

**SIMULATED EFFECTS OF INDO-PACIFIC LIONFISH (*PTEROIS
VOLITANS AND P. MILES*) INVASIONS ON PARROTFISH (SCARIDAE
FAMILY) POPULATIONS ON CORAL REEFS IN THE CARIBBEAN**

An Undergraduate Research Scholars Thesis

by

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ABSTRACT

Simulated Effects of Indo-Pacific Lionfish (*Pterois volitans* and *P. miles*) Invasions on Parrotfish (Scaridae Family) Populations on Coral Reefs in the Caribbean

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The introduction of invasive species in marine environments is rare but detrimental to the existence of native species. The Indo-Pacific lionfish species (*Pterois volitans* and *P. miles*) recently has invaded coral reefs across the Atlantic and Caribbean at an alarming rate. One keystone species currently being affected by the lionfish invasion is the parrotfish (Family Scaridae). The parrotfish plays a vital role in the stabilization of coral reef ecosystems by preventing a phase shift from coral to macroalgal dominated reefs. Our objective was to study the dynamics of parrotfish populations in response to the lionfish invasion in the Caribbean. Using published literature to obtain recent demographic parameters for both the lionfish and parrotfish, we developed an age-/stage-structured population dynamics model for each species, and finally integrated the two models by adding negative effects the lionfish population had on the recruitment rate of the lionfish model. The integrated model was used to quantify the potential effects of lionfish invasions on parrotfish population dynamics on coral reefs in the Caribbean. After 120 months post-invasion, projections show that the parrotfish population will be on the onset of decline, while the lionfish population will continue to grow exponentially. If the lionfish invasion continues at its current rate, our model suggests that there will be a direct

deleterious effect to the Scaridae population; potentially leading to the compositional downfall of the coral reef ecosystem as we know it.

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CHAPTER I

INTRODUCTION

Among the six major ecosystems of the world, the marine realm, which covers 71% of the Earth's total area, provides the largest inhabitable space for living organisms. The marine ecosystem is composed of multiple interacting trophic levels, which play a crucial role in the primary production of organic matter. The ocean's production of plant biomass represents one of the most important ecological roles for our biosphere, as it provides the basic food source for all living organisms, and ultimately humans. The stability of the marine ecosystem is of utmost importance, as its essential for food, raw materials, renewable energy, and climate regulation. However, this stability depends on the maintenance of global biodiversity and species richness levels, owing to the high inter-connectivity of marine species. Connectivity has become a defining characteristic of marine ecosystems (Carr et al., 2003) as its represents the exchange of individuals among marine populations across habitats. This interdependent relationship among marine species highlights the important role 'balance' plays in the continuum of the ecosystem. The 'balance' of the marine ecosystem can be attributed to presence of various ecologically important organisms such as, keystone, foundation, and indicator species. Keystone species are species whose abundance determines the integrity of the community and its unaltered persistence through time, that is, stability (Paine, 1969). For example, Sharks are an important predator keystone species, as they control the distribution and population of prey species. When removed from an ecosystem, the food web can change drastically thus causing a trophic cascade. Foundation species play a role in creating and maintaining habitats, which support a multitude of other species. Indicator species are organisms, which respond immediately to environmental

changes in its ecosystem, thus able to provide early warning when a habitat is stressed. Without the presence of these species, or changes in relative abundance, the marine ecosystem would undergo detrimental transformations. Therefore, it's critical to understand the role of biodiversity and species richness in the stability of the marine ecosystem to better understand how to protect these ecological systems from unexpected additions.

The introduction of a new species is one of the leading causes of the global biodiversity crisis (Wilcove et al., 1998). Invasive species pose a harmful threat to marine environments, as they are capable of dramatically altering community composition and ecosystem function (Stachowicz et al., 1999). Due to these species ability to act synergistically with other environmental stressors, such as, climate change, overexploitation, habitat modification, and pollution, their invasion ranks them as one of the four greatest threats to the world's ocean. With their rapid adaptation and high habitat flexibility, invasive species have the potential to severely modify native indigenous biota. Currently invasive species are altering the evolutionary pathways of native species through unprecedented predation, niche displacement, competition, and ultimately extinction (Mooney & Cleland, 2001). Invaders can also be known to cause functional extinction, where individuals of the native population are hunted to such low numbers that they are unable to play their role in the ecosystem. Extinction can also be a product of niche displacement, which occurs when two species (native and invader) compete for the exact same resources, eventually ending with the demise of the unsuccessful competitor. We can examine the underlying functionality behind niche displacement through scientist G. F. Gause's competitive exclusion principle, which states that two species cannot coexist if they occupy the same niche (Gause et al., 1964). The introduction of these new predators has contributed to numerous documented extinctions of long-term resident species (Davis, 2003). Once established

