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A Review of Present and Alternative Lionfish Controls in the Western Atlantic

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

A REVIEW OF PRESENT AND ALTERNATIVE LIONFISH
CONTROLS IN THE WESTERN ATLANTIC

By

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ABSTRACT

Lionfish (*Pterois volitans* and *Pterois miles*) are the first recorded invasive piscivore in the Caribbean and have become a threat to native species. As generalist consumers, lionfish have a broad diet and reduce prey and competitor abundance and juvenile recruitment. To confront this problem, this paper serves to review all of the current and alternative future controls available to manage lionfish populations in the Western Atlantic and determine where focus is lacking. Derby and cull efforts are the only management efforts in place and are not effective in their current state as these local events have short-term benefits, but lionfish populations recover quickly. Alternative strategies to culls include the use of biological controls and genetic engineering. Both strategies have their associated risks and ethical concerns, but may provide significant levels of control. Biological control agents include the introduction of parasites or disease from their native range that specifically target lionfish or the recovery and conditioning of natural Western Atlantic predators to consume lionfish. Genetic modification is gaining public acceptance for use against pest species and therefore, if made as safe as possible, could provide some of the best results for controlling lionfish. Quantitative analysis of derby and cull data revealed that focus is lacking in key locations throughout the Western Atlantic such as Cuba and the Meso-American Barrier Reef. The vast majority of derbies were located along the U.S. Eastern and Gulf coast. However, lionfish controls must implement in regions of the greatest larval connectivity to reduce the amount of larval recruitment and subsequent recovery of adult populations after local removals. Monthly, basin-wide removals of 20% lionfish biomass were determined to be the most effective strategy, reducing lionfish biomass to near-zero levels in only 36 months. Therefore, to effectively reduce lionfish biomass in the Western Atlantic, an international strategy is needed to produce management efforts in all regions simultaneously.

Keywords: lionfish, invasive species, derbies, culling, biological control, genetic modification, larval connectivity

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INTRODUCTION

Invasive species are a major threat to both indigenous species and global economics. The United States Department of the Interior spends \$100 million annually on invasive species prevention, but invasives still cost the US an estimated \$120 billion each year (US Fish and Wildlife Service, Pimentel et al. 2005). Zebra mussels cost US hydroelectric facilities alone \$250-300 million and invasive insects cause \$13 billion in damages to U.S. crops each year (Pimentel et al. 2005). Invasive species annual costs are estimated at £1.8 billion (\$2.3 billion) for the UK (Kelly et al. 2013) and in Canada the cost of a single invasive in the Great Lakes, the sea lamprey, costs roughly \$22 million Canadian dollars (Colautti et al. 2006). Of the 50,000 non-native species that exist in the United States today, many have been introduced intentionally including invasive plants for their food and resources or ornamental purposes (Pimentel et al. 2005). Non-indigenous fish are typically introduced to create stocks for commercial fisheries (Semmens et al. 2004). However, Williams and Meffe (1998) state that of all non-natives introduced roughly 60% of terrestrial vertebrates, 40% of fishes and 40-50% of mollusks cause harm to other organisms.

Methods of Introduction and Range of Lionfish

Despite the multiple paths of invasion attributed to international trade and transport, marine fish invasions are rare or not often reported (Semmens et al. 2004). The first documented invasive marine fish in the Caribbean region is the lionfish, specifically the Indo-Pacific red lionfish (*Pterois volitans*) and devil firefish (*Pterois miles*) (Meister 2005, Ruiz-Carus et al. 2006, Schofield 2009, 2010), but the method and timing of introduction is not clear. Theories of introduction include transport via ballast water and aquarium escape (Whitfield et al. 2002, Semmens et al. 2004, Kulbicki et al. 2012, NOAA). Ballast water has been identified as a primary vector for marine and aquatic invasions and has been identified as the cause of the zebra mussel invasion in the Great Lakes (Wonham et al. 2000, US Fish and Wildlife Service). *Pterois volitans* was one of the top 10 most valued marine fish imports to the US in 2003 (Cristina Balboa 2003, Ruiz-Carus et al. 2006). This high ornamental value in the hobbyist and aquarium trade suggests that aquarium release is likely the cause. Introduction can occur by several

means, including dumping of unwanted organisms, drainage of water containing organisms and escape from tanks or fish farms during storms (Padilla and Williams 2004).

Since their introduction in the 1980s, lionfish have rapidly expanded throughout the Western Atlantic. Mitochondrial DNA screening of lionfish throughout the Caribbean suggests that their genetic diversity is relatively low compared to their native counterparts (Betancur et al. 2011). Only one haplotype was observed for *P. miles* in the Western Atlantic, while 38 haplotypes were previously detected in the native range (Kochzius & Blohm 2005). Similarly, nine invasive haplotypes were found for *P. volitans* while there are 36 native haplotypes (Hamner et al. 2007, Freshwater et al. 2009). This low genetic

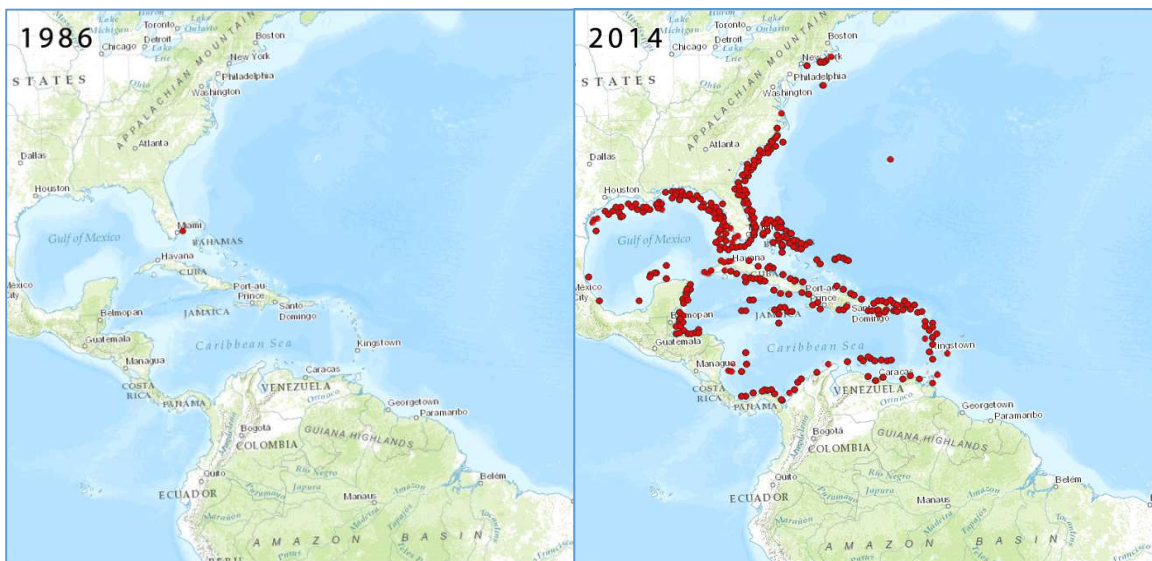


Fig. 1: USGS Lionfish Invasion Status from 1986 and 2014. Red circles indicate lionfish reports. Reprinted from Invasive Lionfish Web Portal.

variability in the Western Atlantic suggests a strong founder effect. A minimum of 12 lionfish (10 *Pterois volitans* and 2 *Pterois miles*) can explain the current haplotypes seen in the Western Atlantic today which suggests multiple releases of lionfish and/or eggs off the coast of Florida.

The first lionfish reported was in 1985 by a lobster fisherman off the coast of Dania, Florida (Schofield 2009). No further reports were made until 1992. Due to lack of reports and information it may be impossible to know exactly where and when the primary invasion event occurred for lionfish in the Western Atlantic. Due to their success as an invader, lionfish quickly established themselves throughout the Western Atlantic (Fig. 1). Lionfish were considered established along the Atlantic coast of the US in 2002,

the Bahamas and Bermuda in 2005, Cuba in 2007, the Turks and Caicos and Jamaica in 2008, and Mexico, Honduras and Costa Rica in 2009. Other sighting locations include the Greater and Lesser Antilles, the British Virgin Islands, Leeward Islands, Nicaragua, Panama, and Venezuela (Schofield 2010). Lionfish have also been observed as far north as Massachusetts, but their range is believed to be limited by cold water temperatures and therefore are not considered established because they are unable survive through the winter (Kimball et al. 2004, Schofield 2010). Although Brazil temperatures are adequate for lionfish establishment to the south, they have yet to be reported likely due to strong northern currents and the Amazon-Orinoco Plume (Luiz et al. 2013). The plume is considered a dispersal barrier for many organisms, but can be crossed via shallow inland mangrove habitat or deep sponge beds below the current. Lionfish in the invaded range are known to inhabit shallow mangroves (Barbour et al. 2010) and have been recorded at depths of 300 m by a ROV (O'Neill 2010). Therefore, lionfish may be able to penetrate the plume barrier by travelling along the inland mangroves or swimming beneath the strong currents at depth which may lead to their establishment along the South American coast.

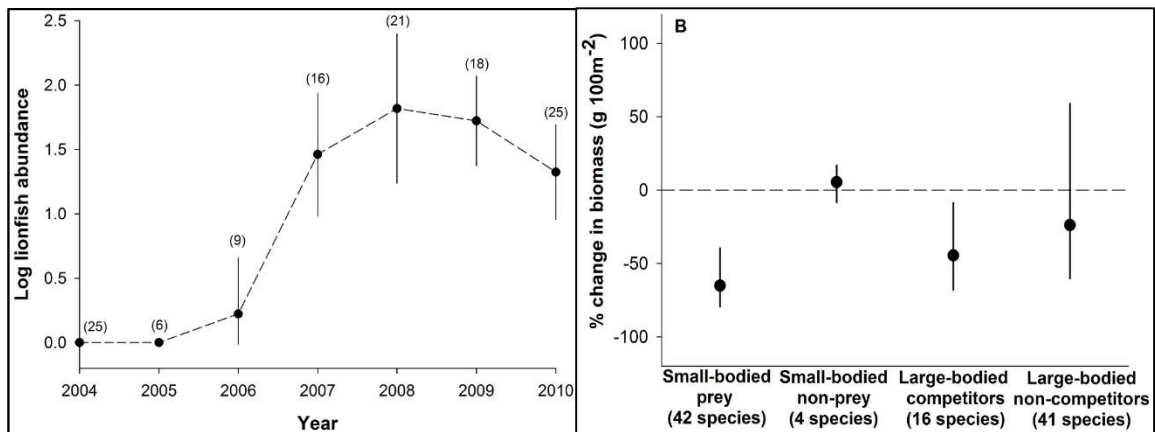


Fig. 2: Lionfish biomass by year off coast of New Providence, Bahamas (left). Change in prey abundance with arrival of lionfish from 2004 to 2010 (right). Reprinted from Green et al. 2012.

Impacts of Lionfish in the Western Atlantic

Piscivorous fish introductions have a large impact on native assemblages primarily due to predator and prey naïveté (Moyle and Light 1996). The lionfish invasion has been devastating to Western Atlantic fish populations (Albins and Hixon 2008, Arias-Gonzalez et al. 2011, Munoz et al. 2011, Green et al. 2012, Albins 2013). Lionfish are

opportunistic feeders that, as adults, consume primarily fish (99%) and do not exhibit a prey preference (Munoz et al. 2011). Green et al. (2012) reported an estimated abundance of 42 fish species in the presence of lionfish in the Bahamas. Nine locations along a continuous reef off New Providence were surveyed from 2008 to 2010 for fish abundance and size. Lionfish prey species were identified from the stomach contents of 567 collected lionfish over the duration of the study. At the conclusion of the study in 2010, lionfish were estimated to comprise 40% of all predator biomass in the Bahamas (Fig. 2). The collected data illustrated that lionfish reduced abundance of small-bodied prey by 65% and the ecologically-similar snappers and groupers (Lutjanidae and Serranidae) by 44% while small-bodied non-prey and large-bodied non-competitors from families Acanthuridae, Echineidae, Haemulidae, Holocentridae, Labridae and Scaridae were unaffected (Fig. 2). Through comparison of the abundance results with analysis of stomach contents, lionfish were determined to reduce prey species abundance in the area by 65% (Green 2012). Prey families found in stomach contents included Apogonidae, Chaenopsidae, Gobiidae, Labridae, Pomacentridae and Serranidae. Though the impact lionfish have on native species may be different by region, it can be assumed that similar results would be found on reefs throughout the Western Atlantic. These results show that lionfish may impact the native biodiversity of the Western Atlantic through reduction of

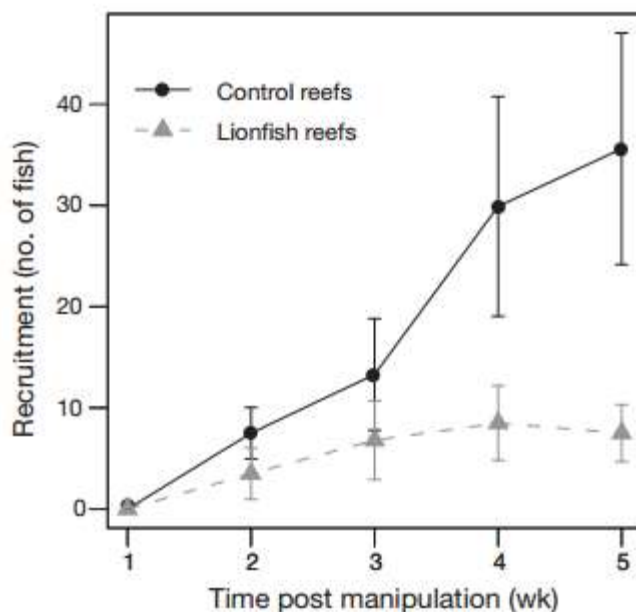


Fig. 3: Recruitment of juvenile fish to experimental patch reefs. Lionfish were transplanted on 10 reefs while another 10 reefs served as lionfish-free controls. Reprinted from Albins and Hixon, 2008.

native species such as snappers and groupers.

