin during the 14-day acclimation period or housed in labeled separate tanks for pre- and post-experiment identification. Lionfish and lane snapper were fed prior to trials *ad libitum* with live grass shrimp and mummichog.

Experimental design

The predation efficiency of the invasive lionfish and the native predator, lane snapper, in differing mangrove habitat complexities was evaluated by artificially simulating mangrove prop roots in laboratory trials. Habitat complexity was experimentally replicated using wooden dowels as non-flexible complexity and clumps of artificial vegetation as flexible complexity. The plots of artificial vegetation were constructed from plastic eelgrass attached to the base of a one-inch piece of wooden dowel. The experimental set-up was made to minimize human interaction and disturbance during the trials.

Trials was conducted in 40-gal all glass aquaria 60 x 60 x 30 cm in size with a blue backdrop surrounding the tank and cardboard lining the bottom to mimic a hard-bottom substrate (Figure 1). A clear plastic partition was used to separate the prey items from the lionfish during the pre-trial acclimation period. Complexity was varied with 0.25-inch diameter wooden dowels

or plastic eelgrass clumps (Figure 2) at four different levels of complexity with each level increasing logarithmically (Figure 3). A control tank was set up with no dowels or eelgrass clumps to test for predation efficiency in open spaces (i.e., replicating a sand flat). Table 1 gives a list of each complexity treatment, number of dowels in the trial area, interstitial space between dowels, and the number of dowels per m². The highest level of complexity, level 3, was determined by estimating the approximate average body size of an individual juvenile lionfish and the average interstitial space between dowels.

Ten prey items of each prey class were chosen specifically for each predator because pre-trial experiments showed that lionfish reached satiation after one hour with ten items of prey. Lionfish are gape-limited predators, so prey items must fit within the gape limit of each study specimen. The total length (figure 4A), maxillary length (figure 4B), and mouth height (figure 4C), were measured from lionfish carcasses collected for another study, and these lengths were used to calculate the gape limit of each lionfish using linear correlation in R (Schmidt and Holbrook 1984). The maxillary length of a lionfish significantly correlated to the mouth height (linear correlation, $t=2.4574$, $p=0.00039$) and can be calculated with equation 1:

$$(1) \text{ mouth height} = 3.62613 + 1.15315 (\text{maxillary length})$$

The maxillary length of the fish is significantly correlated (linear correlation, $t=5.38363$, $p=0.00398$) to the total length of the fish and can be calculated with equation 2.

$$(2) \text{ maxillary length} = 0.00845 + 0.11252 (\text{total length})$$

Thus, we can determine the gape limit of the lionfish by using equation 3.

$$(3) \text{ mouth area} = 3.62613 + 1.15315 (0.00845 + 0.11252 (\text{total length}))$$

Each predator study specimens was starved for 48 hours prior to the start of a trial to ensure that the digestive tract is empty (Fishelson 1997). The overall health of the focal predator was assessed prior to the start of a trial (i.e., coloration, eye clarity, and fin and body condition). Any individual that appeared to be sick, in declining health, or have injuries due to capture and/or handling stress were not used for the trial and were removed and placed in a quarantine tank for recovery. A plastic partition was placed in the middle of the experimental tank prior to start of a trial where the focal fish was placed on one side of the partition and prey on the opposite side for a 1- to 2-hr acclimation period. At the conclusion of the acclimation period, the partition was removed and the predator was allowed to interact with the prey items for one hour. After the 1-hr test period, any remaining prey items were removed and the number of prey items

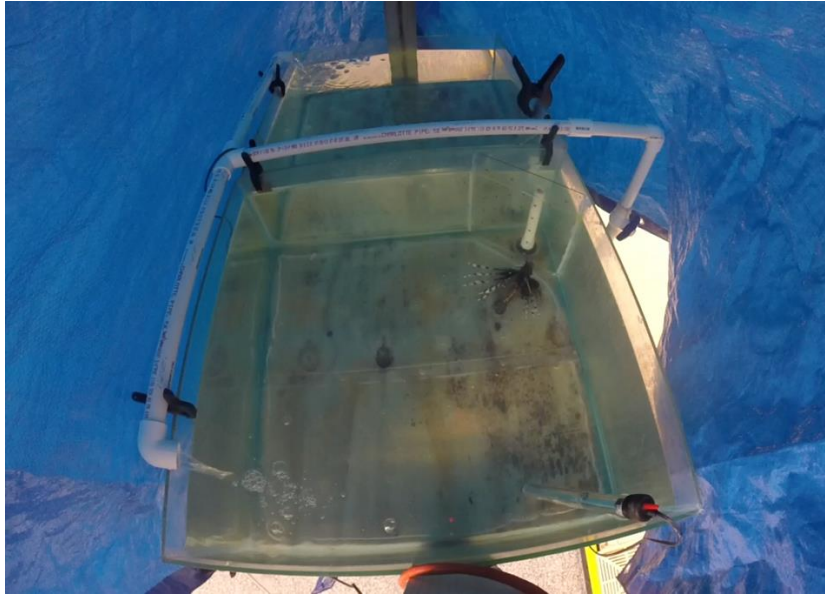


Figure 1. Picture of a trial in progress taken from above using a GoPro Hero 3 camera.

