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The ecological and socio-economic impacts of the lionfish invasion in the Southern Caribbean

by

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ABSTRACT

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

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THE ECOLOGICAL AND SOCIO-ECONOMIC IMPACTS OF THE LIONFISH INVASION IN THE SOUTHERN CARIBBEAN

Fadilah Zafirah Ali

The Indo-Pacific lionfish (*Pterois volitans*) is a venomous, voracious predator with a high dispersal capactity. In the space of 30 years, it has infiltrated an array of habitats, inhabited a depth range of > 300 m and exceeded the size and density reported in the native range, demonstrating the difficulty of effective lionfish management. If left unmanaged, lionfish pose a significant, but still uncertain, threat to Caribbean ecosystems thereby warranting the need for effective and efficient, tailored management schemes. Since their confirmation in Bonaire and Curacao in October 2009, an extensive monitoring program was established by the author in collaboration with CIEE Research Station Bonaire whereby >11,000 lionfish were documented and their population dynamics, reproductive and feeding ecology analysed in relation to local management strategies. The types of education and management strategies applied were evaluated based on their benefits and limitations to make recommendations for areas early in the invasion timeline. Finally efficiency of removal activities in Bonaire and Curacao were assessed and suggestions made on when and how often to remove lionfish. Socio-economic questionnaires were conducted to determine the profile and motivations of lionfish hunters, and a cost-benefit-analysis performed to assess economic effects of the invasion. Knowledge gained from this research is beneficial for tailoring future management through recommendations of which lionfish to remove, how often and which tools, methods and groups are most effective. This work revealed that dusk was the most effective time for lionfish removal and that by focusing removal efforts in the 15 – 25m depth range, this allowed for the depletion of a higher proportion of individuals in the 101 -200mm size class. This research also revealed how valuable a prepared and rapid response to management was and how important a dedicated volunteer removal effort is to controlling the lionfish populations in the future.

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DECLARATION OF AUTHORSHIP

I, **FADILAH ALI** declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

The ecological and socio-economic impacts of the lionfish invasion

I confirm that.

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. None of this work has been published before submission

Signed. Fadilah Ali

Date. 26th September 2017

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Definitions and Abbreviations

ABC Islands	Aruba, Bonaire, Curaçao Islands
BNMP	Bonaire National Marine Park
CIEE	Council on International Education Exchange
ELF Tool	Eradicating Lionfish Tool
INNS	Invasive Non Native Species
REEF	Reef Environmental Education Foundation
SCUBA	Self Contained Underwater Breathing Apparatus
STINAPA	Stichting Nationale Parken

Chapter 1: INTRODUCTION

Second only to habitat loss and fragmentation, invasive species are considered to be the most important cause of global biodiversity loss (Vitousek et al. 1996; Parker et al. 1999; Mack et al. 2000; Stachowicz et al. 2002; Park 2004; Altman and Whitlach 2007) except on islands where they are considered to be the greatest threat (Clout and Veitch 2002; Clavero and Garcia-Berthou 2005). The term 'invasive' is often used interchangeably with alien, exotic, or non-native/non- indigenous-species, however, non-native species are only considered invasive when they cause some form of ecological or economic harm (Table 1.1) (Lovell and Stone 2005; Didham et al. 2007; Havel et al. 2015). Based on these definitions, lionfish (*Pterois volitans* and *P. miles*) are classed as invasive species. Not all non-native species actually become 'invasive' as some are unable to prosper in the new environment and die off naturally (Parker et al. 2003). Others may survive, but have minimal impact without destroying or replacing any native species and are referred to as being naturalised (Lovell and Stone 2005). Not all introduced species actually demonstrate invasiveness, but certain attributes enhance invasiveness (Table 1.2). The predisposition for invasiveness may be due to genetic factors, ecological factors (i.e. the presence/absence of competitors) or a combination of both (Sakai et al. 2001).

Table 1.1. Definitions of non-native, naturalised and invasive species

Term	Definition
Non-native	A species that does not naturally occur within an area, i.e. it has not previously occurred within the area or its introduction has resulted from human influence (Lodge et al. 2006; Holmberg et al. 2015; Kernan 2015)
Naturalised	A species that becomes established, after being introduced, in a self-maintaining population (Manchester and Bullock 2000). However, these species do not have any major or measurable impact on the native community (Kernan 2015)
Invasive	A non-native species which once established can spread and cause ecological or economic harm and may sometimes threaten human health (Born et al. 2004; Lovell and Stone 2005; Didham et al. 2007; Havel et al. 2015; Kernan 2015)

Table 1.2. General attributes of invasive species

Attribute	General Description
Abundant and wide distribution	Generally, common and widely distributed within its native range. Introduced species which rapidly achieve high densities may have greater establishment success and dominate invaded communities and thereby exclude the native species (Ricciardi and Rasmussen 1998; Didham et al. 2007).
Generalist and able to withstand wide environmental tolerance	Possesses the ability to feed on a wide range of food and withstand a broad range of physical conditions including temperature and salinity. Some often possess a quiescent stage which is well adapted to dispersal and/or surviving extreme conditions (Ricciardi and Rasmussen 1998). This phenotypic plasticity allows colonists to cope with a range of environmental conditions, and are subsequently able to colonise new areas (Sakai et al. 2001; Parker et al. 2003).
Competitive ability	Generally able to outcompete and/or overwhelm native taxa by developing dense populations which is achieved by invasive species having a higher reproductive output and growth rate and/or an immunity to parasites, predators and disease (Ricciardi and Rasmussen 1998; Sakai et al. 2001). Invasive species generally compete with native species for food, space, light, water, resting and nesting areas (Emerton and Howard 2008).
High genetic variability	High genetic variation allows individuals the ability to evade any potential genetic problems associated with possessing a small population size (Sakai et al. 2001). If multiple introduction events have occurred from separate regions of the native range, these multiple foci will have a subsequent influence on the structure of genetic variation in the newly invaded range (Parker et al. 2003).
Short generation time and rapid growth	Possesses the ability to direct more resources to growth & reproduction and thereby reduce and/or eliminate native species through predation & competition (Bax et al. 2001).
Early sexual maturity and high reproduction	Generally achieved either by producing many offspring (or propagules) or by nurturing fewer progeny but with a higher efficiency (Ricciardi and Rasmussen 1998).
Rapid dispersal and pioneering ability	Introduced species that are the first to colonise and utilise a disturbed or vacant habitat and which spread widely are more likely to affect multiple native species over large areas of their native range and drive some of them to extinction. However, the relationship between invasiveness and impact has never been quantified (Didham et al. 2007).
Commensal with human activity	Introduced species whose dispersal patterns are enhanced by human activities (e.g. ship ballast water transport or fouling on boats) tend to be more successful (Emerton and Howard 2008).