in a habitat, the impacts of invasive marine species are often irreversible due to their high predation efficiency. Therefore, there is a substantial chain of impacts these newly introduced invaders pose to the continuum of native species populations in the marine ecosystem. There are various ways species become established beyond their native location, in particular, marine species have used the help of the continuous ocean to migrate to different locations around the world, but ever since modern technology, humans have facilitated other marine species to relocate to new habitats by hitchhiking on large boats. Also the exotic pet trade has also allowed other species into non-native habitats by accidental or intentional release. Once non-native species are relocated they could die off due to competition, survive without environmental impact, or take over as harmful predators. Usually successful invasions are uncommon, but due to sea temperature rise by global warming, non-native species have been able to successfully migrate to a wider range of previously colder habitats. As populations of invasive marine species continue to grow at an unprecedented rate, it is essential we examine the ecological functions of the marine ecosystem, which these newly introduced species are both directly and indirectly threatening.

Although there are not many marine invasive species recorded, there is one invasion currently unraveling. The Indo-Pacific lionfish species (*Pterois volitans* and *P. miles*) were recently introduced from their native range to the Western Atlantic, as several individuals were accidentally released from an aquarium during Hurricane Andrew in 1992 (Albins & Hixon, 2008). By 2001, lionfish had spread expeditiously as populations were established along the US Atlantic coast from Florida to North Carolina, and were reported as far north as Rhode Island (Hines et al., 2011). Marine invasions are near impossible to eradicate once established, and these lionfish have demonstrated how difficult they are to control after they successfully

bloomed across the Atlantic Ocean. To date, the lionfish is the most successful invader, due to their intense proliferation across the Western Atlantic, Caribbean, and Gulf of Mexico (Johnston & Purkis, 2015). Their remarkably high reproductive rate is a result of their ability to spawn year-round, with an annual fecundity of over 2 million eggs (Morris & Whitfield, 2009). Lionfish are also able to disperse long distances during their larval and egg stage, which then disperse further by riding ocean currents. These characteristics, coupled with the lack of natural predators, and a voracious appetite, makes lionfish densities surpassed some of the native species with as much as 1,000 lionfish per acre in some regions. Lionfish can be dangerous to hunt because they have venomous spines. Along with the spines, lionfish have a range cryptic colored stripes that serve as camouflage by breaking up the outline the fish when viewed from far away, this allows them to sneak up on prey and avoid predators. Lionfish are carnivorous and they do not have a food preference, they can eat up to 90% of their body weight every day and some eat up to 50 small fishes per day. Lionfish feed on a variety of commercial fish, crustaceans, and native fish that help maintain the health of the reef by grazing on algae. This demonstrates how lionfish have a direct predatory impact because these smaller reef fishes perform special ecological services on the coral reefs. Their immense appetite makes lionfish successful invaders and harmful predators, if they continue to populate they can dramatically affect native ecosystems and local fishing economies. Studies have shown they can reduce the abundance of small native reef fishes by up to 95% at some invaded sites in the western Atlantic and Caribbean region (Cote et al., 2013), this proves the entire marine ecosystem is at risk of (1) severe extinctions of native fish, (2) degradation of coral reef ecosystems if algae are not kept by the grazers, and (3) impacts on commercial fisheries species like on snappers, groupers, shrimps and crabs.