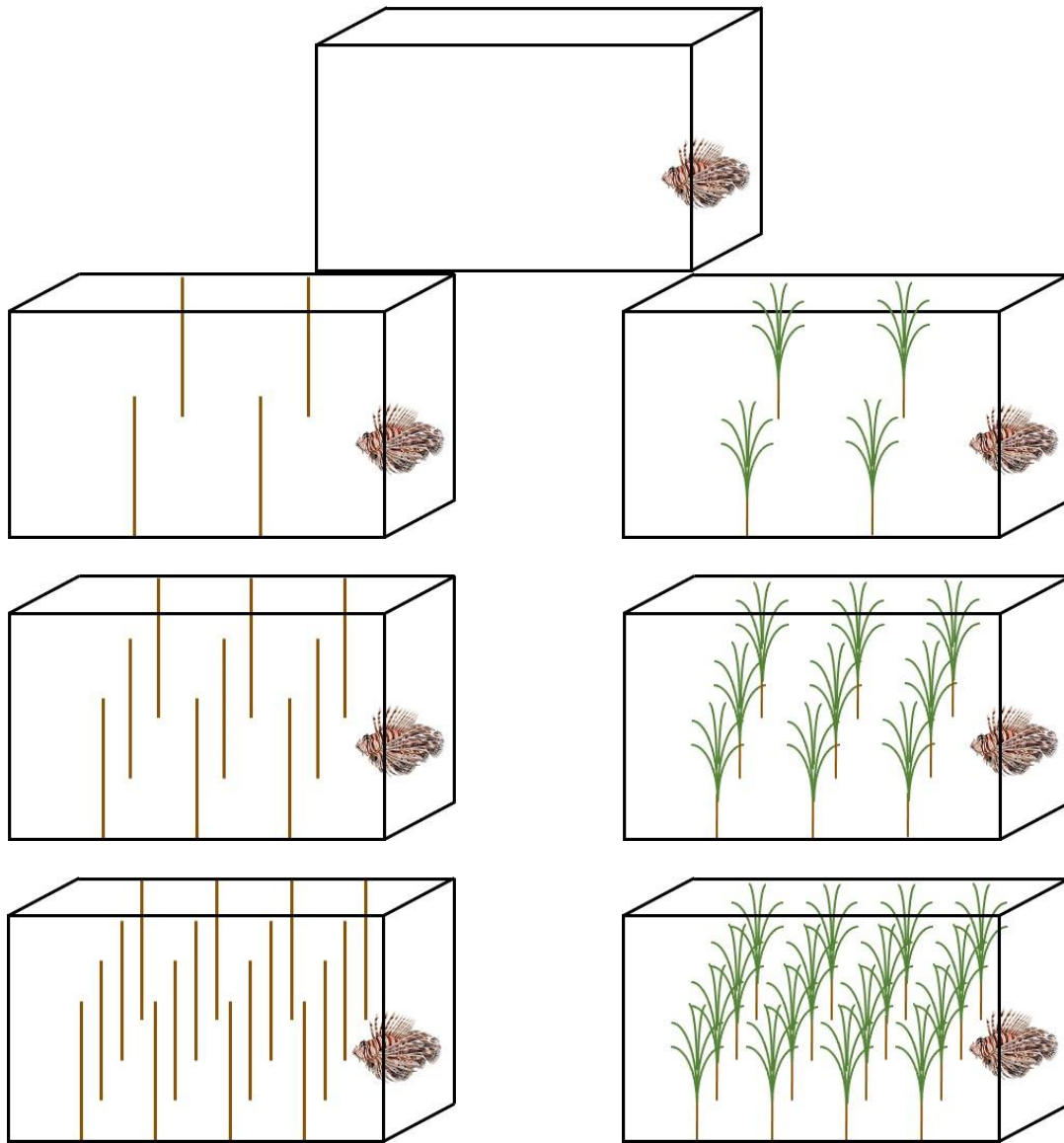


Figure 2. Diagram of the lab set-up with varying complexities. The left side of the diagram uses wooden dowels to vary complexity while the right side of the diagram uses plastic eel grass to vary complexity. The top row represents the control or level 0 complexity, the second row represents level 1 complexity with 4 dowels per m^2 , the third row represents level 2 complexity with 9 dowels per m^2 and the fourth row represents level 3 complexity with 16 dowels per m^2 .

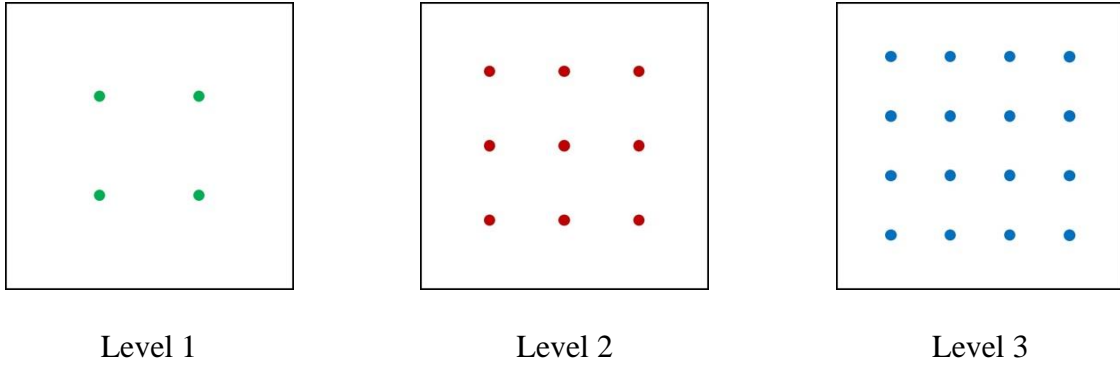


Figure 3. Distribution of artificial complexity within the trial tank for the three levels of complexity used in experiments.