Albins and Hixon (2008) reported on the effect of lionfish on juvenile recruitment at Lee Stocking Island (LSI) in the Bahamas, spanning the mid-1990s to the first lionfish appearance in 2005. The lionfish population increased significantly by 2007 with over 100 lionfish spotted at LSI. In the summer of 2007, 24 new lionfish recruits were observed

at LSI over a 70 day period. This is the equivalent of 24 lionfish ha^{-1} per day, but this rate is based on the patch reefs at LSI and therefore may be different for continuous reefs. Juvenile recruitment of other species was reduced by an average of 79% after 5 weeks (Fig. 3). Recruitment was measured as fish less than 5 cm in length after 5 weeks compared to initial observations. Twenty-three of 38 species that recruit to these reefs were negatively affected by the presence of lionfish. These include, but are not limited to *S. tigrinus*, *H. melanurum*, *H. maculipinna*, *S. aurofrenatum*, *C. glaucofraenum* and *G. thompsoni*. For example, *H. melanurum* and *C. glaucofraenum* recruitment rates were reduced from 4.3 to 0.3 and 11.9 to 4.4 (fish reef^{-1}), respectively, in the presence of lionfish. Further research at Bahamian patch reefs showed that lionfish also reduce prey populations by up to 97% with the largest declines in *C. glaucofraenum*, *S. leucostictus* and *G. thompsoni* (Albins 2013). By comparison, a native predator, the Coney grouper, reduce these same prey populations by 36%. Lionfish growth rates are over 6 times that of the coney grouper and their negative effect on species richness was nearly two-fold greater than the effect of native grouper. This suggests that lionfish exhibit more rapid growth, a broader diet and a greater ability to outcompete native predators which led to their successful invasion of the Western Atlantic.

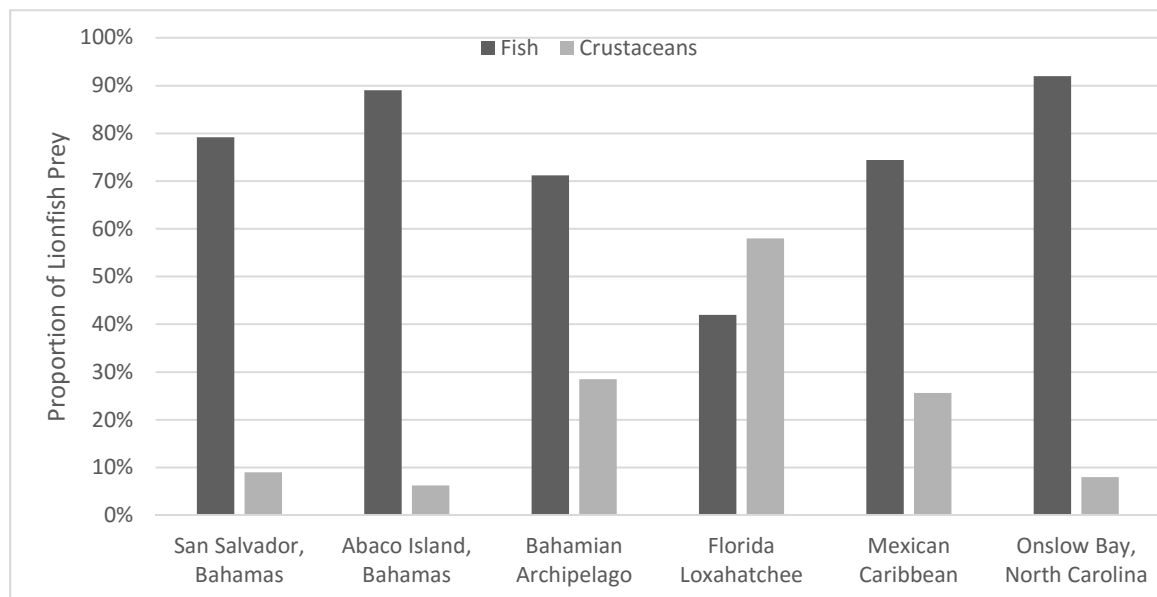


Fig. 4: Proportion (%) of major food groups in lionfish diet in 4 locations in the Western Atlantic. Fish and crustaceans were the only two food groups in all regions except the Bahamian archipelago, where molluscs represented 0.3% of lionfish diet.

Lionfish prey varies slightly based on region, but may be explained by their generalist hunting behavior. When comparing lionfish prey from several regions within the Western Atlantic, it is clear that lionfish generally prey more heavily upon fish than crustaceans at many locations (Fig. 4). The Loxahatchee River in Florida is an exception with a higher reliability on crustaceans, but this is likely due to the smaller average size of lionfish. The three most important prey groups in the estuary were determined to be the Panaeidae shrimps, Palaemonidae shrimps, and unidentified teleosts with 88% of the stomachs containing shrimp (Jud et al. 2011). Within the estuary, lionfish size ranged from 23 to 185 mm with an average size of 92.1 mm, suggesting that the majority of lionfish are small and/or juveniles. In a study by Morris and Akins (2009) in the Bahamian archipelago, it was determined that lionfish only consume prey between 0.02% and 48% of their total body length. A greater proportion of crustaceans, primarily shrimps, were also found in the Bahamas when evaluating only the stomach contents of smaller lionfish. The study by Jud et al. (2011) in the Loxahatchee took place in 2010 and 2011 and lionfish were first observed in the Loxahatchee in 2010. Therefore the lionfish population may consist of smaller juveniles and recruits and therefore the higher proportion of crustaceans found in the Loxahatchee estuary may be attributed to the smaller size lionfish in this region.

Table 1: Proportion of prey fish from several sites in the Western Atlantic. The Florida Loxahatchee River is excluded because specific data on stomach contents was not given.

Top Prey Fish from the Western Atlantic	
Family	Proportion of Prey Fish
Onslow, North Carolina	
Haemulidae	41.78%
Serranidae	14.48%
Scaridae	13.37%
Carangidae	8.64%
Blenniidae	6.13%
Mexican Caribbean	
Labridae	26.40%
Gobiidae	20.00%
Scorpaenidae	12.80%
Scaridae	10.40%
Apogonidae	7.20%
San Salvador, Bahamas	
Mullidae	29.17%
Gobiidae	25.00%
Labridae	12.50%
Labrisomidae	8.33%
Scaridae	4.17%
Abaco Island, Bahamas	
Labridae	29.00%
Pomacentridae	26.00%
Scaridae	14.00%
Haemulidae	12.00%
Blenniidae	8.00%
Bahamian Archipelago	
Gobiidae	27.08%
Labridae	14.58%
Grammatidae	13.89%
Apogonidae	10.07%
Pomacentridae	5.90%

The differences in lionfish prey between regions may be explained by regional prey abundance. For example, in Onslow Bay, North Carolina, Haemulidae was found in lionfish stomachs at the greatest proportion of 41.78% of all prey fish consumed (Munoz et al. 2011), while Labridae was found at 29% of all fish prey consumed at Abaco Island in the Bahamas (Table 1, Layman and Allgeier 2012). Being generalists, the difference between prey choices for lionfish between regions therefore suggests a higher abundance of different families at the study sites. Some similarities do exist due to the extensive range of these families throughout the Western Atlantic, but may also be a result of some minor prey preference. Labridae was the primary prey fish in both the Mexican Caribbean (26.4% of all prey fish consumed) and Abaco Island (29.0%) (Valdez-Moreno et al. 2012). They appeared in relatively large proportions of lionfish diet in four of the five locations, suggesting abundance throughout the Western Atlantic. Scarids were also a large part of lionfish diet in North Carolina (13.4%), the Mexican Caribbean (10.4%), San Salvador (4.2%), and Abaco Island (14.0%) (Layman and Allgeier 2012, Pimiento et al. 2013). In contrast, goatfish (family Mullidae) were unique to San Salvador across all study sites.

Due to their rapid growth and broad diet, lionfish may be altering food webs in the Western Atlantic and are considered a major threat to coral reef systems (Gonzalez et al. 2011, Green et al. 2012). Through the use of models it is possible to estimate the trophic impact that lionfish may have on Caribbean reef systems. A model designed by Gonzalez et al. (2011) uses the Ecopath with Ecoism approach. This modeling technique is used primarily to investigate the impact of policy decisions, but can also be used to analyze food web structure related to the impact of nutrients, functional groups such as parasites and apex predators, and invasive species. Data was used from the Alacranes Reef, an isolated atoll in Campeche Bank north of the Yucatan Peninsula where fishermen have reported 260 lionfish caught between July 2010 and February 2011. The model begins at near-zero lionfish biomass ($0.01 \text{ metric tons km}^{-2}$) with abundance and proliferation eventually increasing to post-invasion levels of $10.5 \text{ metric tons km}^{-2}$. Pre-invasion fish community data at Alacranes Reef was used as the starting point for reef community structure while the post-invasion values were estimated through comparison of biomasses observed in Bahamian reefs by Côté et al. in 2009 and 2010. In the early

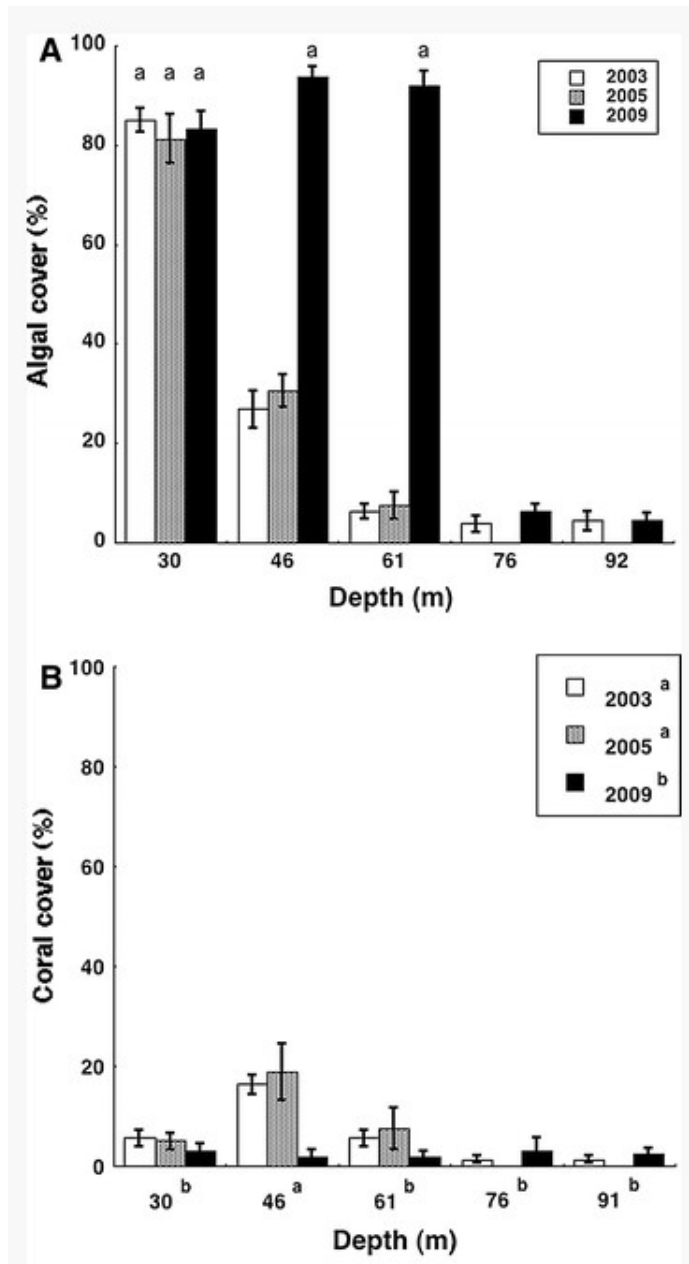


Fig. 5: Percent algal and coral cover in 2003, 2005 and 2009. Algal and coral cover varied significantly at 46 and 61 m depth. Reprinted from Lesser and Slattery 2011.

predation and competition for prey.