Without a doubt, the extreme characteristics that lionfish hold combined with their insatiable appetite, could definitely lead to major disruption of the native food web and ultimately destabilize coral-reef ecosystems (Holian, 2012). This unparalleled lionfish invasion represents a major potential threat to reef ecosystems in the Caribbean by decreasing the survivability of native reef animals through predation and competition. According to an experiment conducted by Albins and Hixon (2008), it was determined that a single lionfish could reduce native juvenile fish populations by 79% over a 5-week period. The effect of the lionfish on native species populations in coral reefs is more than twice when compared to similar sized native predators such as the native grouper (*Cephalopholis fulva*). Juvenile fish are among the most susceptible prey for this predator species resulting in an increase in early mortality of native fishes, which ultimately leads to a huge decrease in adult populations of ecological importance such as herbivores. As a result, communities being invaded by lionfish are slowly emerging a destabilized coral-reef ecosystem. One experiment indicated how the introduction of lionfish was capable of reducing overall recruitment of native coral-reef fish by nearly 80%, in addition an observational study demonstrates 65% decline, on average, in native fish biomass in just over 2 years following the invasion of lionfish (Green et al., 2012). In an experiment where patch reef communities were controlled to investigate the effects of the invasive lionfish, it was found that along with decreasing native species recruitment the lionfish population also causes a reduction in local native species richness as opposed to native grouper predators alone (Benkwitt, 2014). However, when both predators are present in a reef patch an extensive reduction in richness occurs. As a consequence of reduction in native species populations both common and rare species are declining leading to an increase in species evenness. With a decline in both species

richness and evenness in the presence of the invasive predator, coral-reef diversity is also declining.

A crucial native reef species that is currently being affected by the lionfish is the parrotfish (Scaridae Family). Herbivorous fishes, namely parrotfish, play a crucial role on coral reefs, as they mediate the competition for space between corals and microalgae. Parrotfish are found in both the deep and shallow reef where they serve their roles as browsers and grazers as they pick up large amounts of inorganic substratum and help maintain algal free substrate at mesophotic depths. Lionfish have several effects on native species in coral reef communities, as they not only affect their abundance but their behavior as well. Eaton et al. (2016) found parrotfish appeared to forage at a very slow rate with the sole presence of lionfish. It was estimated that it decreased their foraging by 50%, which could prompt a huge effect on the reef ecosystem as parrotfish are among the most efficient foragers. Being a very abundant and successful predator, the lionfish's diet is primarily composed of fish (71%), which coincidentally remain in the same ten families including Scaridae. A fish survey from 2003 to 2009 found the density of the Greenblotch parrotfish to be completely depleted from 0.064 fish per m² to 0 with fish per m² the introduction of the lionfish. Since parrotfish are keystone species to the coral reef communities, any alteration to their abundance and ability to perform their important ecological roles has a great impact in the resilience of these environments. Phase shift to algal dominated communities at mesophotic depths has been one of the most drastic results to occur with the massive loss of herbivore species such as the parrotfish, leading to the decline in corals and sponges in reef systems. With less coral and sponges present, fewer habitats are available for the amount of herbivorous fish needed to help recover the reefs, therefore making it even more difficult for coral reefs to regain health (Lesser & Slattery, 2011). Due to the additional pressures

coral reefs are presently facing, e.g., coral bleaching, crown-of-thorns, and eutrophication, the role of these reef fish are becoming increasingly vital as these factors eventually lead to a phase shift from coral to macroalgal dominated reefs (Bellwood & Hoey, 2008). Although complete eradication of lionfish is virtually impossible due to the magnitude and speed of their dispersal, control methods need to be proposed and implemented (Morris et al., 2011). Therefore, it is critical to evaluate the potential effects lionfish have on native reef fish populations, i.e. parrotfish, in order to understand the threat that they pose to the stability of the marine ecosystem.

CHAPTER II

METHODS

Unlike the Pacific region, the Caribbean environment is more heterogeneous due to local effects and patchy distribution of coral, seagrass, and sedimentation (Mumby, 2006). The contiguous biogeographic region containing the Caribbean coral reefs, known as the “greater Caribbean”, extends from the Bahamas and along the NE coast of South America. Coral reefs in the Caribbean are among the best studied in the world, with an abundance of information available on the reef status since the 1950’s (Hughes 1994). These long-term observations provide a foundation for analyzing the role of rare phenomena’s such as marine invasions and their effect on the trend of coral cover and biodiversity over time.

In order to uncover the possible threats lionfish may have on the parrotfish population in the Caribbean; three different models were constructed using vital rates from previous published journals. The models were projected using STELLA® ecological modeling software. The first model was developed using the following equation (1):

$$\mathbf{AdultsL}(t) = \mathbf{AdultsL}(t-dt) + (\mathbf{JuvenileLSurvival} - \mathbf{AdultLMortality}) \times dt \quad (1)$$

Where **AdultsL** is the recruitment density of lionfish per hectare at time of (t), and **dt** is the deaths at time (t). **JuvenileLSurvival** is calculated by multiplying the recruitment density of juvenile lionfish (**JuvenileL**) times the survival rate (**SR**) of the juvenile lionfish.