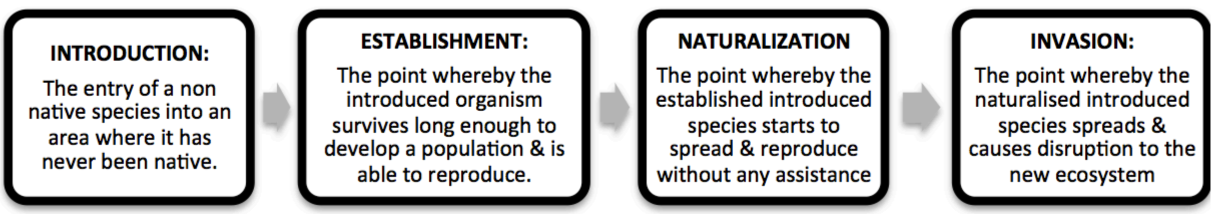


Figure 1.1. Stages in the invasion process (Modified from Emerton and Howard 2008)

The physical nature of the environment, trophic resources, resident species diversity, the range and intensity of biological physical disturbance, the minimum habit size along with other factors help to mediate most invasion events (Carlton 1996b). The 'tens rule' for invasive species (Williamson 1999) states that on average, 10% of the species succeed in each of the 3 transitions (i.e. from imported to introduced; from introduced to established; and from established to species with negative socioeconomic effects) (Figure 1.1) (Garcia-Berthou et al. 2005). Hence, the chance of an introduced species actually becoming invasive is about 0.1% (Emerton and Howard 2008). Invasion success is affected by characteristics of the invader (intrinsic growth rates, trophic status, reproductive life history) and attributes of the recipient community (degraded habitat, productivity and species interactions) (Semmens et al. 2004; Holmberg et al. 2015).

1.1 The threat of invasive species

There remains is still general uncertainty regarding the nature of their impacts on native species and ecosystems, and also how these impacts may be lessened or reversed via human intervention (Park 2004). Additionally, many threats can act synergistically to cause declines and extinctions. Thus, even if invasives are associated with other problems, and not the primary cause of extinction or a major contribution to the decline of species, they still have the potential to cause great harm (Gurevtich and Padilla 2004). Furthermore, some invasive species work synergistically, so that the environmental modifications caused by one species would provide further opportunities for other future non-native species to invade, referred to as an 'invasional meltdown' (Park 2004; Bax and Thresher 2009). Marine invaders, like other invasive species undoubtedly affect receiving communities (Grosholz and Ruiz 2009), but their consequent impacts are not uniform and are instead context dependent and influenced most strongly by invader attributes and the structure and diversity of the invaded habitat (Strayer et al. 2006; Ricciardi et al. 2013; Thomsen et al. 2011). Introduced species have the ability to cause great ecological harm including local suppression of a single native species; reduction of genetic diversity and biotic homogenization; change in community structure and ecosystem function through the extinction of native species; and altering of primary production levels (Grosholz et al. 2000; Ricciardi et al. 2000; Stachowicz et al. 2002; Chornesky and Randall 2003; Garcia-Berthou et al. 2005; Sloan and Turingan 2014). The effects can be both pervasive and varied, as factors such as the genetics, population size, diversity, community structure and biogeochemical cycles are affected (Strayer et al. 2006). Economic losses occur due to costs of border inspections to prevent invasion; eradication programmes, ongoing control, habitat restoration and a reduction in productivity (Hoddle 2002). Mack et al. (2000) suggest that biotic invasions generally cause three main categories of economic impact.

1. Loss in potential economic output
2. The direct cost of combating invasives. includes all forms of quarantine, control and eradication
3. Costs of combating invasive species which are threats to human health. either as direct agents of disease, vectors or carriers of the disease or parasites (Mack et al. 2000).

The consequent social impacts of invasive species include a decrease in employment in affected economic activities (fisheries, aquaculture, tourism) and also a decrease in people's welfare due to the reduced quality of their environment and natural surroundings (Bax et al. 2003; Bax and Thresher 2009).

By suppressing native species populations and further altering habitats and ecosystems, invasive species have contributed to the imperilment of nearly half of the plants and animals now considered rare, threatened or extinct (Chornesky and Randall 2003; Armon 2015; Montgomery et al. 2015). The environmental damage and the associated economic losses caused by invasive species can amount to hundreds of billion of dollars per year (Hoddle 2002; Strayer et al. 2006) and this damage manifests itself via a reduction in biodiversity, modification of trophic structures, and the overall deterioration of healthy ecosystems (Hoddle 2002). However, only a few introduced species establish themselves, with an even smaller percentage becoming widespread, high-density pests that are responsible for a vast array of negative impacts (Kolar and Lodge 2001; Parker et al. 2003; Finnoff et al. 2006; Marsico et al. 2009). Although marine invasions have been increasing in incidence (Ruiz et al. 1997; Kindinger 2014), most marine invaders tend to be invertebrates; making marine fish invasions rare (Cohen and Carlton 1998; Whitfield et al. 2002; Byrnes et al. 2007), but still possessing great potential to cause grave ecological impacts (Hellman 2007; Albins and Hixon 2008; Raymond et al. 2014).