Table 1. Comparison of the number of dowels between the 4 treatments expressed as the experimental area of the trial tank (60 x 60 cm) and the corresponding number of dowels per m².

Complexity Level	No. Dowels · exp. area ⁻¹	Average Interstitial Space	No. Dowels · m ⁻²
0	0	0	0
1	4	19.9 cm	7
2	9	14.9 cm	15
3	16	11.9 cm	27

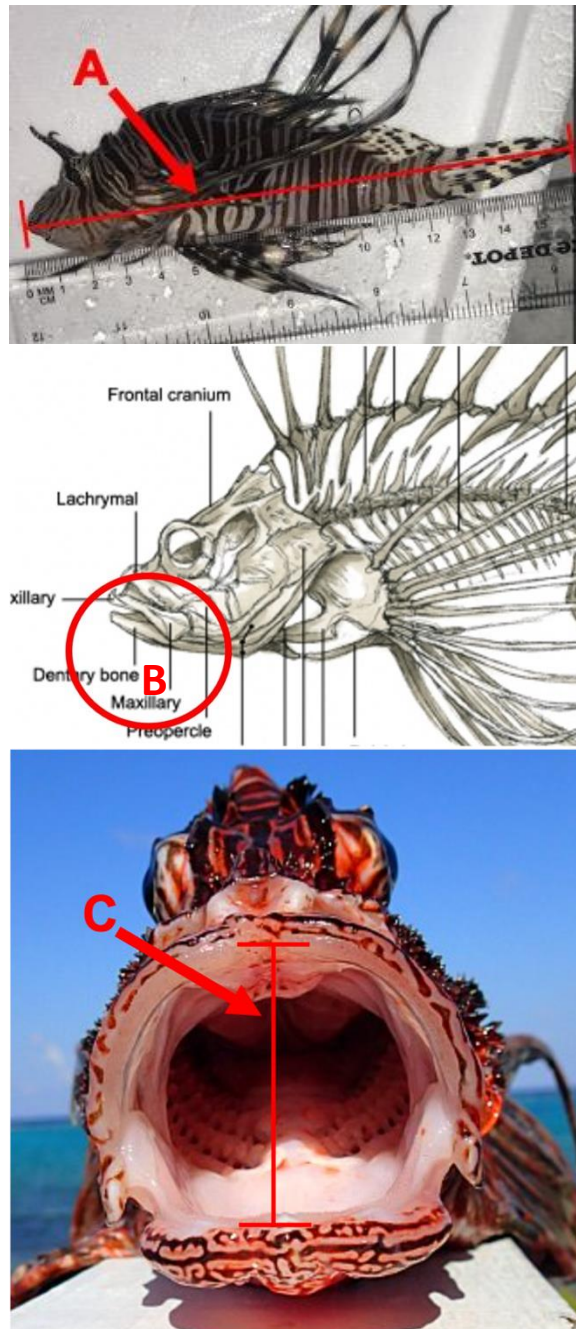


Figure 4. Lionfish total length measurement (A), maxillary length measurement (B), and mouth height measurement (C). Photographs by A. Kimbrel (top), Terryl Whitlatch (middle) and N. Coles (bottom).

consumed was recorded. Predation efficiency was measured by the number of prey items consumed divided by the total number of prey items available (Flynn and Ritz 1999). Habitat complexity was measured in two ways: (1) average interstitial space size between each dowel divided by the total size of the predator (Sp/Pr), and (2) the total structural cross-sectional area, or total amount of cover, provided by the dowels divided by the habitat area (C_t/A_t) (Bartholomew et al. 2000). The Sp/Pr ratio is used to measure predator maneuverability within a habitat while C_t/A_t measures the amount of area within the habitat that the structure obstructs from view or cover within the habitat that prey can hide behind (Bartholomew et al. 2000). The results were analyzed using R with nested mixed models with the number of dowels being the fixed factor, the tank as the nested factor, the randomly chosen predator as the random affect, and the total length of the predator as the covariate. Each combination of temperature, complexity type, complexity level, and prey type were replicated five times.

Analyses

Factorial ANOVAs were used to analyze the effect of habitat complexity, temperature and prey on predation efficiency. All data was considered non-parametric because it did not meet the parametric assumptions of normality and homogeneity, so a Kruskal-Wallis rank sum test was used to analyze the results. Following a significant Kruskal-Wallis test. Non-parametric pairwise multiple comparisons was also used to examine differences between groups using Dunn's test of multiple comparisons. To control the family-wise error rate, p-values were adjusted using the holm method. Binomial generalized linear models were used to analyze the effects of predator size, the Sp/Pr ratio, and the C_t/A_t ratio on predation efficiency. All analyses were run in the program R, and statistical significance assessed at 0.05.

Results

Influence of habitat complexity on lionfish predation efficiency

A total of 169 individual lionfish ranging from 82 mm to 215 mm (\bar{x} length = 146.88 mm) were tested throughout the experimental trials. An analysis of variance was conducted on the influence of four independent variables (complexity level and type, temperature, prey type) on the predation efficiency of lionfish in a controlled environment. Complexity level included four levels (control, 1, 2, 3), complexity type included three levels (control, flexible, non-flexible), temperature included four levels (15°, 20°, 25°, 30°), and prey type included three

levels (shrimp, gambusia, fundulus). In a comparison of all four variables, a Kruskal-Wallis test showed that all four of these variables significantly affect the predation efficiency of lionfish in a controlled environment ($H(56)=131.31$, $p=5.477*10^{-8}$) (Figure 5A).