AdultLMortality is calculated by multiplying the adult parrotfish recruitment density (**AdultsL**) multiplied by **1-AdultsLSR**. Recruitment density is the measure of new individuals contributing

to the population through migration or progeny. The demographic data used includes estimates (Table 1) of the species' egg reproduction, recruitment value, mortality and survival rates for larvae, juvenile, and adults. A monthly-time step model ran with an initial recruitment density of 40 fish per hectare, for 120 months.

The second model illustrates the parrotfish population growth prior to the lionfish invasion using the following equation (2):

$$\mathbf{AdultsP(t) = AdultsP(t-dt) + (JuvenilePSurvival - AdultPMortality) \times dt} \quad (2)$$

Where **AdultsP** is the recruitment density of parrotfish per hectare at time (**t**). The equation for the parrotfish recruitment density was the same as the one used for the lionfish, with the pertaining parameters to the parrotfish population.

Table 1. Default parameters use in the lionfish population growth model.

Parameter	Value	Unit	Reference
Eggs	35,315	months	(Morris, Shertzer, Rice, 2011)
Recruitment	1,412,600	months	
Larval Mortality (%)	99%	months	(Morris, Shertzer, Rice, 2011)
Juvenile Mortality (%)	92.90%	months	(Morris, Shertzer, Rice, 2011)
Adult Mortality (%)	2%	months	(Morris, Shertzer, Rice, 2011)
Larval Survival Rate	0.00003	months	(Morris, Shertzer, Rice, 2011)
Juvenile Survival Rate	0.071	months	(Morris, Shertzer, Rice, 2011)
Adult Survival Rate	0.949	months	(Morris, Shertzer, Rice, 2011)
Density Dependent Variable	-0.02994	months	

Vital parameters were also used in the model to develop the population growth curve including adjusted values pertaining to the parrotfish listed in Table 2. Due to the inability to find consistent data across literature, estimations were used to distinguish between the different age classes of parrotfish. As a result, the 3 stages: larvae, juvenile, adults, were determined by fork length in measurements of 0-2 cm, 3-15 cm, and >15 cm respectively. The two separate models were individually configured in order to compare the population's growth trends prior to the lionfish invasion across the Caribbean.

Table 2. Default parameters use in the parrotfish population growth model.

Parameter	Value	Unit	Reference
Eggs	159,563	days	
Recruitment	8,217,469	days	
Larval Mortality (%)	97.72%	months	
Juvenile Mortality (%)	97.72%	months	
Adult Mortality (%)	21%	months	
Larval Survival Rate	0.022757	months	
Juvenile Survival Rate	0.022757	months	
Adult Survival Rate	0.79	months	(Rooij & Videler, 1997)

The two individual species models were integrated in order to quantify the potential effects of the lionfish population on the recruitment density of the parrotfish. Due to the ambiguous relationship between the two species, we decided to include a converter, which incorporates the negative effects adult lionfish have on the parrotfish recruitment density. This value was calculated by computing the recruitment loss measured in a group of five species belonging to the Scaridae family. The following species were used collectively to gauge the net recruitment loss per km²: *Cryptotomus roseus* (-0.2), *Scarus taeniopterus* (0.1), *Sparisoma*

atomarium (-0.1), *Sparisoma aurofrenatum* (-2.6), *Sparisoma viride* (-0.5) (Albins, 2008). The summation of these values were then multiplied by the adult lionfish recruitment density (**AdultsL**) and converted into recruitment loss per hectare in order to keep all data uniform. The incorporated model, as seen in figure 1, ran at a monthly-time step for 120 months. The projected population trend for each species were then graphed, where we were able to observe the lionfish population and parrotfish population post invasion.