Similarly, lionfish predation on juvenile parrotfish and other herbivores may produce a trophic cascade that can shift coral-dominated communities to algal-dominated communities (Albins and Hixon 2013). Removal of herbivores has been documented to cause algae to outcompete and reduce recruitment of corals (Mumby et al. 2006). This is a worse-case scenario described by Albins and Hixon (2013) in which the combined

stages of the model with near-zero lionfish biomass, small omnivorous reef fish are the dominant fish group and jacks, sharks and rays are apex predators. As lionfish biomass rapidly increased, small and intermediate carnivorous and omnivorous coral reef fish biomass decreased by 40-69% while sharks, rays, scombrids, jacks, and small scarids and gobiids biomass decreased by 28-35%. Some groups exhibited a 14-47% increase in biomass with the proliferation of lionfish including blenniids, groupers, scarids, and engraulids. Together, these results suggest that the presence of lionfish causes changes in reef community and food web structure by releasing some groups from predation and competition pressures and hindering others through direct

effect of fishing pressure on large species and lionfish predation on smaller juveniles of the same species causes a significant change in trophic structure from coral-dominated to algal-dominated reefs. This scenario is becoming apparent in local regions where they have extended their range below 61 m depth, such as Bock Wall in the Bahamas. At Bock Wall, lionfish have begun to induce a phase shift from coral-dominated to algal-dominated communities (Lesser and Slattery 2011). Surveys were completed on Bock Wall at depths of 30, 46, 61, 76, and 92 m in 2003, 2005 and 2009 (Fig. 5). There were significant changes in algal and coral cover at both 46 and 61 m. Percent algal cover at 61 m depth was 6% in 2003, 8% in 2005, and 92% in 2009 while coral cover was 6% in 2003, 8% in 2005, and less than 2% in 2009. No lionfish were observed at Bock Wall until 2009 and therefore their arrival seems to be the cause of this rapid change in community structure. SIMPER analysis by Lesser and Slattery (2011) indicated that lionfish alone have a significant effect on species composition at this site including a decline in herbivorous fish. Eleven of the 16 herbivorous fishes found at Bock Wall in 2003 were no longer present in 2009. Native predators also disappeared; an average of 11 Nassau and 6 Hind grouper were found on transects between 2003 and 2006. However, with the arrival of lionfish in 2009, grouper were completely absent from this site. Through changes in community structure, lionfish may cause the already threatened coral reefs to eventually shift to an algae-dominated food web.

Lionfish present a rapidly growing threat to the ecology of the Western Atlantic and therefore all management strategies must be considered. Basin-wide eradication of *Pterois miles* and *Pterois volitans* is no longer possible as they are widespread and well established. Therefore, effective management strategies must be designed to reduce lionfish populations to a minimum and preserve native biomass at a regional level. Focusing management efforts on regions of greatest lionfish connectivity, namely source and sink populations, can greatly amplify results (Johnston and Purkis 2015). Johnston and Purkis (2015) forecasted that with international collaboration, lionfish biomass would reach near-zero with 20% monthly culls throughout the Western Atlantic. This capstone will provide a review of contemporary and theoretical lionfish management strategies in an attempt to enhance management strategies currently in place. It will also provide a

regional, quantitative analysis of control/removal studies in order to determine where focus is lacking.

METHODS

To identify all possible lionfish controls, scientific literature was reviewed primarily from online databases using Google Scholar advanced searches and other databases through Nova Southeastern Library access. Any reliable lionfish information was considered which included publications as well as information from general websites linked to lionfish, such as the REEF, U.S. Fish and Wildlife Service (FWS) and Lionfish Hunting. However, websites were primarily used to support published information. Searches were be focused on both the native and invasive range to compare lionfish status in both regions.

A comparison of lionfish prey by location in the Western Atlantic was completed to determine similarities and differences between prey choices. Data was taken from six studies at different locations. To account for different methods of measurement in each study, proportions of prey were used as a percentage of lionfish total diet by number. The top five prey fish families where then determined for five of the six studies because one did not provide specific information. The information was provided in chart and table form for comparison between regions.

The regional, quantitative analysis of control/removal studies was completed following the larval connectivity work by Johnston and Purkis (2015), which was used as a guide to the connectivity linkages between sub-regions in the invaded range of lionfish. The study identifies locations where controls should be focused in order to reduce lionfish abundance. Furthermore, quantifying the extent of lionfish control/removal studies revealed high risk areas that are lacking focus. Data was collected from published research studies and lionfish derby-like events. Events and study sites were grouped into the regions and sub-regions described by Johnston and Purkis (2015). The range and magnitude of removal events was considered if available. The regions with highest control activity were then compared to the regions of highest priority to reduce lionfish numbers in order to determine where focus is lacking. These areas are suggested as priorities for further research and culling events to optimize management efforts.

REVIEW

Native and Invaded Range

Prior to their establishment in the Western Atlantic, little was known about lionfish other than their value in ornamental trade. In order to create the most effective management strategies, a comprehensive understanding of lionfish is required. Research on invasive species tends to be focused in the invaded range, but information regarding their ecology and distribution in the native range is pertinent to their management (Hierro et al. 2004). For lionfish, information about predatory behavior and habitat in the native range of the Indo-Pacific can be used to create more focused control strategies in the

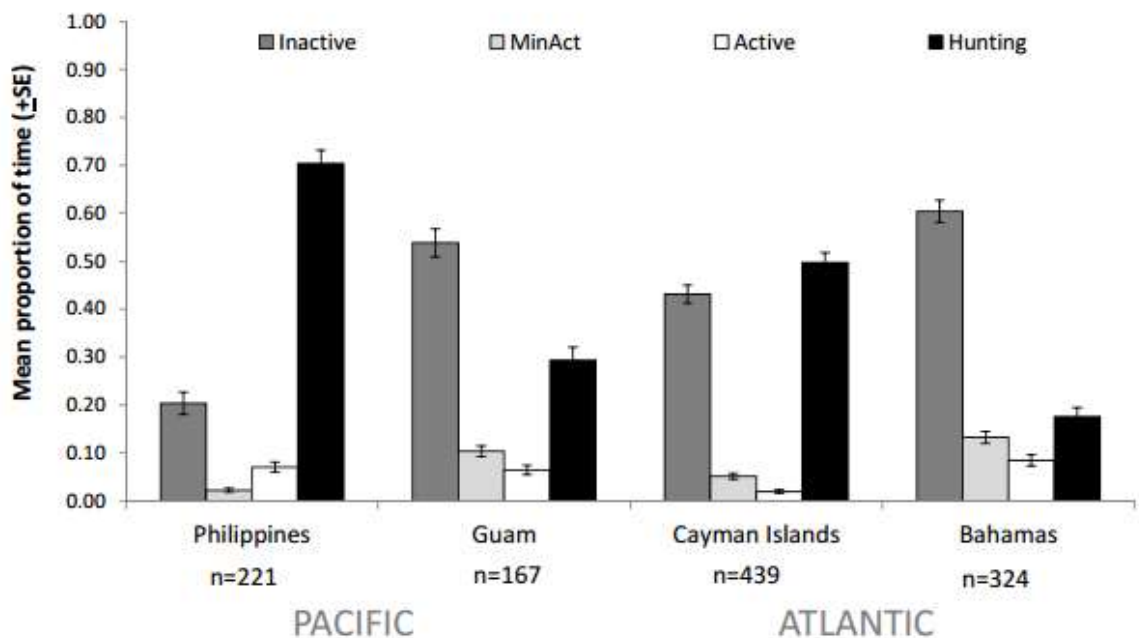


Fig. 6: Lionfish activity between Pacific and Atlantic Oceans. Lionfish exhibit similar patterns at different magnitudes between oceans. Reprinted from Cure et al. 2012.

invaded range (Kimball et al. 2004, Cure et al. 2012, Kulbicki et al. 2012), but further research is still needed to explore the native characteristics of this species.

Based on research completed by Cure et al. (2012), predatory behavior of lionfish was compared between native reefs in Guam and the Philippines and invaded reefs in Cayman Islands and Bahamas. It was discovered that hunting patterns did not differ dramatically between oceans, but rather between regions within each ocean. Lionfish were observed to be more active in the Philippines and Cayman Islands than Guam and the Bahamas. This suggests that there is no interoceanic difference between native and

invasive lionfish activity patterns. However, lionfish generally spent more time inactive and less time hunting between oceans (Fig. 6) and prey choices were significantly different between native and invasive lionfish. Mean prey size of invasive lionfish was double that of native lionfish. Lionfish exhibited a much broader diet with an average 1.6 taxa killed per 1000 min in the Atlantic and 0.9 in the Pacific. Only two fish families were targeted in their native range (Pomacentridae and Trichonotidae), while six fish families were targeted in the Atlantic (Apogonidae, Blenniidae, Gobiidae, Labridae, Pomacentridae and Scaridae). Their broader diet includes the ecologically important juvenile parrotfish in the Atlantic, which are not preyed upon in the Pacific.

Aquaculturists note that determining reef mates for lionfish is difficult because they will consume almost anything that fits in their mouths including ornamental shrimp, crabs and fish (“Lionfish Careguide” n.d., Marini 2002). Fishelson (1997) and Maljkovic (2010) also researched predation rate between oceans and found Pacific and Atlantic lionfish consume an average of 8.5 g and 13 g of fish per day, respectively. This difference may be attributable to predator and prey naiveté in the Atlantic (Côté 2013, Diller et al. 2014). While they do have a broad diet, lionfish also exhibit a high resilience to starvation, losing only 5-16% of their body weight after 3 months of starvation (Fishelson 1997). These attributes make lionfish an effective invader because they are able to consume a broad diet and survive in conditions where prey are scarce.

In the Indo-Pacific, lionfish have had time to reach a relative equilibrium compared to their recent expansion in the invaded Atlantic. Therefore it may be possible to estimate their future distribution in the Atlantic and focus management efforts by comparison with native lionfish. A study completed by Kulbicki et al. (2012) looked at population density and distribution patterns of lionfish in their native range (Fig 7). *P. volitans* and *P. miles* distributions were estimated based on a series of observations in the Pacific and, while they were relatively rare throughout the Indian and Pacific oceans (3.6 fish ha⁻¹ and 0.17 fish ha⁻¹, respectively), density was highly variable by region and increased with distance from the Indo-Pacific biodiversity center. For example, the highest regional density in the Pacific was found at Rapa in French Polynesia at 7.2 fish ha⁻¹ with much of the Pacific having no lionfish. In the Indian Ocean, highest densities were found near the Red Sea at greater than 20 fish ha⁻¹. These differences may be

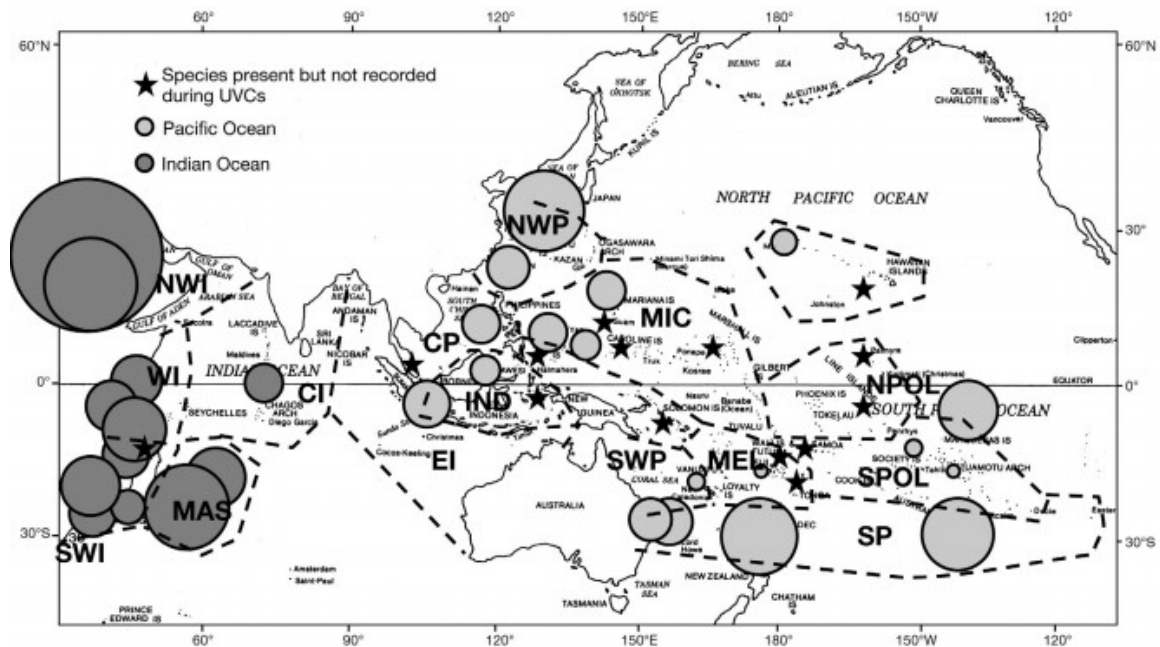


Fig. 7: Density of lionfish in the Indian and Pacific oceans. Area of circles is proportional to observed density. Stars represent lionfish present, but density was not recorded. Reprinted from Kulbicki et al. 2012.

attributable to any number of factors such as competition and/or predation of lionfish, suitable habitat, depth, temperature, or reproductive requirements, which could reveal any number of possible alternatives for lionfish control in the Atlantic. More research in their native range is needed to understand this distribution.