Invasive species also have the potential to work in combination with other processes such as climate change which can often intensify their impacts (Mainka and Howard 2010). Climate change has the ability to affect core biological processes and thus can affect the future spread, demography, life histories, density and intensity of impact of invasive species (Gritti et al., 2006; Hellman et al., 2008; Mainka and Howard 2010). Aquatic ecosystems will be especially affected since climate change can increase water temperatures, affect flow patterns but also increase the frequency of storms (Poff et al. 2002; Rahel and Olden 2008). Climate change can also affect species distributions where the impacts of some species can decline and therefore no longer be classed as an invasive species. In other cases, some non-native species can become invasive, whilst other native species can shift geographically to areas which they do not usually occur and therefore become non-native and have the potential to become invasive (Hellman et al., 2008). However, the traits that enhances a species' ability to become invasive often enhances their potential to outcompete native species under climate change (Mainka and Howard 2008).

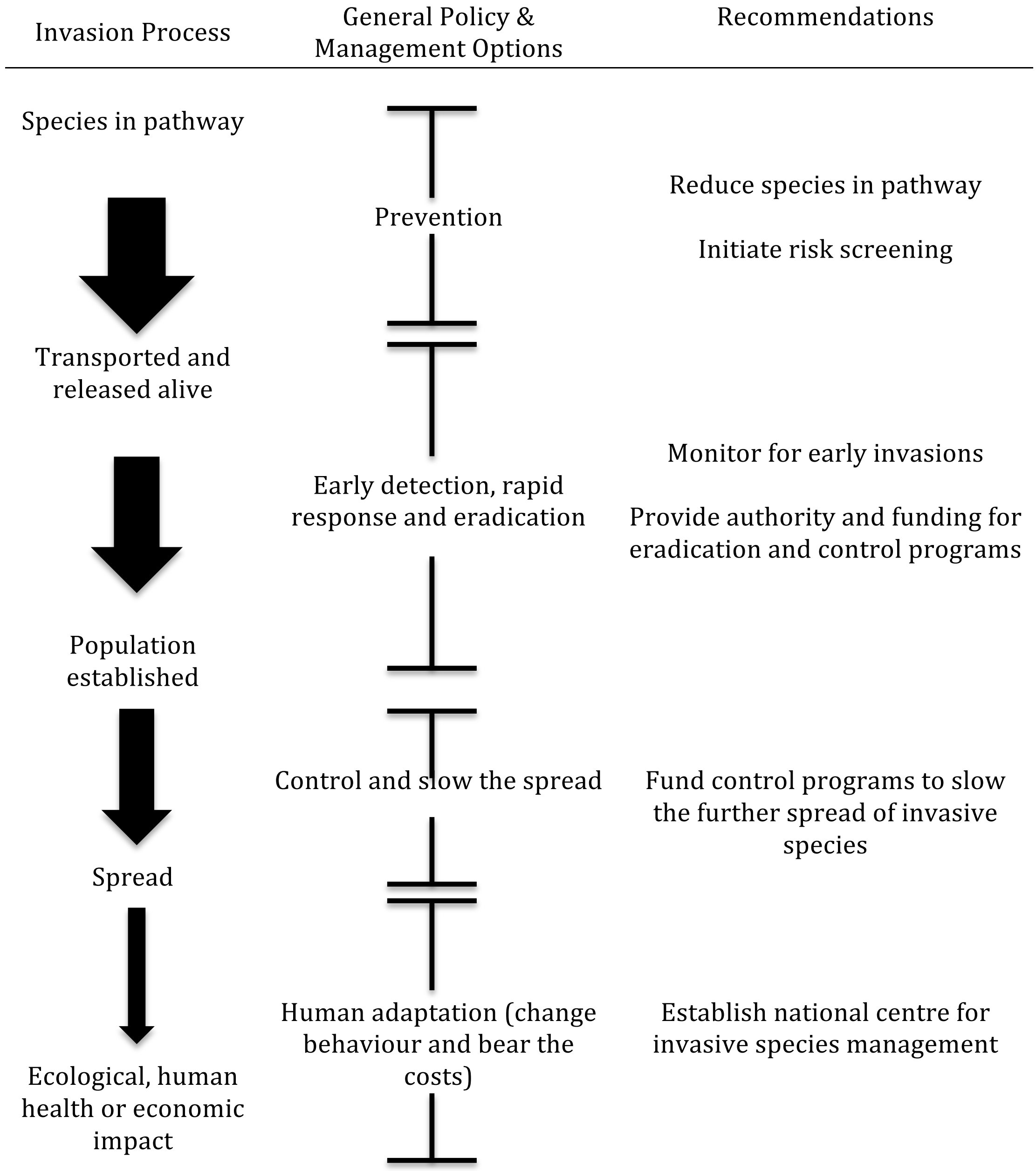


Figure 1.2. Management options and specific recommendations for various stages of the invasion process (Modified from Lodge et al. 2006)

1.2 Managing invasive species

Unlike terrestrial invasions, the available experience and techniques to handle marine invasions are often limited (Bax et al 2001; Secord 2003; de Leon et al. 2013) thereby explaining why only a few marine invasives have been completely eradicated from their non-native range (Culver and Kuris 2000; Genovesi 2005; de Leon et al. 2013). Generally, with marine invasive species there is little time to respond, and this is especially exacerbated due to the open nature of most marine environments (Bax et al. 2001; Simberloff et al. 2000; Thresher and Kuris 2004; Johnston and Purkis 2011; de Leon et al. 2013). Hence, interception and removal of pathways are the only effective strategies for reducing future impacts (Molnar et al. 2008). As the invader spreads, the options available to eradicate the invasive species, drastically decreases over time (Bax et al. 2001; 2003) and the longer the delay, the greater the area needed to be treated (Simberloff et al. 2000) (Figure 1.2).

Based on a precautionary perspective, it has been argued that all introductions should be treated as being potentially harmful to identify and target high-risk vectors (Floerl et al. 2005). However, although only a few introduced species actually establish self-sustaining reproductive populations (Randall 1987; Semmens et al. 2004), very few of these have actually been studied, and most of this research on the impacts on native species and ecosystems tends to occur decades after the original introduction (Bariche et al. 2004; Albins 2015). However, the lionfish invasion in the Caribbean is an exception and is quickly becoming one of the most highly studied invasive species (Côté et al. 2013). Possessing most of the attributes listed in Table 1.2, lionfish were listed as one of the top 15 global conservation issues of all time (Sutherland et al 2010; Loerch et al. 2015). Furthermore, their introduction and vast expansion has been deemed as one of the worst marine invasions in the Caribbean of all time (Sutherland et al. 2010; Hoo-Fung et al. 2013; Anton et al. 2014; Cure et al. 2014; Pusack 2014; Johnston and Purkis 2014; Layman et al. 2014; Raymond et al. 2014; Sloan and Turingan 2014).