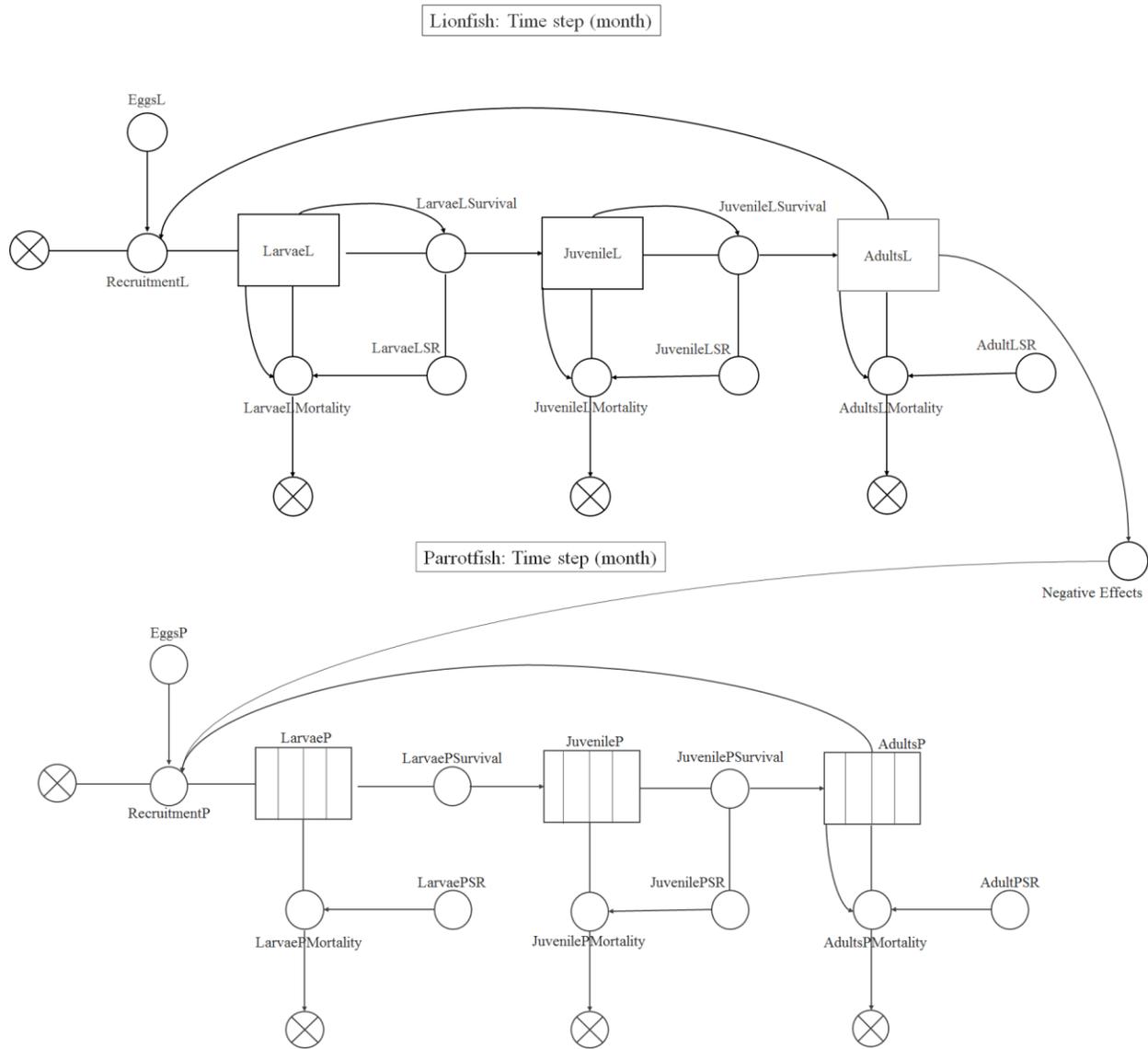


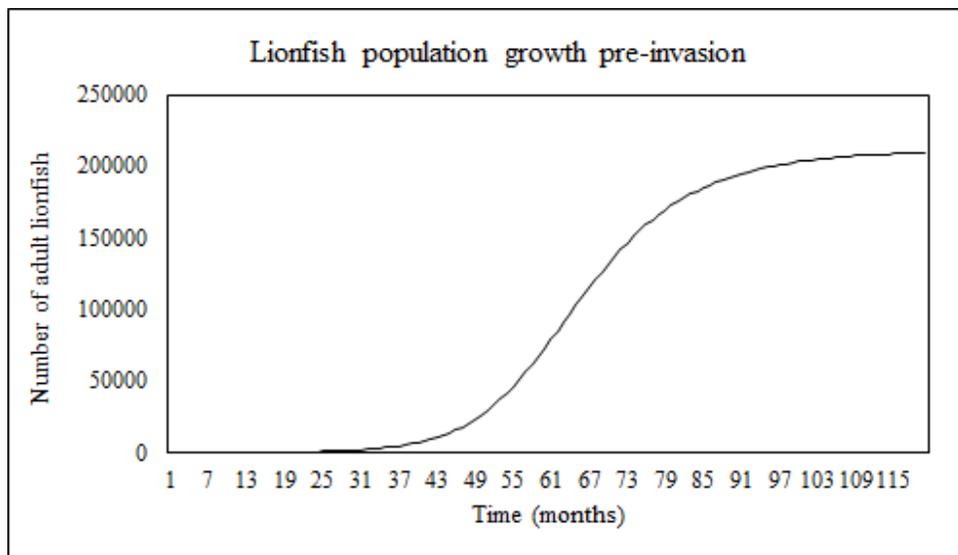
Figure 1. The figure above represents a predator-prey model incorporating both the lionfish and the parrotfish theoretical populations.

CHAPTER III

RESULTS

Results for the baseline simulation lionfish population prior to invasion ran with an initial recruitment of 40 fish per hectare for 120 months (Graph 1). The graph predicts a logistic growth for the lionfish population without incorporating the amount of parrotfish that contribute to their diet. Because there is no reliable data of the current Lionfish population, our population growth is