Kulbicki (2012) also studied lionfish habitat and depth preference in the Indo-Pacific and found that they preferred reefs, soft substrates, seagrass and algae beds, mangroves and estuaries. Regarding depth, highest densities from trawl catches were in the 10-20 m depth range (mean 0.68 fish ha⁻¹) with deepest recorded catch at 75 m. In the southeastern U.S., Meister et al. (2005) observed lionfish via submersible dives at depths of up to 99 m. The difference in depth between oceans may be attributed to environmental conditions in the southeastern U.S. and lionfish share a common establishment pattern with Atlantic reef fishes. Reef fishes that are observed in shallow waters are established on reefs up to 100 m depth off the coast of the southeastern U.S. It is also important to note that in the Indo-Pacific, *P. volitans* and *P. miles* share a relatively small area in western Indonesia, but are otherwise separated; *P. miles* are observed in the Indian Ocean and *P. volitans* are observed in the Pacific (Kulbicki et al. 2012). However, the reasons behind this separation are not well known. It is perhaps due to environmental differences and physical limitations of each species. In the Western

Atlantic, *P. miles* are restricted to northern regions such as Bermuda and the U.S. while *P. volitans* can be found throughout the Caribbean, Bermuda and East Coast U.S. (Betancur et al. 2011). In order to fully understand the physical limits of these species and better estimate their future expansion in the Atlantic, more research is required.

Thermal tolerance is one characteristic that can be used to estimate geographic expansion in the Atlantic. In the Pacific, lionfish have broad ranges spanning from 35°S to South Korea at 35°N with sea-surface temperature averages at both locations being roughly 19°C with a minimum winter temperature of 14°C (Kulbicki et al. 2012).

Kimball et al. (2004) conducted a study in the southeastern US to determine thermal tolerance of *Pterois volitans* and *Pterois*

miles and estimate their potential northern, southern and offshore limits in North America. Kimball et al. (2004) discovered the lethal minimum temperature for lionfish to be 10°C with feeding cessation beginning at 16.1°C. Comparing these to average sea-surface temperatures in the Atlantic, the geographic range for lionfish is from just north of Cape Hatteras, throughout the Gulf and Caribbean and south along the coast of Brazil, while offshore range in North America is limited by the 200 m isotherm continental shelf break at an average 12°C temperature.



Fig. 8: Range of thermal tolerance for Lionfish in the Western Atlantic based on average annual sea surface temperatures (SST)

Current Controls

Local fishing derbies and culls are the only active management strategies used to control lionfish populations at present (Harrell n.d.). Derbies are typically held by organizations and can help spread awareness of the lionfish problem while removing lionfish on a local scale. REEF and the Florida Fish and Wildlife Conservation Commission (FWC) sponsor summer lionfish derbies several times a year at several

different locations to assist in the management of lionfish off the coast of Florida and train divers on how to properly collect and handle the invasive fish. Teams are formed and register to compete in derbies of which winners will receive cash prizes based on the number and/or size of lionfish caught. In REEF events alone, 16,134 lionfish were reported removed since 2009 with the largest removal of 3,542 occurring in 2011. The lionfish caught during derbies are either donated for research or sold to restaurants. REEF and the FWC sponsor many other organizations or tournaments throughout Florida, which generally run from March through September each year (“2016 Lionfish derbies” n.d.).

Targeted removals have proven to significantly reduce lionfish densities to minimal levels and reduce the average size of remaining lionfish at the local to regional level (Frazer et al. 2012). Removals conducted by Frazer et al. (2012) off Little Cayman Island resulted in 229 lionfish caught at Blacktip Boulevard. This reduced lionfish density from 175 fish ha⁻¹ to 13 fish ha⁻¹ in 7 removals over 209 days. This type of local removal relieves predatory stress on larger prey species such as juvenile Nassau grouper and parrotfish and increases native biomass by 50-70% (Green et al. 2014). However, this is only a temporary solution. The long-term effects of such removals can be estimated through the use of models. Modeling overfishing of stock density estimates (Côté 2009, Morris and Whitfield 2009) showed that annual overexploitation rates of 35-65% or 157-293 lionfish ha⁻¹ were required to significantly reduce spawning stock, while cessation of overexploitation led to recovery in only six years (Barbour et al. 2011). Another simulation by Johnston and Purkis (2015) showed that monthly removals of 20% of lionfish biomass are necessary to significantly reduce lionfish abundance, which will be discussed later in this paper.

In the Lesser Antilles, monthly culls were performed in Martinique over the course of one year, each time removing an average of 74% of the observed population (Tregarot and Marechal 2014). The culls were performed on large, continuous reefs and small, isolated reefs. Density on the isolated reefs was reduced over time as culling continued throughout the year, but densities remained relatively stable on continuous reefs despite the large numbers of lionfish removed each month, suggesting year-round

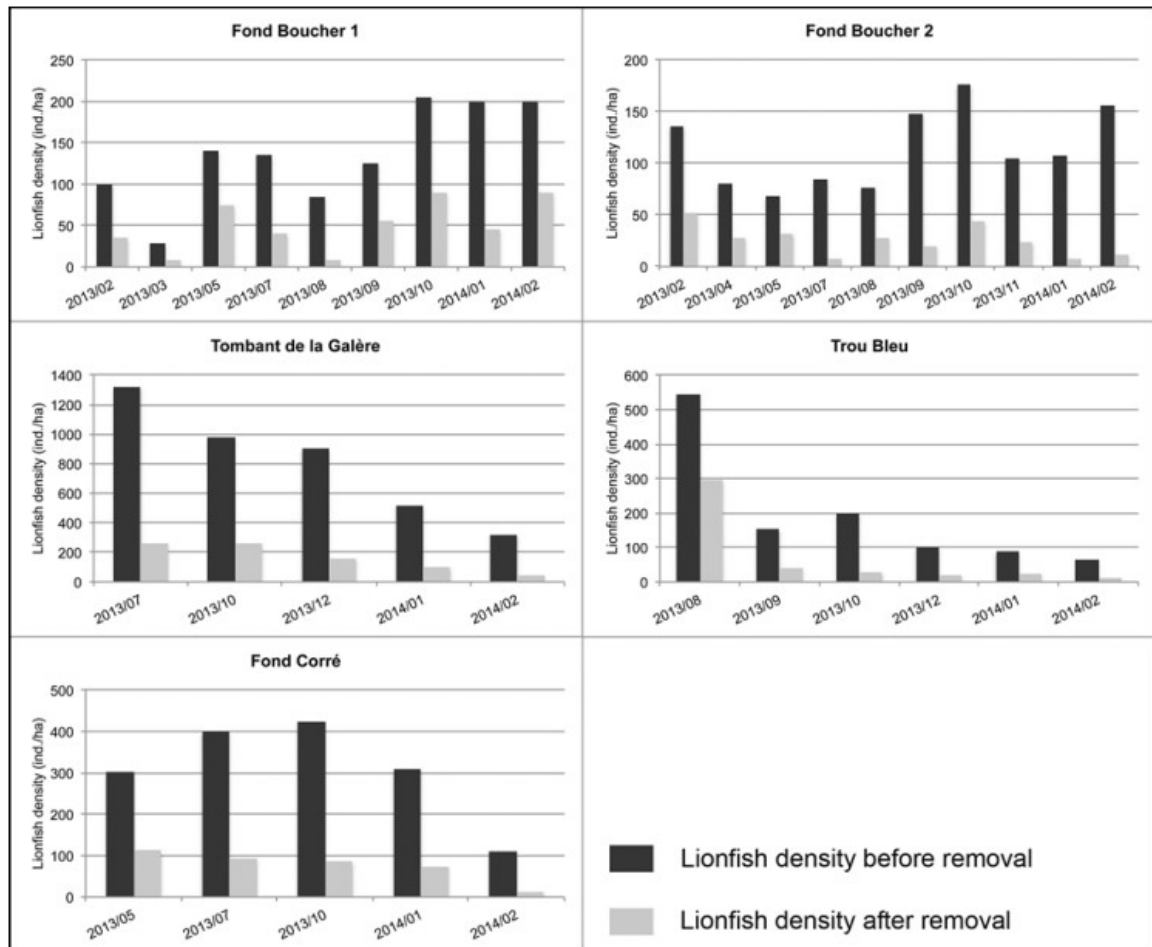


Fig. 9: Surveys of lionfish before and after targeted removals at several sites on the west coast of Martinique. Fond Boucher 1 and 2 are the continuous reefs which exhibited relatively stable lionfish densities despite large removals each month. All others are isolated reefs which show a negative trend in removals as density decreased. Reprinted from Tragarot and Marechal 2014.

recruitment (Fig. 9). Immigration is possible, but is contradicted by the observations of Jud and Layman (2012) and others that lionfish exhibit high site fidelity. Fifty-five lionfish of varying size categories were tagged along about 2 km of the south shoreline of the Loxahatchee estuary and recaptured or sighted over the course of 10 months. Over 73 total recapture/sighting events, the majority of lionfish hardly moved between captures. Roughly 56% were found within 0.5 m of their previous location and an additional 18% had moved less than 10 m. The greatest distance covered by a single lionfish was 420 m after 67 days suggesting that very few lionfish migrate to other locations and the stable density observed by Tregarot and Marechal (2014) is more likely due to larval recruitment than immigration. Therefore focus on specific regions with high larval connectivity should be prioritized to optimize culling efforts (Johnston and Purkis 2015).

Other cost-effective alternatives, such as the lionfish challenge award programs offered by the FWC, encourage recreational divers and fishermen to harvest invasive lionfish. These are important to consider, but still only tend to cover specific locales. The 2015 lionfish challenge allowed individuals to catch one extra spiny lobster each day of harvest season that they also take ten lionfish although this may lead to declines in lobster populations (FWC). In 2016, the FWC began the Statewide Lionfish Challenge that runs from May through September and provides one entry into a raffle for every 50 lionfish caught (FWC Lionfish Challenge). Prizes include fishing licenses, fuel cards and dive tank refills. Dive shops may also volunteer to provide an effective alternative. The Red Lionfish Hunt hosted by the Ocean Frontiers Dive Shop in the Cayman Islands dedicates one dive boat to lionfish culling every Monday afternoon (Ocean Frontiers). This has been ongoing since 2010 and provides interested divers with the education and resources to obtain a Lionfish Culling Certification.

Another organization known as Robots in Service of the Environment (RISE) is currently in development of submersible lionfish hunting robots that aim to autonomously control lionfish populations in the Western Atlantic (RISE). Seeking to eventually operate like the Roomba vacuum, the robots are controlled remotely. However, the developers aim to make the submersibles easy to operate so minimal training is required. The robots originally used traditional spears for culling, but newer models use a shocking probe. Though still in development, this may provide an interesting alternative to widespread culling.

Culling may provide significant lionfish control at a local and/or regional scale, but it can also affect lionfish behavior over time (Côté et al. 2014). As a response to heightened predation pressure, prey species tend to change their behavior to compensate and ensure highest survival rates. After intense culling by humans, therefore, lionfish exhibit greater avoidance behavior in the presence of divers and also hide during daylight hours when divers are typically present. Côté et al. (2014) imposed varying levels of culling pressure at 8 patches off Eleuthera in the Bahamas in order to study these behavior changes. Lionfish exhibited significantly more hiding behavior and less activity during daylight hours and tended to be more active and less hidden during dawn hours (6:40 am to 7:30 am) on culled reefs compared to uncultured patches. Lionfish also

exhibited greater avoidance behavior on culled patches with mean alert distance twice that of lionfish on unculted patches. This difference is only 25 (unculted) vs 50 (culled) cm, but could affect close range spearing and netting success. This analysis suggests that lionfish may change their behavior in response to human predation and repeated cullings may become more difficult over time. There is also concern that lionfish in frequently culled regions may move to deeper water. Considering the size of the affected area and short length of recovery, culling events are unreasonable and expensive tasks that can only be applied at small scales to protect biodiversity at the local level. Therefore, alternative methods should be explored for long-term solutions.

Fisheries and Human Consumption

Lionfish harvest by divers could provide significant impact on lionfish populations (Morris and Whitfield 2009). The idea of lionfish consumption has started to make headway and wholesale dealers are purchasing lionfish for sale in restaurants (FWC n.d.). This may be the most cost-effective method of lionfish control in areas with large lionfish populations and of high ecological importance as restaurants may see lionfish as profitable and therefore the demand will increase (Morris and Whitfield 2009). Many wholesale dealers have low or no minimum and high maximum delivery requirements and accept lionfish daily to accommodate all interested parties. Lionfish hunting may come in the form of trap, net or spear fishing, with spear fishing and hand-held netting currently being the most effective as they do not produce bycatch. If at some point a larger lionfish fishery was to develop, it could provide significant regional management of the invasive species.

Morris and Whitfield (2009) explain that lionfish meat is perfect for many dishes and is served as a delicacy in Mediterranean cuisine. If a demand for lionfish is created, harvests may become widespread and provide management. Publicizing this information, however, is quite difficult. For recreational fishermen or restaurant chefs who are interested in catching and/or cooking lionfish, the Reef Environmental Education Foundation (REEF) provides instructional guides and videos on catching, handling and filleting procedures as well as some cooking recipes. REEF also provides lionfish drop-off locations for divers that wish to donate their catch for research. Paul Greenberg, an

author for Food&Wine magazine, wrote about the lionfish problem in an attempt to inform the public of this potential exotic food and convince divers to become lionfish hunters (Paul Greenberg). Publicizing the problem to diving enthusiasts will not eradicate lionfish, but lionfish removals even in small, infrequent numbers may have some demographic impact.