When only considering the type of complexity (i.e., dowels vs. plastic eelgrass), a Kruskal-Wallis test showed that complexity type marginally affects lionfish predation efficiency, ($H(2)=6.0254$, $p=0.0492$). However, the level of complexity (i.e., the number of dowels placed in the environment) was found to significantly affect predation efficiency ($H(3)=10.1$, $p=0.0177$). Non-parametric pairwise multiple comparisons between complexity groups showed that the only significant differences occurred between the control and level 2 complexity (dunn test holm method, $p_{adj.}=0.0358$). This shows that lionfish were most efficient when there is no complexity in the environment and the least efficient at level 2 complexity, with a total of nine dowels in the environment (Figure 5B).

Influence of temperature and prey behavior on lionfish predation efficiency

Temperature overall was found to significantly affect lionfish predation efficiency ($H(3)=25.079$, $p=1.486*10^{-5}$). Non-parametric pairwise multiple comparisons between groups showed that significant differences occurred between 15° and 20° (dunn test holm method, $p_{adj.}=4.3988*10^{-3}$), 15°C and 25°C (dunn test holm method, $p_{adj.}=9.3792*10^{-3}$), and 15°C and 30°C (dunn test holm method, $p_{adj.}=6.0759*10^{-6}$). Lionfish were most efficient at a temperature of 15°C, the lowest temperature included in trials and least efficient at a temperature of 30°C (Figure 5C).

Type of prey (shrimp, Fundulus, and Gambusia) was found to significantly affect lionfish predation efficiency ($H(2)=14.982$, $p=5.582*10^{-4}$). Non-parametric pairwise multiple comparisons between complexity groups showed that the only significant differences occurred between shrimp and Gambusia (dunn test holm method, $p_{adj.}=0.0004$). Lionfish were most efficient with shrimp as prey, and next most efficient with Fundulus as prey. Lionfish were least efficient with Gambusia as prey (Figure 5D).

Other variables that were measured was the total length of the focal predator, predator maneuverability using the Sp/Pr ratio, and the amount of cover provided in the habitat using the C_i/A_i ratio. A binomial GLM test showed that predator size ($p=0.4884$), Sp/Pr ($p=0.1368$), and C_i/A_i ($p=0.254$) does not significantly affect lionfish predation efficiency (Figure 6).

Comparison of predation efficiency in differing mangrove habitat complexities to native species

A total of 15 individual lane snapper ranging in length from 120 mm to 185 mm (\bar{x} length = 144.87 mm) were tested in the predation trials. An analysis of variance was conducted on the influence of three independent variables (complexity level and type, temperature) on the predation efficiency of lane snapper in a controlled environment. A Kruskal-Wallis test showed that all variables significantly affect predation efficiency of lane snapper in a controlled environment ($H(27) = 100.5$, $p = 2.128 \times 10^{-10}$). When considering each factor individually, temperature significantly affects lane snapper predation efficiency ($H(3) = 90.955$, $p < 2.2 \times 10^{-16}$). However, complexity level and type does not significantly affect lane snapper predation efficiency ($H(3) = 0.711$, $p = 0.8706$ and $H(2) = 0.3367$, $p = 0.8451$, respectively).

Comparison of temperature and prey behavior on predation efficiency to native species

Since lane snapper did not consume any prey fish during trials, only the lionfish trials using shrimp as prey will be considered for comparison to lane snapper. Lionfish consumed significantly more prey shrimp than lane snapper ($p = 0.2596 \times 10^{-5}$). Temperature does significantly affect predation efficiency in both predators but differently. Lionfish were the most efficient at 25° followed by 15°, 30°, and 20°, respectively, while lane snapper are most efficient at 30° and efficiency decreases with decreasing temperature (Figure 7C). While the level and type of complexity significantly affects lionfish predation efficiency, complexity level and type has no significant effect on predation efficiency in the native lane snapper (Figure 7A and 7C).

Other variables that were measured was the total length of the focal predator, predator maneuverability using the Sp/Pr ratio, and the amount of cover provided in the habitat using the C_i/A_i ratio. A binomial GLM test showed that predator size ($p = 0.2004 \times 10^{-6}$) and the Sp/Pr ratio ($p = 6.599 \times 10^{-3}$) significantly affected predation efficiency between lionfish and lane snapper (Figure 8).

Animal Husbandry

A total of 275 lionfish were collected during the duration of this study, although only 30 were used in repeated experiments. The main problem with our lionfish in captivity was mortalities. Many of the lionfish have died shortly after arrival, which may be a result of either