based on population density per hectare in order to obtain a population trend. The population trend for the baseline simulation presents a monthly increase of 1759 lionfish per hectare.

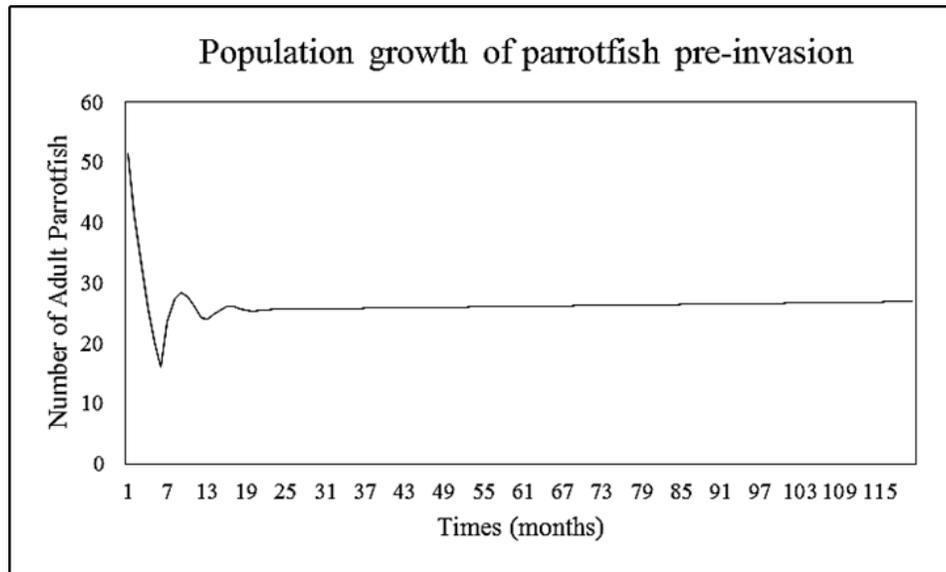
Graph 1. The graph below represents a projection of the lionfish population growth prior to invasion in the Caribbean.



In the same manner, the parrotfish population was also based on an initial recruitment of 40 parrotfish per hectare. The simulated growth of the parrotfish prior to the invasion of the lionfish (Graph 2) shows a declining population trend that slightly oscillates until it reaches a