Exploring Alternative Biological Controls

Through the careful evaluation of an invasive species' native range, it is possible to find biological control agents suitable for control in the invaded range. For example, the United States Department of Agriculture (USDA) currently deploys terrestrial invasive controls based on species relationships in native ranges (USDA APHIS 2009). The Emerald Ash Borer (*Agrilus planipennis*), or EAB, is a beetle that was projected to cause \$10 billion in economic damage to North American forests (USDA APHIS 2009). Three parasites from the beetle's native range in China were deemed compatible with the insect's invaded range in North America and released starting late 2007. The introduced parasites successfully slowed the spread of EAB, but did not cause declines in their abundance (Jennings et al. 2015). Models suggest that parasitism will need to be increased roughly 30-65% through further releases of the parasites to reduce EAB biomass (Jennings et al. 2015). By investigating what native controls lionfish have in their native range, it may be possible to find biological controls that can be implemented in the Western Atlantic.

However, the use of alien species as biological control agents requires extreme caution. In the early stages of EAB invasion in North America in 2002, the USDA conducted eradication efforts including quarantines and removal of ash trees (USDA APHIS 2015). This strategy was changed to management efforts once EAB populations were widespread. EAB is native to southeastern Asia so the USDA looked for parasitoids in China that specifically target EAB eggs and larvae as biological control agents. Only after 5 years of quarantined research in China and Michigan were test releases completed for the parasitoids in Michigan. Small, controlled releases were conducted and monitored for 60 days after which the parasitoids were not considered a great threat to other native species. They were soon after released in larger numbers to combat EAB. This procedure

outlines the extreme caution and time that is required when dealing with release of more invasive species in order to support management of another.

Biological controls can become failures if the agent competes with or attacks other native species and/or does not reduce targeted invasive species density (Myers 2000). A well-known example of a biological control failure is the 1935 introduction of cane toads, *Rhinella marina*, in Queensland, Australia to control scarab beetles, a sugarcane pest (Australian Government 2010). Their introduction as a control led to their establishment and rapid spread across northern Australia. The toads have since become a threat to other native species, where they compete with native predators for prey and shelter and are also toxic to naïve predators (TSSC 2005).

Another example is the Asian lady beetle, *Harmonia axyridis*, which is a polymorphic species native to central and eastern Asia that is exceptional at thriving in different environments (Soares et al. 2008). It has been released in multiple countries including the US to combat pest insects (Roy et al. 2007). However, the beetle is considered invasive in many cases, preying on and having greater foraging efficiency than native species, leading to changes in community composition (Soares et al. 2008). The EAB parasitoids can currently be considered a failure, although as the parasitoids populations increase through reproduction or further releases they may become more effective. Therefore, extensive, controlled experiments must be done in advance to determine if a non-native biological control agent is both viable and effective enough for safe release.

Species-specific agents such as natural predators, parasites or disease may provide the best option as biological control agents for lionfish management. However, due to the limited information available on species interactions with lionfish in the native range, few options are available. These include the natural predators to lionfish in the Indo-Pacific, including coronetfish (Bernadsky and Goulet 1991), sharks, grouper, large eels, frogfish and other scorpionfish (Lionfish Hunting), but these species are all moderate to large piscivores and are therefore too dangerous for release because they may lead to biological control failures. Further research to identify potential *Pterois*-specific agents may be beneficial in producing effective management strategies in the Western Atlantic.

Western Atlantic: Native Predators

Other possibilities for control rely on native species in the Caribbean such as the implementation of no-take zones or conditioning native predators like Nassau grouper and nurse sharks to consume lionfish (Maljkovic et al. 2008, Mumby et al. 2011, Mumby et al. 2013, Diller et al. 2011). Native grouper have been documented with lionfish in their stomachs and fishermen believe that native grouper are preying on lionfish (Maljkovic et al. 2008). However, the ability of native predators to control lionfish populations is a controversial topic and more research is required (Valdivia et al. 2014). Evidence exists to support both arguments and therefore this possibility for lionfish management needs to be explored.

Strict reduction in fishing of native predators (i.e., groupers and snappers, for example) and implementation of no-take zones (Sadovy 1997, Chiappone et al. 2000, Sala et al. 2001) may provide benefits to lionfish control. Grouper populations have been under severe pressure since before the 1970s when commercial grouper fisheries were established (Sadovy 1997, Chiappone et al. 2000, Sala et al. 2011). This also means that grouper populations were in steep decline during the onset of the lionfish invasion which may in part explain their rapid expansion in the Western Atlantic. Landing data from the 1970s shows Nassau grouper as the primary target of grouper fisheries, which comprised

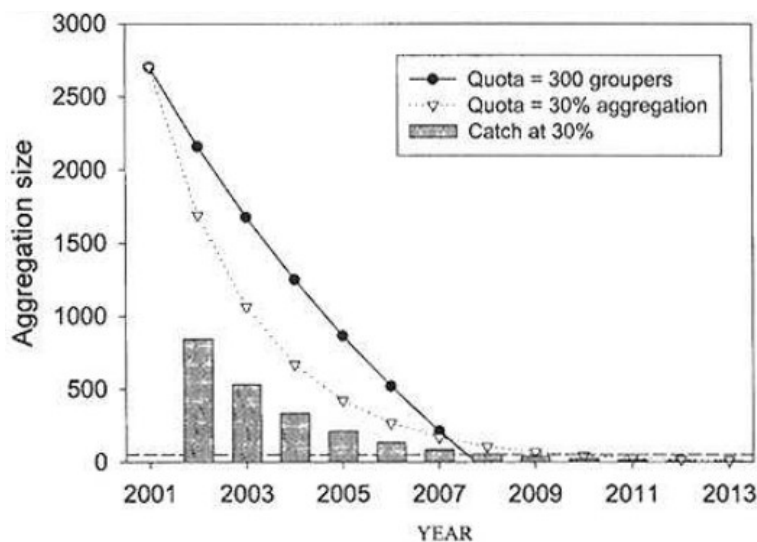


Fig. 10: Models of the Nassau grouper fishery on Glover's Reef in Belize. The two models are for two different quotas, 300 groupers or 30% of aggregation size. The bars are equal to grouper aggregation when quota is 30%. The dotted line indicates profitability of grouper fishery for a single vessel. Reprinted from Sala et al. 2011.

roughly 70% of total grouper landings (Sadovy 1997). Annual landings decreased rapidly from several thousands to less than 100 by 1990 at aggregation sites in the Bahamas. Grouper spawning aggregations in Belize declined from 15,000 to 3,000 in 25 years with high fishing quotas still in effect in 2011 (Fig.

10, Sala et al. 2011). In Bermuda, the decline was much quicker with Nassau grouper landings reduced from 29,100 kg to 1,800 kg in 6 years (Sadovy 1997). Cuba experienced a decline from 2,768,000 kg in 1960 to 766,000 in 1981, and Florida fishermen reported approximately 0.18 Nassau grouper per trip in the early 1980s compared to 0.01-0.03 fish per trip by the mid-1980s. Since their decline, grouper have struggled to recover in part due to the lionfish invasion, but also because they are still caught by fishermen. The implementation of no-take zones, however, has been successful in grouper recovery (Chiappone et al. 2000, Mumby et al. 2011).

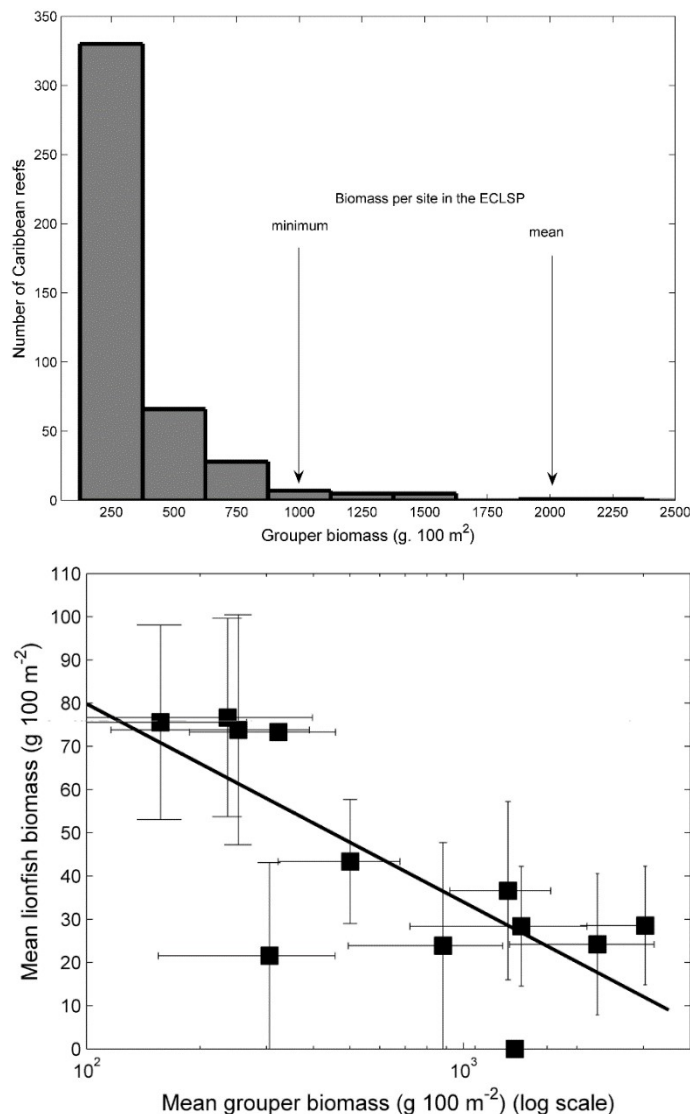


Fig. 11: Top: Average grouper biomass based on AGGRA assessments throughout the Caribbean. Arrows indicate minimum and mean grouper biomass in the ECLSP. Bottom: negative relationship found by Mumby et al (2011) between grouper and lionfish biomass. Reprinted from Mumby et al. 2011

No-take zones or protected areas completely prohibit fishing or have fishing regulations associated with them. One such location is the Florida Keys National Marine Sanctuary. The sanctuary is broken up into several zones to reduce conflict between recreational users such as divers and anglers. Hook-and-line and spearfishing is allowed in the sanctuary, but it is heavily regulated by the FWC to reduce impacts (Florida Keys National Marine Sanctuary). These regulations have helped grouper biomass increase within the sanctuary, but it still remains low due to the difficulty and lack of enforcement (Chiappone et al. 2000). Enforcement of catch regulations are difficult because they are expensive and time-

consuming, which can lead to illegal catches and reduce the effectiveness of the protected area.

One of the most restrictive areas is the Exuma Cays Land and Sea Park (ECLSP), where grouper have managed to recover due to a 20-year fishing ban (Chiappone et al. 2000, Mumby et al. 2011). Entrance to the park is only allowed with a scientific collecting permit. Mumby et al. (2011) calculated native grouper and invasive lionfish biomass along 30 km of reef of the Exuma Cays in the Bahamas. Sites were chosen within the ECLSP and to the north of the park where restrictions do not exist. These sites were chosen based on similar habitat (*Montastraea* reef) and depth of 7 - 15 m and had previously been surveyed for biomass as part of the Atlantic Gulf Rapid Reef Assessment Program (AGRRA). Average grouper biomass in this area was estimated at 2000 g per 100 m², far exceeding the average for the rest of the Caribbean. According to AGRRA assessments, the majority of Caribbean reefs had grouper biomass closer to 250 g per 100 m² (Fig. 11). Through their analyses of protected and non-protected sites, Mumby et al. (2011) determined that lionfish biomass had a significant, non-linear negative relationship with grouper biomass (Fig. 11). Lionfish biomass was reduced 50% with grouper biomass of 800 g per 100 m² and lionfish density was reduced to only 30% of its highest value when grouper biomass reached 1,516 g per 100 m². This implies that high numbers of native grouper may effectively reduce lionfish biomass either through predation or competition. Therefore, it is important to consider the beneficial effects of no-take zones and/or protected areas when designing lionfish management strategies.

Native predators and prey are naïve towards lionfish (Côté 2013, Diller et al. 2014), but conditioning native Nassau grouper and nurse sharks to consume lionfish may be possible (Diller et al. 2014). Caribbean predators may not recognize the antipredator behavior of lionfish resulting in fewer predatory events. Greater abundance of grouper has been tied to reduced lionfish abundance in specific regions (Chiappone et al. 2000, Mumby et al. 2011). If native predators can be conditioned to consume lionfish then they may therefore be able to help control lionfish in the Western Atlantic. Diller et al. (2014) studied the effects of conditioning on native predators. 132 lionfish were caught, sedated, secured by monofilament lines to lead weights and left overnight over multiple trials. The process was not determined fatal or stressful to lionfish because they survived longer than

24 hours in tanks and individuals were observed swimming slowly or resting during the experiment. Through video surveillance, many predatory events were observed. Lionfish consumed were roughly 50 - 200mm in length, with more lionfish consumed on reefs than seagrass beds (Fig. 12). This is likely due to native predator size and accessibility in the shallower locations. It is also possible that lionfish with total lengths greater than 200mm are not chosen by native

predators and therefore are safe from predation in the Western Atlantic.

Adult-sized lionfish can grow up to 450 mm in length, so the majority of adults may be avoided (NOAA).

However, conditioning may be a viable option to enhance current culling efforts and extend their length of effectiveness. Culling events tend to focus on larger individuals, reducing mean total length of lionfish

in an area and exposing more targets for native predators. In the study, predation rate was greatly enhanced on intensely culled reefs (Fig. 12, Diller et al. 2014). This may be attributable to the reduced size of lionfish in the culled area and/or prior conditioning of local natives by consumption of injured or killed lionfish.