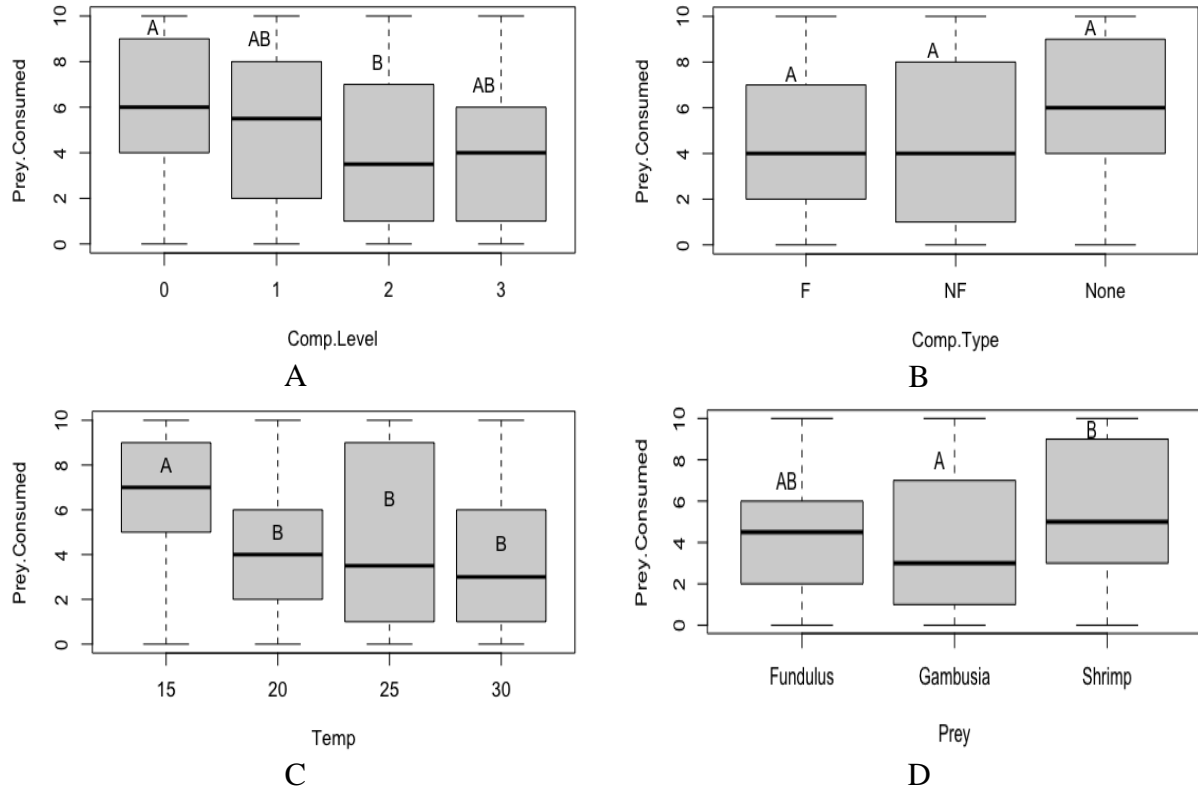
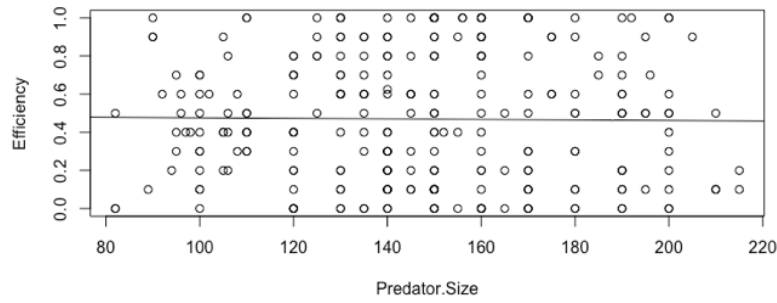
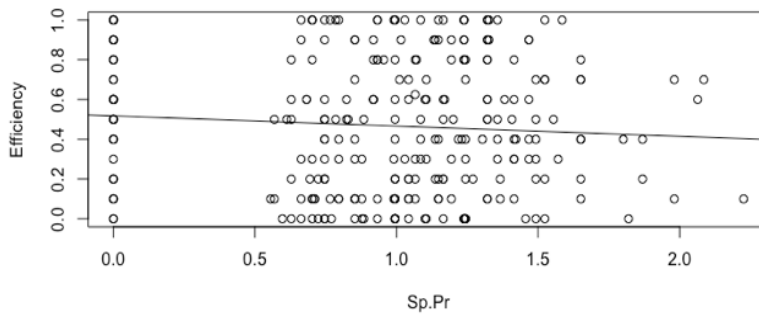


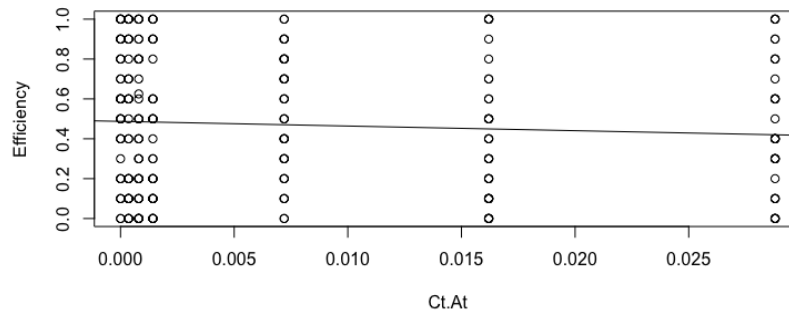
Figure 5. Graph of the effect of complexity level, denoted by Comp.Level, (A), complexity type denoted by Comp.Type, (B), temperature denoted by Temp, (C), and prey type denoted by Prey (D) on lionfish predation efficiency using the number of prey consumed by lionfish within the one-hour trial period denoted by Prey.Consumed.



A



B



C

Figure 6. Graph of the effect of predator size denoted by Predator.Size (a), predator maneuverability within the habitat using the Sp/Pr ratio denoted by Sp.Pr (b), and amount of cover provided within the habitat using the C_t/A_t ratio denoted by Ct.At (c), on lionfish predation efficiency denoted by Efficiency.