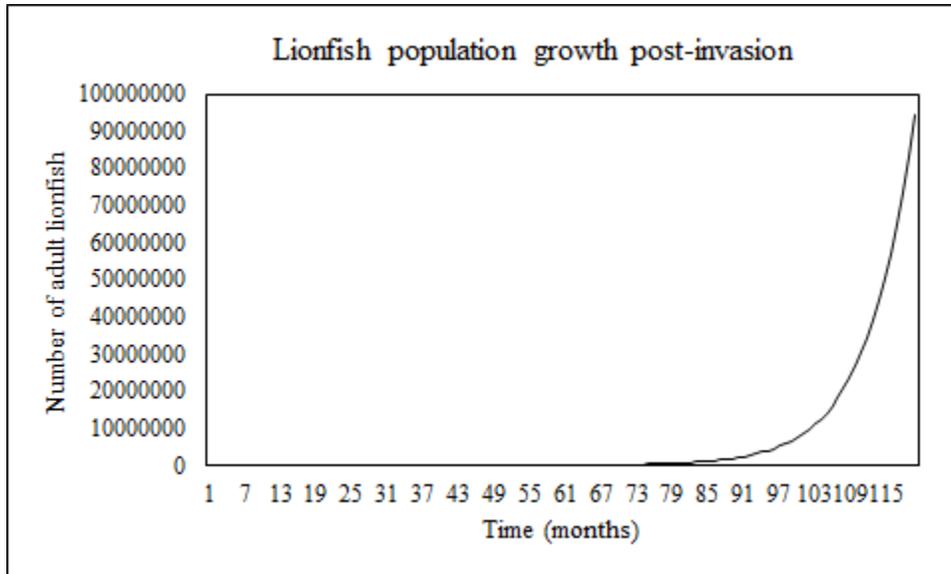
stable population. The population trend estimates a population density of 25 parrotfish per hectare, which is a decline from the initial population.

Graph 2. The graph below represents the projection of the parrotfish population growth prior to the lionfish invasion in the Caribbean.

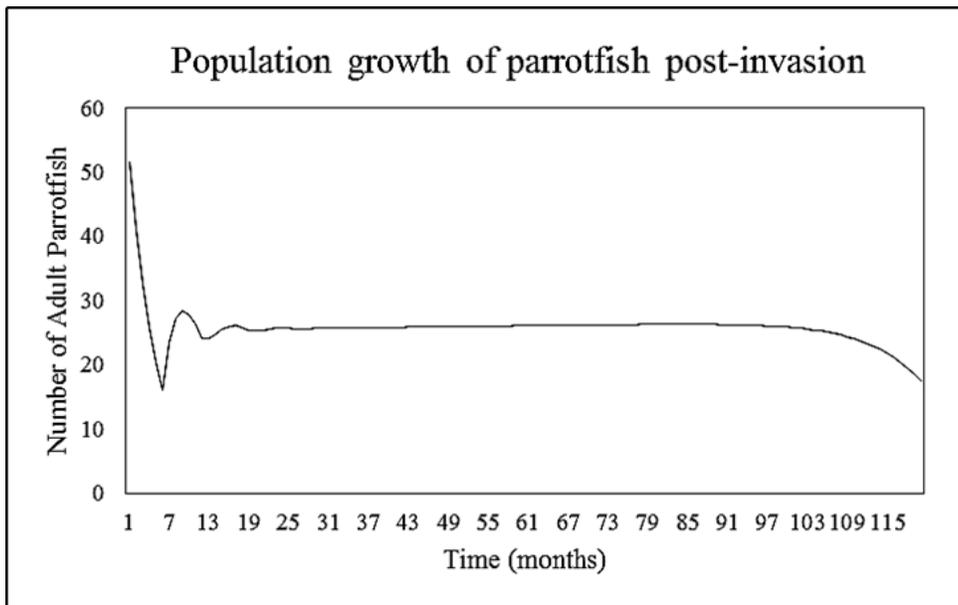


After integrating the two population models by calculating the negative effects the lionfish have on the parrotfish recruitment rate, two different population trends derive for each species. The lionfish population density experiences an exponential increase post invasion (Graph 3). This trend suggests further prolific advancement of the lionfish population after the incorporation of both populations. When looking at the population density of the parrotfish after the lionfish invasion (Graph 4), a similar trend appears but with the exception of a later decline in the parrotfish density. This trend exposes the threats the lionfish present to the parrotfish population and anticipates possible threats to the coral reefs as a result from this symbiotic relationship.

Graph 3. The graph below represents the projection of the lionfish population growth following their invasion in the Caribbean.



Graph 4. The graph below represents the projection of the lionfish population growth following the lionfish invasion in the Caribbean.