Management strategies must be careful to include native predators as biological controls because evidence also exists against their effectiveness. Thorough research is still needed to determine if native predators can reduce lionfish abundance throughout the Western Atlantic. John Bruno (2013) provided a direct critique of Mumby's research in the Exuma Cays. Bruno explains that native predators do not significantly reduce lionfish biomass, but instead lionfish biomass in the Exuma Cays area is about 1/10 of the values reported throughout the Caribbean due to unknown environmental factors. Valdivia et al. (2014) examined the effectiveness of native, large-bodied predators in controlling lionfish on Caribbean coral reefs. Seventy-one coral reefs were surveyed in the Bahamas, Cuba, and the Mesoamerican Barrier Reef for fish abundance. Data was incorporated into

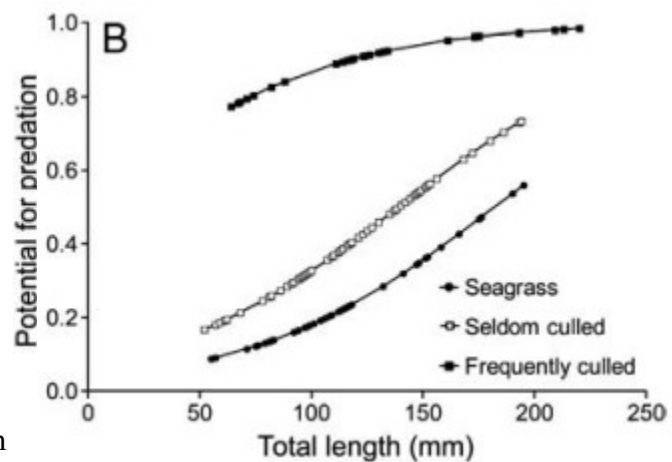


Fig. 12: Potential predation on tethered lionfish in seagrass, on frequently culled reefs, and on seldom culled reefs. Predators include Nassau grouper and nurse sharks. Reprinted from Diller et al. 2014.

a statistical model to estimate the effectiveness of large-bodied predators such as Nassau, tiger, black and yellowfin grouper on lionfish abundance. The model estimated that greater predator biomass did not affect lionfish abundance even when considering fishing pressure and habitat. Instead, the model predicted that site-specific characteristics had a significant effect on lionfish abundance, such as wind exposure, habitat type and human proximity. Across all 71 sites, lionfish abundance varied significantly with roughly equal grouper biomass. In comparison, the reduction in lionfish biomass found by Mumby et al. (2011) was less than 1% of the total range of lionfish biomass found across all 71 sites in the Caribbean. Due to the large regional differences in lionfish biomass throughout the Caribbean, these results suggest that differences in biomass are primarily due to differing environmental factors and not native predator control. Mumby et al. (2013) accepted that the relatively low lionfish biomass in their limited study area may be due to other factors and that it is unlikely that grouper can control lionfish throughout the Caribbean in their current state. However, the effects grouper have on lionfish biomass can only be measured in small, limited areas such as the Exuma Cays in order to account for as many environmental factors as possible. Therefore, although the reduction was less than 1% of the total range of lionfish biomass across the 71 sites surveyed by Valdivia et al. (2014), the negative effects observed were significant for their limited study area and should be considered (Mumby et al. 2013).

With evidence both in support of and against the effectiveness of native predators, their influence on lionfish in the Western Atlantic needs to be revisited. If deemed an effective control, the implementation of no-take zones or protected areas that regulate landings of large-bodied predators may assist and prolong the effect of current management efforts, specifically local and regional culling events. Native predators that have been conditioned by culling may, over time, consume more lionfish and therefore provide long-term management.

Controls: Genetic Engineering

Genetically engineering for control of invasive species is a highly debated topic, but provides the possibility for greater management of lionfish. With these techniques, local to regional extinction of invasives such as lionfish may be possible, but there are

risks involved and long-term effects must be considered (Langin 2014). Genetic modifications can be made either through breeding or genetic engineering and are commonly used in crops to increase yield and resistance to pests (Wolfenbarger and Phifer 2000). For example, the genetic engineering of algae has been proposed by Radakovits et al. (2010) to produce large quantities of renewable biofuels in the form of biohydrogen, alcohols, diesel fuel, and alkanes. Some other examples of genetically engineered crops include corn, soybeans, cotton, potatoes, tomatoes, wheat, alfalfa, tobacco, rapeseed, and rice (USDA 2014). These types of genetic modifications are aimed towards increasing the capabilities of organisms for some benefit. However, when targeting invasive species like lionfish, genetic modifications would be made to reduce the ability of the invasive species to be successful.

Genetically modified organisms (GMOs) have several ethical concerns and are considered a possible threat to environmental and human health (Prakash et al. 2011). For this reason, GMOs such as crops must follow State guidelines and also be approved at the Federal level by the USDA, U.S. Environmental Protection Agency (EPA) and the U.S. Food and Drug Administration (FDA) (USDA 2014). Further to this, the USDA's Animal and Plant Health Inspection Service (APHIS) provides careful testing of each GMO because the modification of any species is considered a threat to natural order and the integrity of species and ecosystems. GMOs are difficult to test thoroughly and therefore consequences can be unpredictable. If transgenic organisms were to escape, modified genes could spread through wild populations (Muir and Howard 2001). The modified individuals may have increased fitness compared to their wild-type counterparts and therefore may induce changes in the natural environment. This scenario would be an invasion in itself where a GMO outcompetes wild-type species and induces a shift in the food web. Intentionally released GMOs may breed with compatible relatives, spreading the modified trait to other native species (Prakash et al. 2011). If the trait was engineered to reduce viability of lionfish and is transferrable to other species, this trait may have a negative effect on native species. There are other species of scorpionfish in the Caribbean, but their compatibility with lionfish are not known. Another risk is that once the GMOs are released, especially into the open marine environment, it is nearly impossible to eliminate them. Any problems associated with the genetic modifications

would persist through the lionfish population. Horizontal gene transfer is one of the most concerning risks associated with release of modified organisms. This involves the transfer of the genetically engineered genes to other organisms, which may produce a new trait or in that organism. This is of particular concern in pathogens that may acquire an increase in fitness and become a threat to human health and the environment. The concerns regarding GMOs are generally aimed towards GMO crops and plants, but apply to all organisms. However, genetic engineering management strategies may become acceptable when considering only marine pest species such as lionfish (Thresher and Kuris 2004).

Genetic modification of pest marine species may be more publicly acceptable than in the past and may have the best chance to protect indigenous species. Thresher and Kuris (2004) provided a review of workshops held by the Australian CSIRO Centre for Research on Introduced Marine Pests, which included representatives of marine stakeholders, conservation groups, fishing industries, international scientists, and local, state and national marine managers to discuss alternative controls for marine invaders. The workshop was held to discuss alternatives to the publicly acceptable controls used for marine invasives that are low-risk and have a low chance of success against established invaders. Alternative controls were considered publicly acceptable for invaders through five categories: environmentally safe, safe for human health, practical, social, and politically attractive. Genetic modification of pests was considered effective, environmentally safe, and safe for human health by workshop participants with uncertainty for the other categories. As a general conclusion, genetic modification of marine pests to reduce their viability was accepted as having the greatest potential to be effective against invasives while also becoming publicly acceptable. Therefore, with the support of stakeholders and the public, genetic engineering of pest species may become a viable control for lionfish in the Western Atlantic.

There are several options for controlling lionfish through genetic engineering (Table 2). These are autocidal techniques meaning that they reduce the ability of a population to produce viable offspring. Control of females reduces total possible offspring and therefore may reduce population sizes. Sex or stage-specific lethality/sterility has been tested on *Drosophila melanogaster* by Thomas et al. (2000), but could potentially be used to control any pest species. This technique is based upon the

Table 2: Autocidal approaches for controlling invasive pests. Reprinted from Thresher 2007.

Approach	Description
Sex or stage-specific lethality/sterility	Construct induces death of offspring at specified stage, or kills or sterilises offspring of one sex, in which case the gene is transmitted through the other sex.
Gender distortion (“daughterless” or “sonless”)	Construct causes offspring to develop as specified sex irrespective of sexual genotype.
Inducible mortality	Construct causes death when externally triggered by, e.g., extreme environmental variability or artificial trigger; construct maintained in population by further stocking.
Pleiotropy “Trojan gene”	Construct pleiotropically has positive effect on one or more fitness components, and negative effects on others, e.g., increases mating advantage while decreasing viability of genetically modified offspring.
Selfish genes	Operational construct, e.g., one that causes gender distortion or sex-specific lethality, is packaged into a genetic element that has a high probability of reproducing itself within a genome, increasing both its spread and that of the construct.

sterile insect technique (SIT), which involves the periodic release of many sterile males that mate with wild-type females and result in no progeny. In theory, this will reduce wild populations and possibly eradicate pest species over time. However, Thomas et al. (2000) discuss a more efficient transgenic technique, RIDL (“release of insects carrying a dominant lethal”). This strategy involves the release of individuals that are fertile and carry a dominant,

repressible gene that is passed on to progeny. The repressible factor would be something not found in nature and only producible in a laboratory setting. For example, tetracycline was used as a repressor by Thomas et al. (2000). Stage-specific lethality is accomplished in males and females when the repressible factor is not present at specific life-stages. In the flies, the cytotoxic gene was expressed under the control of a heat shock protein, Hsp26 which is expressed in both male and female flies. When breeding the GMO insects, all progeny inherited the modification and did not survive without the tetracycline repressor. The experiment also tested the expression of the cytotoxic gene with a fat-body enhancer, Yp3 (Thomas et al. 2000). Yp3 is expressed only in females

during the larva and adult stages. All female progeny perished with the Yp3 modification, but males survived because they do not exhibit Yp3 expression. Male progeny are therefore carriers of the cytotoxic gene and continued to produce no female progeny. A similar technique designed by Schliekelman and Gould (2000) uses the same idea in which dominant genes kill or sterilize only female offspring while males become carriers. If translated to lionfish, this could become a powerful technique in reducing and/or eradicating lionfish populations throughout the Western Atlantic. Male carriers of the gene would eradicate all female progeny and reduce population sizes over time.

Another genetic technique involves gender distortion for which a patent was filed in 2001 (Thresher et al. 2002). The technique was developed as a strategy to control populations of exotic animals through manipulation of sex ratios. It is intended to be used in producing safe, male-only stocks in farming operations as well as reducing exotic pest populations. The designed genetic construct is inserted into the target organism at the proper locus and is activated during the sex-determination stages of development. It inhibits the targeted gene for sex differentiation resulting in a greater numbers of males. Similar to the previous method, the modification is transferred to progeny so males would persist and carry the modification to future generations, eventually resulting in reduced populations due to lack of females. Thresher et al. (2002) also explain that this procedure is humane, safe, cost-effective, and potentially effective against well-established invasive populations. The construct is described as species-specific and therefore is safe to use against exotic pests without harm to native species. It is also considered humane and cost-effective as it provides long-term control without the suffering of animals and can be achieved through low cost release programs while the construct spreads through the wild population.

A third genetic engineering technique that can cause gender distortion or sex-specific lethality is the insertion of 'selfish' genes (Burt 2003). These genes have a high chance of reproduction within the genome and therefore a high chance of spread to future generations. The simplest of selfish genes are homing endonuclease genes (HEGs) and are naturally occurring. They encode enzymes that cleave sequences not containing the HEG, into which the HEG is then inserted. This process can be manipulated by having the HEG cut a targeted essential gene sequence and insert itself to recreate a knockout

mutation. The gene would be chosen so that the knockout mutation would have no effect when the gene is the dominant trait, but be fatal when recessive. The gene could be chosen from several that express the gene at specific stages, such as the larval stage. Therefore, when expressed at the specified stage, the gene would induce mortality.

Instead of using a repressor to repress activation of genes, inducible mortality of individuals is possible when they are exposed to an external trigger (Grewe 1997). This technique was proposed as an alternative to carp control in Australia. A fatality gene linked to a reporter are incorporated into the genome of the target pest. Releases of modified pests then spread the genes to offspring in the natural population. The reporter gene allows for identification of individuals with the fatality gene in order to estimate percent integration in natural populations. Finally, once the desired levels of integration have been reached, the trigger can be released locally to induce mortality. This will have to be considered carefully as anything released into the system may affect native species. However, by allowing the fatality gene time to spread, significant reduction of lionfish populations may be accomplished. One complication of this method is that 100% introgression of the gene for carp in Australia was estimated to take roughly 28 generations, suggesting that complete eradication will be a long-term goal. It may be longer or shorter in the Western Atlantic depending on several factors including reproduction rate, growth rate and number of isolated populations. The transgene might also affect individual fitness and mating ability. Other challenges include finding the proper transgene and trigger for lionfish, development of a broodstock and periodic release throughout the basin. However, Grewe (1997) explains that given the current state of technology, this method can be easily used to combat pest species. Incorporating multiple constructs at various loci may improve the chance of inheritance and therefore reduce the time needed to reach the desired level of integration into the wild population. To do so, interbreeding of transgene carriers would produce fish with multiple copies of the kill gene at different locations. This is due to the low chance that construct integration will occur in the exact same location for all individuals. By using this method, local or even regional to basin-wide removal of lionfish may be possible.