1.3 Introduction to the lionfish species complex (*Pterois volitans* and *P. miles*)

Native to the Indo-Pacific region, two species of lionfish have been confirmed within the introduced region (Kojis 2009; Morris et al. 2010). *Pterois volitans*, commonly referred to as the red lionfish and *P. miles,* also known as the devil firefish are both members of the Scorpaenidae family (MacIsaac et al. 2016). Though they are primarily an aquarium fish in most parts of the world, they have been used as a food fish in some areas of their native range (Ruiz-Carus et al. 2006). *Pterois* has a native range extending from Southern Japan, south to Lord Howe Island, throughout Indonesia, Micronesia and French Polynesia (Whitfield et al. 2002; Ruiz-Carus et al. 2006; Gonzales et al. 2009) (Figure 1.3). Although *P. volitans* and *P. miles* are genetically distinct (Kochzius et al. 2003; Côté et al. 2013), they are extremely hard to distinguish visually (Freshwater et al. 2009; Côté et al. 2013) since *P. volitans* has one more

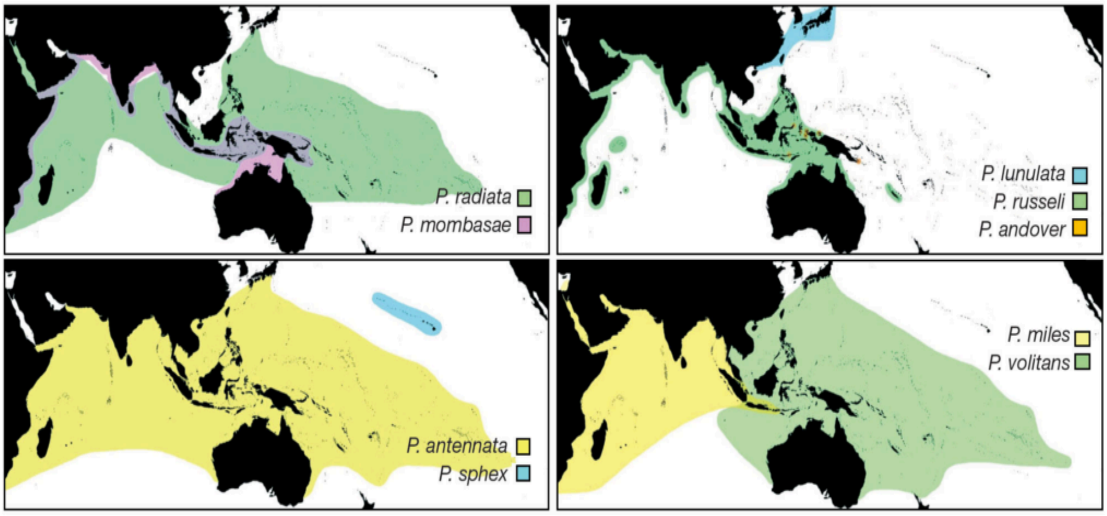


Figure 1.3. Geographical distribution of *Pterois spp.* in their extensive native range

Source. Kulbicki et al. (2012)

dorsal fin ray as well as an additional anal fin ray (Schultz 1986; Kletou et al. 2016). Throughout this thesis, the species complex *P. volitans / P. miles* will be collectively referred to as lionfish.

1.4 Morphology of lionfish

Lionfish possess distinctive brown, red, maroon and white stripes or bands which cover their head and body, large ornamental fan-like pectoral fins and 12-13 dorsal spines, 9-12 dorsal rays, 3 anal spines, 5-8 anal rays, 12-18 pectoral rays, one pelvic spine, 5 pelvic rays and 24 vertebrae (Allen and Eschmeyer 1973; Morris et al. 2009). Although *P. volitans* and *P. miles* are almost identical, they can be differentiated from other related members of the *Pterois* genus due to the horn like projections on their heads. These tentacles are proposed to mimic algae or small fish to lure prey closer or even as an apparatus for sexual signalling (Syngajewski et al. 2004). The upper and lower jaws of lionfish are lined with 2 rows of tiny teeth, with a secondary cluster located on the upper roof of the mouth. The function of these features is believed to be for grasping prey for consumption (Syngajewski et al. 2004). Fishelson (1997) suggested they have a potential lifespan of approximately 4-10 years, with adults reaching a reported maximum size of 45cm and 1.0 to 1.2kg in body weight. However, to date lionfish larger than 45 cm are increasingly being reported with the largest recorded specimen measuring 48 cm in total length (WLHA 2014). Lionfish are proposed to have a growth rate ranging from 0.4 – 1.1mm/day (Benkwitt 2013; Albins 2015; Pusack et al. 2016) and it was suggested that their growth rate declined with increasing size (Akins et al. 2014).

1.5 Venom

Like other scorpaenids, lionfish are venomous and possess a highly developed venom apparatus located within their dorsal, ventral and anal spines (Figure 1.4) (Prithiviraj et al. 2014). The venom glands are covered in skin and are partly enclosed by anterior-lateral grooves of each spine and extend three quarters of the distance from the base of the spine towards the tip (Morris 2009; Prithiviraj et al. 2014). Thus once an envenomation occurs, the skin is compressed, thereby squeezing the venom gland, leading to the injection of venom (Prithiviraj et al. 2014). The toxin in lionfish venom contains acetylcholine which affects neuromuscular transmission and has been known to cause cardiovascular, neuromuscular and cytolytic effects in animals, including humans (Morris 2009). Lionfish use these venomous spines to deter predators but the potency remains unknown as no fatalities have been observed or documented.