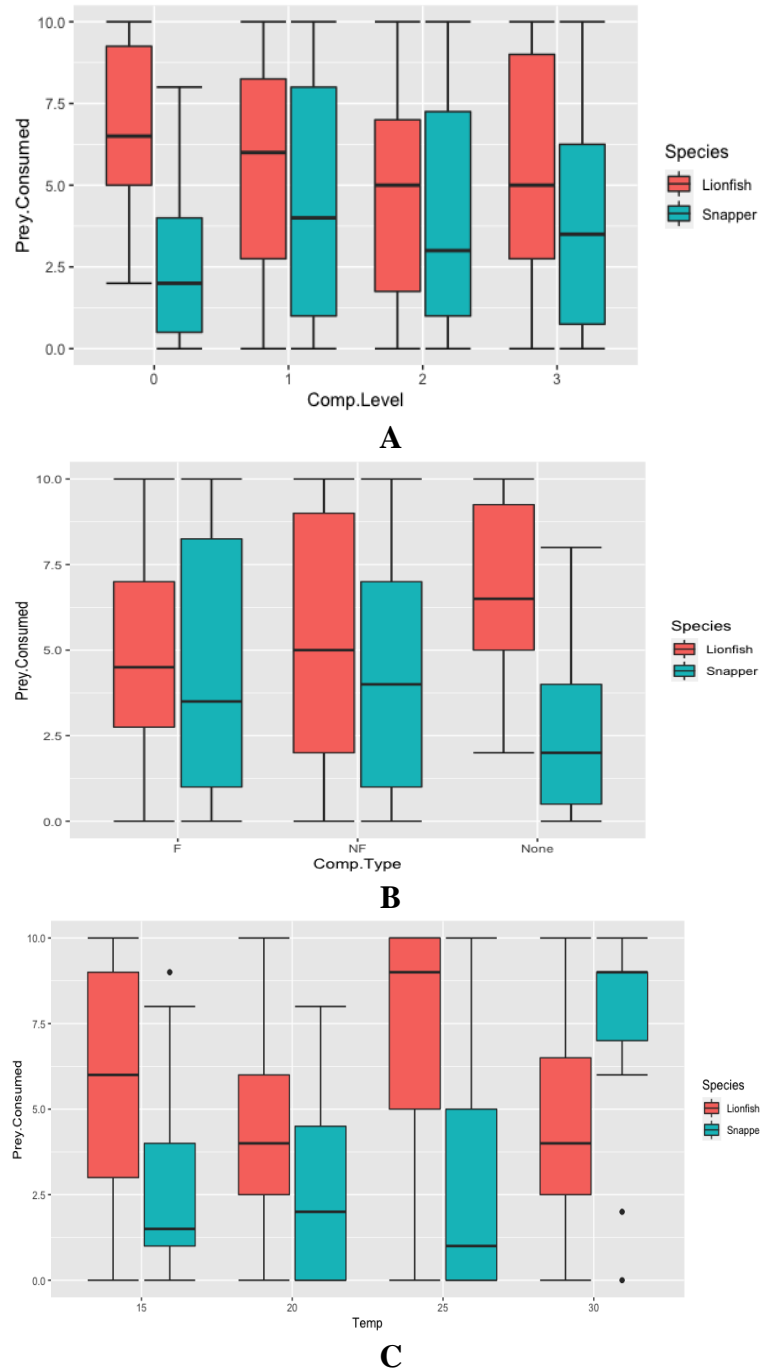
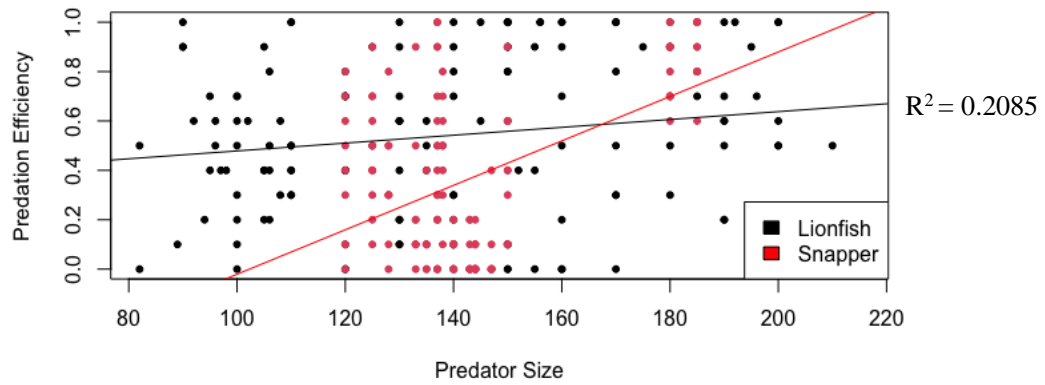
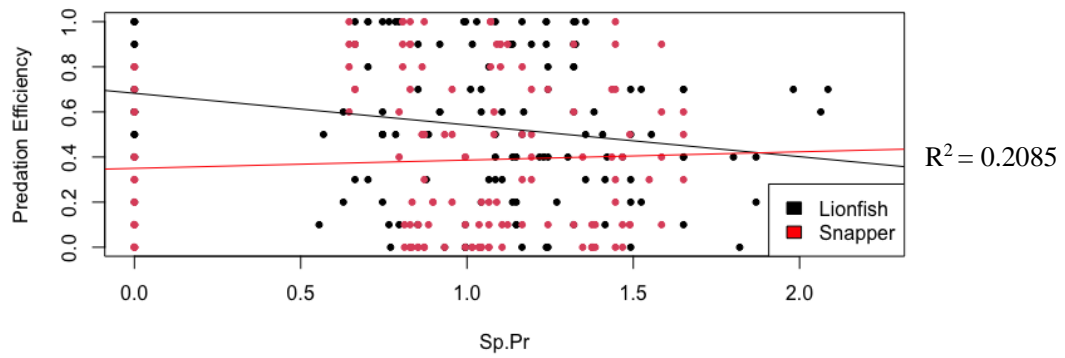