Using genetic modifications can have adverse effects on species and may reduce their viability and therefore effectiveness. The trojan gene hypothesis developed by Muir

and Howard (1999) does the reverse. The genes are developed so that they enhance the ability of the pest species to mate but reduce the viability of offspring. The technique was tested with Japanese rice fish, *Oryzias latipes*. The transgenic fish were created by inserting the human growth hormone gene with a salmon promoter, sGH. They were then compared to wild-type rice fish to determine the differences in four categories: viability, development, fecundity and sexual selection. A predictive model was then used to estimate the results from the trojan genes being incorporated into the wild population. The transgene produced significant differences in male mating success and offspring viability, which would allow for local extinction of wild-type populations. Offspring viability was reduced regardless of sex. The model predicted that transgenics that reduced offspring viability alone would result in the elimination of transgenics from the wild-type population and have little effect. However, the combination of increased male mating success with reduced offspring viability instead resulted in local extinction of wild-type populations. Wild-type populations were reduced by 50% in six generations and were estimated to be completely eradicated in 40 generations. Trojan genes provide a unique opportunity in which transgenic lionfish may outcompete wild-type lionfish in the Atlantic. This strategy is not directly harmful to the species and can therefore be considered ethical. Instead, lionfish numbers will slowly decline over time due to the decreased viability of offspring.

The genetic techniques discussed here have the potential to reduce the impact of or completely eradicate pest species such as lionfish. For example, by using female-specific mortality genes, populations may disappear over time through the loss of females in the wild population. It is possible, however, that these techniques may not reach all lionfish in the Caribbean Basin due to the existence of isolated populations or inability of genetic engineered lionfish to breed. However, trojan genes provide a unique opportunity that enhances the modified individual's ability to breed while simultaneously reducing the viability of its offspring. Further research must be completed in order to produce the most effective genetic techniques suited to the lionfish problem. Combinations of the above or new methods may be discovered, and the possibility for genetic control in the now widespread lionfish invasion must be considered. Traditional controls may significantly

impact lionfish on local to regional scales, but show little promise of basin-wide management or eradication of the non-indigenous species.

Focusing Management

Although there are many controls available for use against lionfish, the fish are too widespread for complete eradication to be possible. Therefore, management needs to be focused in specific regions that may significantly impact lionfish numbers in order to provide both the most cost-effective and efficient means of lionfish removal in the Western Atlantic. Johnston and Purkis (2015) developed an international strategy that outlines specific regions where controls should be focused in order to better manage lionfish populations. The research is based on larval dispersal by currents throughout the Atlantic and explains why local controls are not particularly effective on lionfish. Lionfish females release buoyant egg masses after courtship and fertilization which are then carried by surface currents (Morris 2009). It is thought that reproduction occurs year-round based on lionfish caught off the coast of North Carolina. The eggs and larvae ride these currents for an estimated 25-40 days, though the exact amount of time is unknown. This allows lionfish larvae to traverse great distances, such as from Bahamas to New England or from the lower Caribbean to the Gulf of Mexico. Their long-distance dispersal ability allows for rapid establishment of new areas and recruitment at the local to regional level throughout the Western Atlantic, making the vast majority of removals ineffective as long term solutions. Therefore, it is pertinent to determine regions of high connectivity that, when control efforts are put in place, will have the greatest effect on lionfish populations throughout the Western Atlantic.

The biophysical model designed by Johnston and Purkis (2015) integrates cull events to forecast lionfish dispersal over time. It covers an area from 39° to 11° N latitude and 94° to 69° W longitude as a 2-dimensional grid comprised of 10 km x 10 km cells. Physical attributes such as sea surface temperature and current velocity were compiled for each cell. Ocean current data was collected from the Hybrid Current Ocean Model (HYCOM) which is commonly used to determine marine connectivity. The model then aimed to simulate distribution of lionfish larvae between regions in order to determine

Table 3: Precincts defined by Johnston and Purkis (2015) and the top 3 linkages for each. Reprinted from Johnston and Purkis 2015.

Precinct	Precinct code	Primary link	Secondary link	Tertiary link	Percentage of total
Carolinas	CAR	MDA	FLK	CBN	95.8
Florida Keys	FLK	EGM	YUC	CBN	99.5
Mid-Atlantic	MDA	FLK	EGM	CBN	94.4
Cuba North	CBN	WBA	CBS	MBR	98.1
Cuba South	CBS	CBN	EGM	MBR	99.6
Western Bahamas	WBA	CBN	NBA	CBS	99.7
Northern Bahamas	NBA	WBA	CBN	CBS	100
Meso-american Barrier Reef	MBR	YUC			100
Yucatan	YUC	MBR	CBS	CBN	99.9
Eastern Gulf of Mexico	EGM	FLK	MBR	YUC	97.8

regions of highest connectivity and therefore the locations at which controls should be placed. The 10 regions, or precincts, were defined as the Carolinas, Florida Keys, Mid-Atlantic, Cuba North, Cuba South, Western Bahamas,

Northern Bahamas, Meso-american Barrier Reef, Yucatan, and Eastern Gulf of Mexico (Table 3). Connectivity between these defined precincts was then calculated through the model simulation.

The modeling approach by Johnston and Purkis (2015) allowed for identification of each precinct as being primarily an exporter, importer or self-recruiter. Precincts were considered exporters if larvae produced within the precinct settled outside of its boundaries and importers if larvae that settled within the precinct came from outside its boundaries. Self-recruitment was considered when larvae settled within the precinct they were produced. The model was run 10 times with randomly located founder populations for each precinct. The founder populations consisted of 10 breeding females for a total of 100 breeding females from each precinct. Each individual larvae was tracked through the grid to determine which regions were considered major exporters or importers. Major linkages were considered as importers that received greater than 95% of all recruits from an exporter precinct. Since all precincts were determined to have 3 or fewer major exporters, exporters were further broken down into primary, secondary or tertiary linkages based on number of larvae contributed.

The model results showed that the Western Atlantic is highly connected through sea surface currents (Fig. 13). However, several precincts show greater larval connectivity than others. The Cuba North and Cuba South precincts were shown to export larvae to 8 of the other 10 locations with Cuba North being the lead exporter. Cuba North was a primary exporter to the Western Bahamas and Cuba South with a secondary link to the Northern Bahamas and a tertiary link to the Yucatan, Florida Keys, Mid-Atlantic, and the Carolinas. Therefore, Cuba North and Cuba South have a large influence on

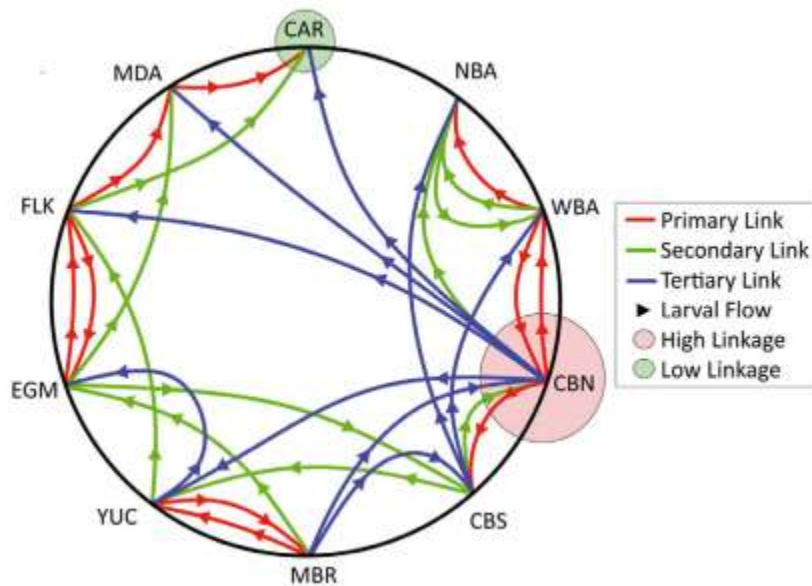


Fig. 13: Connectivity between precincts as determined Johnston and Purkis' (2015) model. Indicated are primary, secondary and tertiary links as well as direction of larval flow. The precinct with highest and lowest linkages are shown (CBN and CAR). Reprinted from Johnston and Purkis 2015.

restocking lionfish to other regions within the Western Atlantic and should be high priority locations for greater lionfish control. On the other hand, the Carolinas precinct did not export lionfish larvae to any of the other precincts, but was instead considered an importer. This that

controls being used in the Carolinas are ineffective for the Western Atlantic as a whole. The Meso-american Barrier Reef was a major exporter just behind Cuba North and Cuba South, making it another high priority location for controls. It is also important to compare the amount of import, export and self-recruitment for each precinct to determine high priority locations. For example, the Florida Keys produced a low quantity of larvae in comparison to many of the other precincts, but over 80% of those larvae were exported suggesting that the Florida Keys would have a somewhat higher priority for placement of lionfish controls. The Mid-Atlantic precinct had the second highest percentage of larval export at roughly 45% with an almost equivalent amount of self-recruitment, suggesting that this location would also have higher priority for controls as it is self-sustaining.

Due to the high level of connectivity between precincts after the proliferation of lionfish in the Western Atlantic, placing intense controls in a single or few precincts may somewhat curb lionfish populations throughout the Atlantic. The model simulated virtual culls within precincts to determine the amount needed to reduce lionfish biomass. Culls were simulated for the Carolinas and its three highest exporters, the Florida Keys, Mid-Atlantic and Cuba North to determine what magnitude of removal would be required to effectively reduce lionfish populations in the four precincts. Simulated annual culls of 50

and 90% in each precinct linked to the Carolinas were ineffective and lionfish populations continued to increase. However, intense monthly culs of 60% in precincts connected to the Carolinas effectively reduced lionfish populations in all four precincts over the 5 year period. The model then simulated the effect of simultaneous culs in all precincts including the Carolinas, which showed that even low-intensity culling events in all precincts significantly reduced lionfish populations in the Carolinas and its exporters

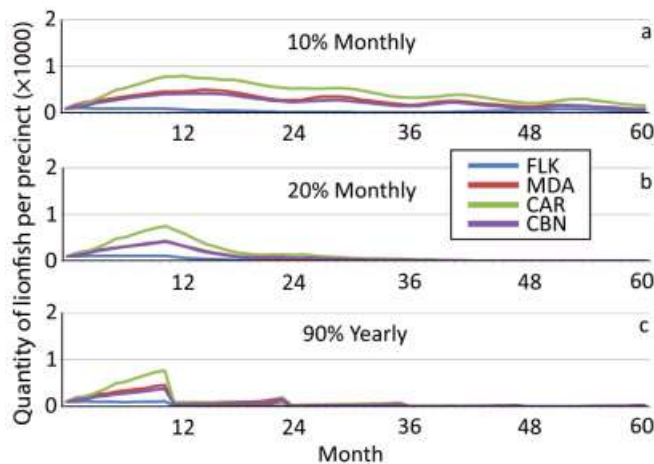


Fig. 14: Five-year plot of lionfish populations after 10% monthly, 20% monthly, and 90% annual culs in the Carolinas as well as precincts highly linked to the Carolinas. Reprinted from Johnston and Purkis 2015.

(Fig. 14). Culms in all precincts at a rate of only 20% monthly vastly reduced lionfish biomass to near-zero levels in only 36 months in the Carolinas, Mid-Atlantic, Florida Keys and Cuba North. Controls in place at few precincts may provide some relief such as the intense 60% monthly cull scenario, but in order to effectively reduce lionfish populations throughout the Western

Atlantic, international collaboration is necessary.

The results from the model designed by Johnston and Purkis (2015) show that local culms such as derby events that reduce lionfish populations at the local level are short lived due to the high connectivity in the Western Atlantic. Therefore, in order to produce longer-term results, an international agreement must be made on the method and timing of control events. This may include culms or any of the other control methods discussed in this review. Currently, regional and international focus on lionfish control is lacking. Derbies and cull events organized by concerned individuals or research organizations tend to be small scale and don't address larval dispersal and repopulation of a reef over a short period of time. Also, the effects of these derbies are not well measured because post-derby monitoring does not usually take place (Côté 2013). It is likely these events curb local lionfish biomass in the short term, but lionfish populations exhibit rapid recovery due to the high larval connectivity throughout the Western Atlantic and are therefore ineffective without international support.

Analysis of Lionfish Control Needs

Focus on lionfish control is lacking throughout the Western Atlantic. Using Johnston and Purkis' (2015) larval dispersal research as a guide, accessible and published cull data shows the majority of precincts are lacking support. Derbies provide easily accessible catch data. Catch data from a total of 86 derbies was recorded from 2009 to 2016 resulting in removal of 60,158 lionfish (Table 4). Catch per derby ranged from 23 to 8,089 and lionfish ranged in size from 24 to 470 mm. 37 derbies took place in the East Gulf of Mexico (EGM), 29 in the Mid-Atlantic (MDA), 7 in the North Bahamas (NBA), 7 in the Florida Keys (FLK), and 6 located outside of all precincts (St. Vincent, St. Croix, St. Lucia, Barbados). 26,701 lionfish were caught in the EGM, 20,320 in the MDA, 7,431 in the NBA, 2,146 in the FLK, and 3,560 in other regions. However, the average number of lionfish caught varied with the NBA having the greatest number of lionfish caught on average at 826 followed by 721 in the EGM, 700 in the MDA, 593 in other regions, and 307 in the FLK. Though this may be attributable to participant effort, it may also be a result of greater lionfish numbers in the NBA due to lack of culling effort in this region. This does not explain, however, the much lower average removals in the Florida Keys. Derbies have a high amount of support and success, but are primarily located in Florida. It is impossible to know the effects of such derbies due to the lack of pre- and post-derby monitoring. With monitoring, it may be possible to learn more about the requirements for proper basin-wide management based on local efforts.