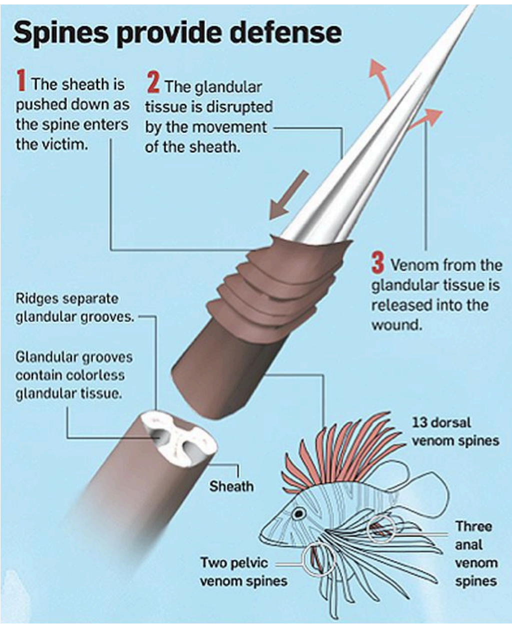


Figure 1.4. Location of venomous spines on lionfish

Source. Morris (2012)

Figure 1.5. Lionfish distribution within the introduced range.

Source. United States Geological Survey (2016)

The greatest misconception which has fuelled fear amongst the public is that the lionfish is poisonous and requires special care and preparation before consumption, or else it can be fatal like the Japanese fugu *(Fugu rubripes)* (Mosher et al. 1964; Nagashima and Arakawa 2014). Considering that their venom is protein based, simply applying heat via cooking denatures the protein and renders the venom harmless (Morris and Whitfield 2009), which accounts for why the application of heat to any lionfish envenomation is the recommended treatment (Vetrano et al. 2002; Badillo et al. 2012; Darlene and Phee-Kheng 2013).

Furthermore, the venom apparatus is located solely within spines and in no part of the body or even at the base of the spine, thus, once the spines are removed, even by bluntly removing the tips, lionfish are safe to handle (Hare and Whitfield 2003; Morris and Whitfield 2009).

1.6 Introduced range and likely range expansion

Lionfish are now established throughout the Caribbean region, the Gulf of Mexico and the coasts of North, South and Central America (Figure 1.5) (Schofield 2009; Morris et al. 2010; Barbour et al. 2011; Côté et al. 2013; Elise et al. 2014) indicating their high dispersal capability. In the 8 years since their arrival in the Bahamas in 2004, an area as large as 7.3 million km^2 in the Atlantic, Caribbean Sea and Gulf of Mexico was invaded by lionfish (Côté et al. 2013; Dahl et al. 2016). Forecasts predict that the lionfish invasion will continue extending in South America towards Brazil (Morris and Whitfield 2012) (Figure 1.6). As the first marine fish invader from the Western Pacific to the Atlantic, lionfish are believed to have been released via unintentional and/or intentional releases from aquaria (Whitfield et al. 2002; Morris et al. 2010; Cure et al. 2012; Johnston and Purkis 2014; Tremain and O'Donnell 2014). Deliberate releases are common, especially when hobbyists cannot relinquish unwanted fish, live release is a more humane alternative to euthanasia (Holmberg et al. 2015). Lionfish are one of the 10 most valuable marine fish imported to the US and also collectively contributes 28% of the total value of imported marine fish which amounts to about USD$3.05 million per month (Ruiz-Carus et al. 2006).

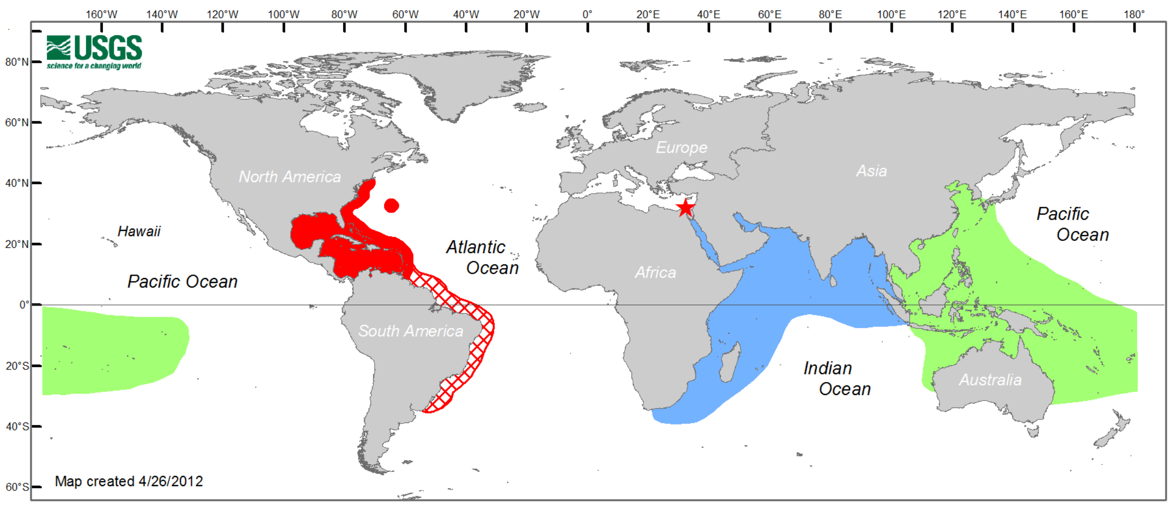


Figure 1.6. Distribution of *Pterois volitans* (green) and *P. miles* (blue) within their native range as adapted from Schultz (1986) and Randall (2005). The red star in the Mediterranean sea denotes migration of *P. miles* via the Suez Canal (Golani and Sonin 1992). The introduced range of *P. volitans* and *P. miles* is indicated in red (adapted from Schofield et al. 2012) whilst the predicted future distribution of lionfish along the coast of South America is indicated in red hatching (adapted from Morris and Whitfield 2009). Source. United States Geological Survey (2012)