CHAPTER IV

CONCLUSION

At the current rate of the invasion, our model suggests that the Indo-Pacific lionfish has a direct deleterious effect on native parrotfish populations in the Caribbean. Our findings demonstrate that direct interactions, initiated by a large-scale predator invasion, can have far-reaching effects on entire reef communities.

The simulated reduction in net recruitment of the parrotfish due to these prolific invaders is an essential component to determining the relationship between lionfish and the stability of the reef ecosystem in the Caribbean. Herbivorous reef species, such as parrotfish, have been recognized as agents of bioerosion as they mediate the competition between coral and macroalgae. Therefore, the possible decline in abundance of these reef species by lionfish could further exacerbate the declining trend recently noted in the Caribbean coral reefs. Not only do lionfish have the ability to reduce recruitment of indigenous species, they also have the potential to act synergistically with current stressors, such as climate change, pollution, and ocean acidification (Albins & Hixon, 2008).

In addition to studying the nonconsumptive effects of lionfish on reef ecosystems, we propose that doing a future study which simulates the non-consumptive and consumptive effects of the lionfish would be highly beneficial for a better understanding of the long term consequences the coral reef ecosystem currently faces.

REFERENCES

- Albins, M. A., & Hixon, M. A. (2008). Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series*, 367, 233-238.
- Benkwitt, C. E. (2015). Non-linear effects of invasive lionfish density on native coral-reef fish communities. *Biological Invasions*, 17(5), 1383-1395.
- Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., & Largier, J. L. (2003). Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications*, S90-S107.
- Côté, I. M., Green, S. J., & Hixon, M. A. (2013). Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biological Conservation*, 164, 50-61.
- Davis, M. A. (2003). Biotic globalization: does competition from introduced species threaten biodiversity. *Bioscience*, 53(5), 481-489.
- Eaton, L., Sloman, K. A., Wilson, R. W., Gill, A. B., & Harborne, A. R. (2016). Non-consumptive effects of native and invasive predators on juvenile Caribbean holian parrotfish. *Environmental Biology of Fishes*, 99(5), 499-508.
- Gause, G. F. (1964). The struggle for existence. 1934. *Williams and Wilkins, Baltimore, MD*.
- Hines, A., Acero, P., Ortí, G., Wilbur, A. E., & Freshwater, D. W. (2011). Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. *Journal of Biogeography*, 38(7), 1281-1293.
- Hoey, A. S., & Bellwood, D. R. (2008). Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*, 27(1), 37-47.
- Holian, P. (2012). INVADERS OF THE REEF. *Earth Island Journal*, 27(1), 22-25.

- Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science-AAAS-Weekly Paper Edition*, 265(5178), 1547-1551.
- J.A. & Whitfield, A.K. (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. *NOAA Technical Memorandum NOS NCCOS*, No. 99. NOAA, Beaufort, NC.
- Johnston, M. W., & Purkis, S. J. (2015). Hurricanes accelerated the Florida-Bahamas lionfish invasion. *Global Change Biology*, 21(6), 2249-2260.
- Lesser, M. P., & Slattery, M. (2011). Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biological Invasions*, 13(8), 1855-1868.
- Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10), 5446-5451.
- Morris, J.A., Shertzer, K.W. & Rice, J.A. (2011) A stage-based matrix population model of invasive lionfish with implications for control. *Biological Invasions*, 13, 7–12.
- Morris, J.A. & Whitfield, A.K. (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. *NOAA Technical Memorandum NOS NCCOS*, No. 99. NOAA, Beaufort, NC.
- Mumby, P. J. (2006). The Impact Of Exploiting Grazers (Scaridae) On The Dynamics Of Caribbean Coral Reefs. *Ecological Applications*, 16(2), 747–769.
- Paine, R. T. (1969). The Pisaster-Tegula Interaction: Prey Patches, Predator Food Preference, and Intertidal Community Structure. *Ecology*, 50(6), 950-961.
- Stachowicz, J. J., Whitlatch, R. B., & Osman, R. W. (1999). Species diversity and invasion resistance in a marine ecosystem. *Science*, 286 (5444), 1577-1579.
- Van Rooij, J. M., & Videler, J. J. (1997). Mortality estimates from repeated visual censuses of a parrotfish (*Sparisoma viride*) population: demographic implications. *Marine Biology*, 128(3), 385-396.

Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience*, 48(8), 607-615.