Figure 7. Graph of the effect of complexity level, denoted by Comp.Level, (A), complexity type denoted by Comp.Type, (B), and temperature denoted by Temp, (C), on lionfish and lane snapper predation efficiency using the number of prey consumed by each predator within the one-hour trial period denoted by Prey.Consumed.



A



B

Figure 8. Graph of the effect of predator size denoted by Predator.Size (a), predator maneuverability within the habitat using the Sp/Pr ratio denoted by Sp.Pr (b), on lionfish (in black) and lane snapper (in red) predation efficiency denoted by Efficiency.

capture/handling stress, barotrauma, and/or secondary effects from an antiparasitic formalin bath (25 mg/L, or approximately 2 drops per gallon) given by the capturing vendor from whom we get most of the experimental animals. However, we have had additional, longer-term mortalities as well that occurred in three broad categories: cloudy eye disease, water quality problems, and an unknown ulcerative skin disease. Several methods were used to attempt to correct these problems including the use of antibiotics, reducing stress and handling times and adding additional mechanical, biological, and chemical filtration methods to maintain good water quality.

Discussion

Currently, physical removal of lionfish is the most commonly used method to control lionfish populations in the Caribbean (Morris et al. 2009). However, there are minimal control measures in areas that are not frequently visited by divers for targeted removals (Valdivia et al. 2014, Cote and Smith 2018). Mangrove habitats, in particular, are not a popular dive location for lionfish hunters possibly due to reduced visibility and high turbidity that is common in mangroves (Lee et al. 2014). The objective of this project was to better understand the predatory effect of lionfish in their most recently invaded habitat. Determining the factors that influence both lionfish and other native competitors' predation efficiency can allow managers to tailor management efforts across all habitat types and complexities to help control the spread and effects of the lionfish invasion.

Influence of habitat complexity on predation efficiency

The complexity of mangroves' intricate prop root systems act as a buffer between predators and prey by providing additional protection for small fishes and invertebrates which leads to a decline in predatory success as habitat complexity increases (Savino and Stein 1982, Minello and Zimmerman 1983). Habitat complexity was shown to have a significant effect on lionfish predation efficiency, although lionfish did not exhibit the expected predation curve. Given the typical inverse relationship between predatory success and habitat complexity, we would expect the ranking of complexity to be by level, from low to high, but instead the complexity level of 2 made lionfish the least efficient. Lionfish are ambush predators, which makes the lower level of complexities an understandably more ideal environment for hunting.

However, at a moderate level of complexity, lionfish were less efficient than at the highest level of complexity. This could be due to an adjustment in hunting strategy of lionfish at the highest level of complexity that is not reached at a moderate level of complexity, the use of naïve prey that act less cautiously in an environment with the highest level of complexity, or the inability of the prey to perceive lionfish as a threat due to their own limited visibility. Furthermore, type of complexity was shown to significantly affect lionfish predation efficiency but only marginally with a p-value close to 0.05 at 0.0492. Comparison between the types of complexity showed significant differences between the control groups and flexible complexity and the control and non-flexible complexity, however there was no significance between flexible and non-flexible complexity groups. This suggests that the type of complexity may not be as important as the amount of complexity in regard to lionfish predation efficiency.

Vision may also be playing a role in reducing lionfish predation efficiency in mangrove habitats. Inshore mangrove ecosystems are one of the most variable and photodynamic aquatic environments due to a variety of factors including wave activity, weather, time of day, vertical mixing, stratification, and sedimentation (McFarland and Loew 1983; Wing et al. 1993; Schubert et al. 2001; Gallegos et al. 2005; Kemp et al. 2005; Horodysky et al. 2010, Hasenei et al. 2020). Furthermore, the dense prop roots and the inherent structure of mangrove forests causes shading over the water which could potentially limit the lionfishes' ability to detect potential prey within the root system. Brightly lit areas, such as that found in open-water seagrass beds, could facilitate better predation efficiency as potential prey would be much easier to detect. However, a recent study has found that lionfish have a visual ecology that is suitable for a wide variety of light environments, with greater sensitivity at lower light levels and excellent visual acuity at higher levels (Hasenei et al. 2020). Additionally, lionfish share similar spectral sensitivities with several species of estuarine fish, suggesting that lionfish would be able to thrive in estuarine environments and effectively detect prey within them (Hasenei et al. 2020). Although lionfish visual systems are suitable for the chromatic properties within mangrove habitats, complexity provided by prop roots is a limiting factor to lionfish predation efficiency.