1.7 Lionfish density

Lionfish densities recorded within the introduced range (Table 1.4) far exceed those reported within the native range (Pusack et al. 2016). It has been proposed that their density is restricted by food availability (Benkwitt 2013) and lionfish in their invaded range have achieved sizes on average 1.5 times longer and 3 times heavier than their native range (Darling et al. 2011; Andradi-Brown et al. 2017). *Pterois* densities ranged between 0.9 – 21.9 ind/ha within the Pacific Ocean (Chou et al. 1992; Suharsono et al. 1996; Chen et al. 2004; Nakamura and Sano 2004; Oxley et al. 2004; Lecchini et al. 2006; Valentine et al. 2008; Grubich et al. 2009; Cure et al. 2014), 1.9 – 28.5 ind/ha within the Indian Ocean (Letourner 1996, 1998; Adjeroud et al. 1998; Letourner et al. 2008; Darling et al. 2011) and 1.7 – 87.3 ind/ha within the Red Sea (Alter et al. 2008; Alter and von Mach 2010; Kulbicki et al. 2012) (Table 1.3). However, within the invaded region, densities vary greatly (Table 3.1) and have been reported as high as 1320 ind/ha within Guadeloupe (Trégarot et al. 2015) and 1470 ind/ha within the Gulf of Mexico (Dahl and Patterson 2014) and as low as 0.6 ind/ha within the Turks and Caicos Islands (Claydon et al. 2012). These densities likely differ due to variations in removal efforts, time since establishment as well as local abiotic conditions such as depth and currents or surge (Benkwitt 2016).

1.8 Genetic and phylogenetic diversity

Molecular analyses by Hamner et al. (2007) have suggested that *P. volitans* is more than an order of magnitude more common than *P. miles* within the introduced range. Through extensive analysis of mitochondrial cytochrome b within the western Atlantic, it was revealed that both *P. volitans* and *P. miles* were involved, however 7% of the specimens were identified as *P. miles* as compared to the 93% identified as *P. volitans* (Hamner et al. 2007). The population is proposed to be a result of a strong founder effect (Betancur-R et al. 2011; Kletou et al. 2016). Through sensitive d-loop diversity analysis which involved a more variable mitochondrial DNA marker, this was used to enhance the detection of any differences amongst populations (Freshwater et al. 2009). The genetic diversity of lionfish within the introduced range is much lower than that in their native range (Hamner et al. 2007) which might suggest that this lionfish invasion is a consequence of either the single release theory (i.e. populations began from a small group) or the multiple release theory (i.e. several releases of individuals with the same genetic haplotype) (Hamner et al. 2007). Multiple introductions supply much needed genetic variation to established populations of invasive species which help to support their viability or allow them to adapt to a new environment (Roman and Darling 2007). Nonetheless, even with diminished genetic diversity and minute founding populations, the invasion of lionfish within the western Atlantic reveals how swift and irreparable invasions can be (Hamner et al. 2007). This also highlights the need for management strategies to regulate the supply of propagules not only before but also after establishment (Roman and Darling 2007).

Table 1.3. Reported lionfish densities within their native range in the Pacific Ocean, Indian Ocean and Red Sea where ± represents the standard error of the mean

Location	Species	Density (ind/ha)	Reference	Location	Species	Density (ind/ha)	Reference
Pacific Ocean				**Red Sea**			
Moorea	*P. radiata*	0.9	Lecchini et al. (2006)	Dahab	*P. miles*	87.3 ± 117.5	
SE Australia	*P. volitans*	2.4	Oxley et al. (2004)	Sharm El Sheik	*P. miles*	7.5 ± 16.1	
Lord Howe	*P. volitans*	2.7	Valentine et al. (2008)	Hurghada	*P. miles*	15.4 ± 34.8	
Brunei	*Pterois spp.*	1.1	Chou et al. (1992)	Marsa Shagra	*P. miles*	13.3 ± 46.2	
Taiwan	*P. volitans*	2.2	Chen et al. (2004)	Marsa Nakari	*P. miles*	18.9 ± 46.9	Kulbicki et al. (2012)
Indonesia	*P. volitans*	2.4	Suharsono et al. (1996)	Jeddah	*P. miles*	1.7 ± 8.2	
Ryuku	*P. antennata*	8.9	Nakamura and Sano (2004)	Dahab	*P. radiata*	36.4 ± 47.7	
Guam	*P. volitans*	3.5	Cure et al. (2014)	Sharm El Sheik	*P. radiata*	25 ± 28.8	
Phillipines	*P. volitans*	21.9		Hurghada	*P. radiata*	15.4 ± 35.1	
Palau	*P. radiata*	13.1	Grubich et al. (2009)	Marsa Shagra	*P. radiata*	10 ± 18.1	
Indian Ocean				Marsa Nakari	*P. radiata*	21.1 40.8	
Kenya	*D. brachypterus*	12.6 ± 30.6	Darling et al. (2011)	Jeddah	*P. radiata*	11.7 ± 22.0	
Kenya	*D. zebra*	1.9 ± 5		Safaga	*P. miles*	20.8	Alter et al. (2008)
Kenya	*P. antennata*	28.5 ± 29.3		Safaga	*P. radiata*	12.5	
Kenya	*P. miles*	25.1 ± 45.7		Safaga	*P. miles*	8.25	Alter and von Mach (2010)
Kenya	*P. radiata*	8.6 ± 22.7		Safaga	*P. radiata*	20.75	
Mayotte	*P. antennata*	2.8	Letourner (1996)				
Reunion	*P. antennata*	3.6					
Reunion	*P. antennata*	16.7	Letourner (1998)				
Reunion	*P. miles*	6.2	Letourner et al. (2008)				
Mauritius	*P. miles*	3	Adjeroud et al. (1998)				

Table 1.4. Reported lionfish densities at various depths and habitats within the invaded region, where the sites in bold font represent the study area of this research and where ± represents the standard error of the mean