Removal events by research organizations are also lacking. There are only few publications that have completed long-term removal studies and report gross numbers (Table 5). However, since pre- and post-cull status is recorded, they provide detailed information so that large-scale models can estimate the required basin-wide effort for lionfish control. 12 culling events resulted in culls from the CBS precinct (10) and other regions (2). Gross numbers of lionfish are not available because lionfish are typically removed based on percent biomass. Many studies work over multiple test areas and remove 0-95% of the estimated lionfish biomass over the course of months to years to monitor the results.

Table 4: Removal data from lionfish derbies held between 2009 and 2016.

Date	Host	Location	Removed	Largest	Smallest	Precinct
Apr-14	Florida Gulf Coast University	Fort Myers	296	388mm	123mm	EGM
May-14	Tampa Bay Spearfishing Club	St. Petersburg	48	436mm	155mm	EGM
May-14	Reef Monitoring Inc	Clearwater	64	343mm	97mm	EGM
May-14	Gulf Coast Lionfish Coalition	Pensacola	1914	392mm	66mm	EGM
Jun-14	Flora-Bama Yacht Club	Perdido Key	99	422mm	155mm	EGM
Jun-14	Gulf Breeze Sertoma Club	Gulf Breeze	101			EGM
Jun-14	Guns and Hoses Spearfishing	Pensacola	310	379mm	112mm	EGM
Jun-14	Gulf Coast Lionfish Coalition	Pensacola	700	391mm	88mm	EGM
Jul-14	Capt. Anderson's Marina	Panama City	452			EGM
Jul-14	Gulf Coast Lionfish Coalition	Pensacola	781	382mm	99mm	EGM
Aug-14	St. Petersburg Underwater Club	St. Petersburg	301	426mm	175mm	EGM
Aug-14	Gulf Coast Lionfish Coalition	Pensacola	1022	380mm	41mm	EGM
Sep-14	Englewood Open	Englewood	25			EGM
Sep-14	Suncoast Spearfishing	St. Petersburg	205	434mm	101mm	EGM
Sep-14	REEF Monitoring Inc	St. Petersburg	473	398mm	151mm	EGM
Sep-14	Gulf Coast Lionfish Coalition	Pensacola	870	395mm	60mm	EGM
Oct-14	REEF	Sarasota	251	374mm	146mm	EGM
Oct-14	Gulf Coast Lionfish Coalition	Pensacola	2394	419mm	47mm	EGM
Apr-15	Naples Spearfishing League	Naples	42			EGM
Apr-15	Tampa Bay Spearfishing Club	Tampa	49	412mm	217mm	EGM
May-15	Diver's Den	Mexico Beach	23			EGM
May-15	Wakulla Diving Center	Crawfordville	51			EGM
May-15	Capt. Anderson's Marina	Panama City	195			EGM
May-15	Discovery Dive World	Destin	700	305mm	75mm	EGM
May-15	Gulf Coast Lionfish Coalition	Pensacola	877	395mm	89mm	EGM
Jun-15	Florida Gulf Coast University	Fort Myers	462	400mm	68mm	EGM
Jul-15	REEF	Sarasota	456	418mm	112mm	EGM
Sep-15	Suncoast Spearfishing	Sarasota	173	406mm	101mm	EGM
Sep-15	Reef Monitoring Inc	St. Petersburg	884	420mm	60mm	EGM
May-16	Naples Spearfishing League	Naples	71	410mm	120mm	EGM
May-16	Florida Skin Divers Association	Belleair Bluffs	655	415mm	103mm	EGM
May-16	Diver's Den	Panama City	728			EGM
May-16	Discovery Dive World	Destin	1930	419mm	98mm	EGM
May-16	Gulf Coast Lionfish Coalition	Pensacola	8089	445mm		EGM
Jun-16	Florida Skin Divers Association	Clearwater	211	394mm	130mm	EGM
Jun-16	Guns and Hoses Spearfishing	Pensacola	370			EGM
Jul-16	REEF	Sarasota	429	385mm	112mm	EGM
Feb-14	REEF	Key Largo	143	445mm	118mm	FLK
Sep-14	REEF	Key Largo	573	435mm	51mm	FLK
Oct-14	Sanctuary Friends Foundation	Marathon	369	470mm	89mm	FLK
Feb-15	REEF	Key Largo	99	407mm	98mm	FLK
Jul-15	Tildens Scuba Center	Marathon	342			FLK
Sep-15	REEF	Key Largo	488	433mm	24mm	FLK
Mar-16	REEF	Key Largo	132	392mm	116mm	FLK
Apr-14	Lionfish Blast	Jacksonville	2068			MDA
Jun-14	Treasure Coast Lionfish Safari	Fort Pierce	581	399mm	97mm	MDA
Jul-14	MCAC Artificial Reef Builders	Port Salerno	512	425mm	139mm	MDA
Jul-14	REEF	Boca Raton	551	423mm	106mm	MDA
Jul-14	REEF	Fort Lauderdale	557	430mm	135mm	MDA
Aug-14	REEF	Palm Beach	639	420mm	70mm	MDA
Aug-14	REEF	Jacksonville	1102	448mm	37mm	MDA
Oct-14	eBoat Listings (REEF)	Boynton Beach	406	389mm	90mm	MDA
Apr-15	Lionfish Blast	Jacksonville	951			MDA
May-15	Force-E Scuba	Pompano	75	406mm	98mm	MDA

May-15 REEF	Fort Pierce	198	419mm	101mm	MDA
May-15 Treasure Coast Lionfish Safari	Fort Pierce	224	393mm	117mm	MDA
May-15 MCAC Artificial Reef Fund	Jupiter	579	444mm	108mm	MDA
May-15 Lionfish Blast	Jacksonville	951			MDA
Jul-15 Andrew "Red" Harris Foundation	Jupiter	119	406mm	148mm	MDA
Jul-15 REEF	Fort Lauderdale	318	435mm	105mm	MDA
Jul-15 REEF	Boca Raton	379	420mm	93mm	MDA
Aug-15 REEF	Palm Beach	236	411mm	112mm	MDA
Aug-15 REEF	Jacksonville	2583	446mm	43mm	MDA
Sep-15 REEF	Dania Beach	166	411mm	60mm	MDA
Sep-15 REEF	Fort Pierce	197	415mm	102mm	MDA
Sep-15 Treasure Coast Lionfish Safari	Fort Pierce	198	419mm	101mm	MDA
Apr-16 Lionfish Blast	Jacksonville	3478			MDA
May-16 REEF	Sebastian	31	384mm	26mm	MDA
Jun-16 MC Lionfish	Jupiter	239	403mm	127mm	MDA
Jun-16 REEF	Boca Raton	655	434mm	82mm	MDA
Jun-16 Treasure Coast Lionfish Safari	Fort Pierce	740	410mm	70mm	MDA
Jul-16 REEF	Palm Beach	337	424mm	24mm	MDA
Jul-16 REEF	Fort Lauderdale	1250	427mm	98mm	MDA
May-14 REEF	St. Vincent and the Grenadines	212	376mm	78mm	N/A
Jun-14 REEF	St. Vincent	989	410mm	33mm	N/A
Nov-14 COREVI	St. Croix	651	420mm	53mm	N/A
Sep-15 REEF	St. Lucia	693	420mm	70mm	N/A
Dec-15 REEF	Barbados	807	440mm	100mm	N/A
Apr-16 REEF	St. Vincent and the Grenadines	208	415mm	113mm	N/A
Jun-09 REEF	Green Turtle Cay, Bahamas	1408	349mm	57mm	NBA
Jun-10 REEF	Green Turtle Cay, Bahamas	914	434mm	47mm	NBA
Jun-11 REEF	Green Turtle Cay, Bahamas	1318	381mm	62mm	NBA
Jun-12 REEF	Green Turtle Cay, Bahamas	771	316mm	50mm	NBA
Jun-13 REEF	Green Turtle Cay, Bahamas	1204	331mm	40mm	NBA
Jun-14 REEF	Green Turtle Cay	908	334mm	51mm	NBA
Jun-14 REEF	Green Turtle Cay, Bahamas	908	334mm	51mm	NBA
Total		60158			

Table 5: Removal data from lionfish publications between February 2011 and June 2014. Gross numbers of lionfish are missing from the majority of publications and were unavailable for use.

Date	Host	Location	Removed	Largest	Smallest	Precinct
Feb-11	Frazer et al. 2012	Little Cayman Island (Bus Stop)	96			CBS
Jan-11	Frazer et al. 2012	Little Cayman Island (Mixing Bowl)	32			CBS
Feb-11	Frazer et al. 2012	Little Cayman Island (Mixing Bowl)	39			CBS
May-11	Frazer et al. 2012	Little Cayman Island (Mixing Bowl)	44			CBS
Jan-11	Frazer et al. 2012	Little Cayman Island (Blacktip Blvd)	100			CBS
Mar-11	Frazer et al. 2012	Little Cayman Island (Blacktip Blvd)	60			CBS
May-11	Frazer et al. 2012	Little Cayman Island (Blacktip Blvd)	44			CBS
Jun-11	Frazer et al. 2012	Little Cayman Island (Blacktip Blvd)	12			CBS
Jun-11	Frazer et al. 2012	Little Cayman Island (Blacktip Blvd)	7			CBS
Aug-11	Frazer et al. 2012	Little Cayman Island (Blacktip Blvd)	1			CBS
2013	Tregarot and Marechal 2014	Martinique (Annual)	1195			N/A
Jun-14	Harms et al. 2014	Cayo Pelotas (Puerto Rico)	22			N/A
Total			1652			

CONCLUSIONS

Johnston and Purkis' (2015) results show Cuba North, Cuba South, and the Meso-American Barrier Reef are major exporters of lionfish larvae with high levels of connectivity to all other precincts and therefore controls should have greater focus in these regions. Only one publication outlined a removal study within the Cuba South precinct and 74 of 86 derby events took place throughout Florida in the East Gulf of Mexico, Mid-Atlantic, and Florida Keys precincts. From this alone it is obvious that the majority of precincts are lacking focus. There were no reported removal events in the Cuba North, Meso-American Barrier Reef, Carolina, and Yucatan precincts. However, unreported data from volunteer efforts in other countries is likely. For example, fishing programs in Bonaire and Curacao started training recreational divers to kill lionfish in 2009, but lack monitoring (León et al. 2013). The lack of effort in both Cuba regions may be skewed due to the recently eased US embargo against Cuba and therefore should be monitored over the coming years. In order to effectively curb lionfish biomass throughout the Atlantic, an international strategy that produces low-effort monthly cullings (20%) throughout the Western Atlantic must be considered (Johnston and Purkis' 2015).

A few countries are already showing support for the fight against lionfish. Costa Rica has showed tremendous support after fishermen started reporting an 87 percent reduction in catch (Arias 2014). In 2012, the Southern Caribbean Traditional Fishermen's Association (APACS) of Costa Rica developed to join the cause. Costa Rica then began the development of the National Commission for the Management and Control of Lionfish in 2014 which was finalized in 2016 to assist with lionfish control efforts (Fenot 2016). This initiative is part of a coordinated effort with Mexico and the International Coral Reef Initiative (ICRI) against lionfish in response to loss of commercially important species (ICRI 2014). The ICRI also helped to form the Regional Lionfish Committee (RLC), which includes members of the UNEP-Caribbean Environment Programme, Centre for Agriculture and Biosciences International (CABI), REEF, government of Mexico, USA, and Dominican Republic. The committee produced the "Regional Strategy for the Control of Invasive Lionfish in the Wider Caribbean" to target all regions within the Caribbean (Gomez Lozano 2013). It seeks to produce a collaboration between all effected governments, reef-reliant industries, society, and

academia in order to encourage research and monitoring, develop an international strategy for control, and generate public support. The collaboration will share strategies and tools for effective lionfish control. Therefore, an international strategy is possible if the proper economic motives are in place. In order for an international strategy to be effective, proper monitoring is key. Many Caribbean islands now have volunteer lionfish programs that attempt to persuade local fishermen to catch lionfish. However, monitoring is absent and therefore pre- and post-removal data does not exist.

Lionfish threaten native species throughout the Western Atlantic. In order to accurately determine what controls to use and the extent at which they must be placed, international collaboration is needed. The creation of a lionfish market may also be key to their control in the Atlantic. Consumption of lionfish is becoming more popular throughout the Caribbean, especially in Florida and the Bahamas (FWC). Lionfish outreach programs such as Friends of the Environment in Abaco, Bahamas, have produced educational TV shows on the proper capture, cleaning and cooking methods for Lionfish (Friends of the Environment). Recreational capture of lionfish may greatly support control efforts (Morris and Whitfield 2009), but further research may reveal more efficient and/or cost-effective control methods that may be worth considering.

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