Lionfish consumed significantly more prey than the native lane snapper as predicted, presumably due to the ability of the lionfish to expand their stomachs to accommodate more prey (Fishelson 1997). Although complexity level and type significantly affected lionfish predation efficiency, these factors had no effect on lane snapper predation efficiency. This finding is

predictable as lane snapper are in their natural habitat within mangrove habitat complexities and have a more stream-lined body shape that offers increased maneuverability within those complex habitats.

Influence of temperature and prey behavior on predation efficiency in mangrove habitats

The effects of temperature on fish behavior and prey consumption rates have been well documented. Although lionfish have a broad thermal range from 10 to 38°C, lionfish exhibit increased activity and feeding behaviors at warmer temperatures (Kimball et al. 2004). While the results of our study showed that temperature significantly affected lionfish predation efficiency, they did not follow the expected predation curve. We expected lionfish to be more efficient at higher temperatures, but the lionfish in our study were most efficient at the lowest temperature regime (15°C) and least efficient at the highest temperature regime (30°C). There are several factors that could have influenced our unexpected results. We encountered several challenges throughout the course of this project, the main problem was with disease-related mortalities, specifically the ulcerative skin disease, which has been a recognized problem in invasive lionfish in Florida waters. Although no lionfish that were visibly sick or lethargic were used in the trials, it is important to note that the ulcerative skin disease seemed to spread and kill lionfish more quickly at higher temperature. It is possible that the focal fish was infected with the ulcerative skin disease but were asymptomatic, but it is important to note that no fish died within 24 hours after participating in a trial.

Another factor that could potentially explain why lionfish consumed significantly more prey at the lowest temperature is the influence of temperature on prey. Adult grass shrimp (*P. paludosus*), for example, have a thermal range of 10 to 35°C but are within their thermal optimum between 18 and 33°C (Anderson 1985). Laboratory studies have found that although grass shrimp mortality does not increase at colder temperatures, shrimp are generally less active at 15 and 20°C and unable to burrow in the sediment at temperatures below 15°C (Stanzel and Finelli 2004). Furthermore, escape speeds of mosquitofish have been shown to be greater at warmer temperatures (25°C and 30°C) and sustained performance of mosquitofish do not decline at warmer temperatures (Grigaltchik et al. 2012). Decreased prey activity at lower temperatures of the prey used in this study could lead to increased predation pressure at those lower temperatures and would explain why lionfish exhibited significantly higher predation rates at the

lowest temperature, 15°C. Meanwhile prey escape speeds may be greater than predator attack speeds at high temperatures resulting in decreased predation pressure at higher temperatures like 25 and 30°C (Johnson and Bennet 1995, Grigaltchik et al. 2012). Future studies using live prey for predation efficiency should also account for potential temperature-mediated changes in prey behavior as well as in predators.

In addition to the effects of temperature on prey, prey behavior and morphology have been used to predict their vulnerability to predation. Several traits including body size and shape, aggregating behavior, and position in the water column are important factors for diet selection in lionfish (Green and Cote 2014). Most vulnerable are the small, shallow-bodied, solitary prey that can be found resting on or above reefs, while aggregating prey found higher up in the water column are much less vulnerable (Flynn and Ritz 1999, Green and Cote 2014). During trials, prey fish like mosquitofish and mummichog aggregated in groups closer to the top of the tank and moved together as a group making them less vulnerable to the lionfish that preferred to stay closer to the bottom of the tank. While the smaller-bodied shrimp remained relatively solitary for the duration of the trials and stayed either on the bottom of the tank or resting close to the bases of the provided complexity. These traits made the shrimp much more vulnerable to predation by lionfish.

Predator size, predator maneuverability within a habitat, and habitat cover do not significantly affect lionfish predation efficiency alone. We would expect that a higher complexity and longer length of lionfish would be the least efficient combination, due to less room to maneuver around while hunting in the environment. However, no major difference was found with varying lionfish lengths and differing complexities, showing that the lionfish's length did not affect their ability to hunt in more complex environments. However, comparing predator size, predator maneuverability within a habitat, and habitat cover between the two predator species shows a different result with predator size and predator maneuverability significantly affecting the efficiency of predation on shrimp prey. This phenomenon can be explained by examining the vulnerability of shrimp within complex habitats. The solitary small-bodied shrimp are significantly more vulnerable to ambush predators like the lionfish. Position within the food chain could also be a factor influencing predation efficiency in lionfish and lane snapper. Lane snapper are considered a mid-level predator and are prey for higher level predators whereas lionfish have very few native predators. Meanwhile, lane snapper are risking their own predation

to forage which could lead to decreased predation rates. These results suggest that the complexity threshold proposed by Nelson and Bonsdorff (1990) may still potentially exist for both lionfish and lane snapper, but that level of complexity was not reached within the parameters of this study and additional tests may be necessary to fully assess their effects on predation efficiency.

Conclusions

Although lionfish have been found in mangrove ecosystems, little research has been done to determine the potential impact the presence of these lionfish may have on the mangrove ecosystem. Habitat complexity, temperature, and prey appear to significantly impacts lionfish predation efficiency in mangrove habitats. The results that we found during this study aligns with previous research that habitat complexity and temperature affects predation efficiency of predators in the mangrove ecosystem, however habitat complexity and temperature affects predation efficiency of the invasive lionfish way more than that of the native lane snapper. As a result, we can conclude that lionfish may not be able to outcompete native predators for available food resources in mangrove habitats although the presence of additional predators may still deplete these resources. These results highlight the need for additional studies within the natural ecosystem on the behavior of lionfish in mangrove habitats, impact on prey species assemblages, and their interactions with other native predators in these critical habitats.

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