Location	Year lionfish found	Year of Study	Depth (m)	Habitat	Density (LF/ha)	Reference
North Carolina, USA	2000	2004	30 - 45	Rock/reef/wreck	21.2 ± 5.1	Whitfield et al. (2007)
North Carolina, USA	2000	2008	N/A	Reef	150	Morris and Whitfield (2007)
North Carolina, USA	2000	2006 - 2010	38 - 46	Hard bottom reef/wreck	176.4 ± 24	Whitfield et al. (2014)
North Carolina, USA	2000	2006 - 2010	15 - 37	Hard bottom reef/wreck	84.6 ± 15	
New Providence, Bahamas	2004	2008	12 - 20	Reef	393 ± 144.4	Green and Côté (2008)
New Providence, Bahamas	2004	2008	5 - 20	Reef	101.7 ± 103	Darling et al. (2011)
Exuma Cays, Bahamas	2005	2010	7 - 15	Reef	3	Mumby et al. (2011)
Lee Stocking Island, Bahamas	2005	2009	30 - 91	Reef	0.053 ± 0.83	Lesser and Slattery (2011)
San Salvador, Bahamas	2005	2009	13 - 17	Reef	13 ± 18	Anton et al. (2014)
Eleuthera, Bahamas	2005	2011 - 2012	3 - 15	Patch Reef	520	Hackerott et al. (2013)
Cape Eleuthera, Bahamas	2005	2011 - 2012	10 - 20	Patch Reef	300 ± 600	Green et al. (2012)
Turks and Caicos Islands	2007	2010	12 - 24	Deep Reef	9.5 ± 5.37	
Turks and Caicos Islands	2007	2010	1 - 5	Seagrass	0.87 ± 0.41	Claydon et al. (2012)
Turks and Caicos Islands	2007	2010	1 - 5	Sheltered Reef	0.52 ± 0.47	
Turks and Caicos Islands	2007	2010	1 - 5	Exposed Reef	0.12 ± 0.13	
Turks and Caicos Islands	2007	2010	1 - 5	Mangrove	0.06 ± 0.1	
Jardines de Reina Reserve, Cuba	2007	2011 - 2012	3 - 15	Reef	150	Hackerott et al. (2013)
Manzanillo, Costa Rica	2008	2011	0 - 7	Reef	162 ± 218	
Puerto Viejo, Costa Rica	2008	2011	0 - 7	Reef	81 ± 80	
Puerto Vargas, Costa Rica	2008	2011	0 - 7	Reef	70 ± 93	Sandel et al. (2014)
Perezoso, Costa Rica	2008	2011	0 - 7	Reef	62 ± 99	
South Coast, Costa Rica	2008	2011	0 - 7	Reef	92 ± 130	
Little Cayman	2008	2011	10 - 27	Reef wall	233 - 650	Frazer et al. (2012)
Little Cayman	2008	2013	18 - 20	Edge of drop off	162.5	
Little Cayman	2008	2013	18 - 19	Reef Inner edge	21.5	Bejarano et al. (2015)
Little Cayman	2008	2013	17 - 18	Reef Mid section	34	
Belize/Mexico Mesoamerica	2008	2012	3 - 15	Reef	160	Hackerott et al. (2013)
Bonaire (Unfished)	2009	2011	15 - 35	Reef	66	
Bonaire (Fished)	2009	2011	15 - 35	Reef	30	de Leon et al. (2013)
Curaçao	2009	2011	15 - 35	Reef	127	
Venezuela	2009	2011	5 - 20	Rock/Coral Reef	25.83± 66.57	Agudo and Salas (2014)
Venezuela	2009	2011	6 - 12	Rock/Coral Reef	30 ± 83.5	Elise et al. (2014)
Venezuela	2009	2013	6 - 12	Rock/Coral Reef	121 ± 164	
Cozumel, Mexico	2009	2010	N/A	Reef	255	Sosa Cordero et al. (2013)
Gulf of Mexico	2010	2013	17 - 73	Natural Reef	49	Dahl and Patterson (2014)
Gulf of Mexico	2010	2013	17 - 73	Artificial Reef	1470	
Saint Pierre Bay, Martinique	2011	2013	13 - 20	Rock/Coral Reef	1320	Tregarot et al. (2015)
Martinique	2011	2013	13 - 20	Reef	480	

1.9 How were they introduced?

A range of pathways have been suggested for biological invasions of marine fish, including natural range extensions, deliberate introductions, unassisted migration across oceans or movement via canals, transport in ballast water and both intentional and unintentional aquarium or aquaculture releases (Whitfield et al. 2002; Hare and Whitfield 2002; Ruiz-Carus et al. 2006; Simmons 2014). Lionfish were first reported in the 1980s along South Florida and have since spread along the South-East United States coast and throughout the Caribbean region (Morris 2009; Johnston and Purkis 2014). Reproduction is likely to be supplying juveniles to the South-East and North-East US continental shelves and Bermuda (Whitfield et al. 2002). Further distribution of lionfish is likely to be restricted by thermal tolerance (Morris 2009) with populations being able to survive off Bermuda, but unlikely to persist north of Cape Hatteras due to cold winter temperatures (Whitfield et al. 2002).

As there is a great distance between the native and invaded range of *P. volitans* (Figures 1.3 and 1.4), natural dispersal and/or movement via canals is unlikely. Additionally, it is improbable that lionfish were released for fishery purposes. Therefore, ballast water or aquarium releases are the two most plausible methods of introduction (Whitfield et al. 2002). Transport via ballast water has led to the successful introduction of 35 fish species globally, of which the most successful species are Gobiidae and Blenniidae (Whitfield et al. 2002). It has been proposed that ballast water may have been responsible for the transfer of *P. miles* from the Suez Canal to the Mediterranean Sea (Johnston and Purkis 2016). Although lionfish have been reported from several harbour areas, there has been no documented evidence of successful introduction of scorpaenids via ballast water transport into the Atlantic/Caribbean region (Whitfield et al. 2002). However, because of the small size of larval lionfish and their 25-40 day larval duration, it is plausible and very possible that lionfish can be successfully transported via ballast water (MacIsaac et al. 2014). Although many harbours within the region may appear to be inhospitable to successful establishment of lionfish, areas such as the Galapagos Islands have been identified as being highly susceptible to the extension of the lionfish invasion (MacIsaac et al. 2014). Thus, although transfer via ballast water is an unlikely vector of introduction of lionfish to the invaded region, it still remains as a valid vector that needs to be investigated further.

Accidental/intentional release from aquaria remains the most likely mechanism of introduction (Semmens et al. 2004; Ruiz-Carus et al. 2006; Hixon et al., 2016), considering the popularity of lionfish as an aquarium fish (Thresher 1984; Hare et al. 2003). Furthermore, off the US coasts, the non-native fish species most commonly encountered by divers are those most regularly imported for the aquarium trade (Semmens et al. 2004; Côté et al. 2013). Reports have suggested that the pigment patterns of individuals caught off North Carolina and other parts of the United States are very similar to individuals from the Phillipines and Indonesia, where 85% of all marine aquarium fishes are imported from (Hare and Whitfield 2003). South Florida especially is renowned as a hotspot for marine introductions (Semmens et al. 2004) whereby more than 30 species of non-native fish have been recorded over the last 15 years (Morris and Whifield 2009; Schofield et al. 2010). Moreover, large numbers of lionfish are continually imported into Florida to supply the aquarium trade with more than 7,500 being imported to Tampa airport within a 6-month period in 2003 (Ruiz-Carus et al. 2006).

It was previously unknown whether lionfish invaded Bahamas by larval transport via ocean currents, or if their introduction was the result of additional aquarium releases (Hare and Whitfield 2003; Morris 2009) due to the lack of strong connectivity and lag between confirmed sightings of lionfish on the US East Coast (2000) and the Bahamas (2004) (Freshwater et al. 2009). However, genetic studies by Freshwater et al. (2009) confirmed that the invasion in Bahamas was a result of larval dispersal originating from US waters (Morris 2009; Morris and Akins 2009). Although there may be debate over introduction events, ocean currents have been confirmed as the transport mechanism for lionfish eggs and/or larvae (Hare and Whitfield 2003; Côté et al. 2013). Their dispersal seemingly occurs during the pelagic larval phase over great distances (Whitfield et al. 2007; Morris et al. 2009). With lionfish larval duration proposed to be between 25-40 days, and a typical larval scorpaenid growth rate of 0.33mm/day, the estimated larval duration is considerably within the transport time of other South-East US shelf species that have dispersed to the North-East US coast and Bermuda (Whitfield et al. 2002). Larvae are transported from the South-East US coast to the North-East US continental shelf via the Gulf Stream, warm core rings and also cross shelf movement. However, transport to Bermuda is quite similar, except that cold core rings rather than warm core rings are involved in this dispersal (Hare and Whitfield 2003). These rings are independent circulatory systems of water that can last for many months

1.10 How do they reproduce?

The lionfish courtship phase consists of a complex series of events involving circling, following and leading (Hare and Whitfield 2003; Ruiz-Carus et al. 2006; Morris 2009) and commences just before dark, and continues well into the night (Morris et al. 2011; Gardner et al. 2015). Males have an elaborate courting display where they use their spines in an agonistic display with other competing males (Ruiz-Carus et al. 2006). Following courtship, the female releases two buoyant egg masses which are fertilised by the male and then ascend to the surface (Fishelson 1975; Morris 2009). Lionfish are broadcast spawners like many other reef fish and have external fertilisation (Fishelson 1975; Côté and Green 2012).

Evidence from specimens captured in North Carolina and the Bahamas suggests that lionfish are reproducing multiple times per months (Johnston and Purkis 2014) and throughout all seasons of the year, without any apparent timing relative to moon/tidal regimes, thereby supplying a consistent and continuous supply of propagules (Department of Marine Resources 2008; Morris 2009). Characterised as oviparous, asynchronous, batch spawners (Morris 2009), lionfish are especially prolific breeders, with one female being able to eject up to 15,000 eggs during a single mating event (Bervoets 2009) and about 2 million annually (Morris et al. 2008; Morris 2009; Albins and Hixon 2011; Biggs and Olden 2011). The eggs are bound in an adhesive mucus which disintegrates a few days later which allows the embryo and/or larvae to become free-floating (Hare and Whitfield 2003; Morris et al. 2009).

The released free-floating egg masses subsequently develop into planktonic larvae (Ruiz-Carus et al. 2006), a feature which allows dispersal by ocean currents (Freshwater et al. 2009). Based on spawning information and the collection of larvae from the water column, lionfish possibly have a pelagic larval stage similar to that of other marine fish species (Hare and Whitfield 2003). Furthermore, assuming this planktonic larval duration of 25-40 days, the Caribbean and Yucatan currents are capable of dispersing larvae into the Gulf of Mexico from regions in the Caribbean where they are already resident (Morris 2009). Settling from the water column to the benthic habitat is proposed to occur at about 12mm (Hare and Whitfield 2003). The juveniles subsequently develop rapidly and begin to hunt actively at approximately 70mm length and have been observed to consume prey up to two-thirds their body length (Bervoets 2009). Lionfish attain sexual maturity at ~100 mm total length for males and ~180mm for females (Morris 2009).

1.11 Where do they live?

In their native range, lionfish occur over coral, sand and hard bottom substrates from the surface to 150m (Whitfield et al. 2002; Ruiz-Carus et al. 2006; Whitfield et al. 2007; Andradi-Brown et al. 2017). Within their invasive range, they have been confirmed in diverse habitats (Pusack 2013; Cure et al. 2014) such as hard bottom, shallow and mesophotic reefs (Whitfield et al. 2007; Albins and Hixon 2011; Biggs and Olden 2011; Lesser and Slattery 2011; Côté et al. 2013); mangroves (Barbour et al. 2010); seagrass (Claydon et al. 2012) and estuarine habitats (Jud et al. 2011, Jud and Layman 2012; 2014). During the day, they linger under ledges and crevices, but may hunt small fish, shrimps and crabs in the open water at night (Ruiz-Carus et al. 2006). Lionfish have the ability to adapt to many different habitats and have colonised areas ranging from 1 – 300m (Côté et al. 2013) on reef walls, patch reefs, rocky areas, hard bottoms, ledges and crevices, mangrove creeks, isolated coral heads, blue holes, ship wrecks, and man-made structures (Ruiz-Carus et al. 2006; Nuttall et al. 2014).

Lionfish tend to live in small groups as juveniles and during reproduction, but disperse and hide in reef shadows when they are adults (Fishelson 1997).

1.12 What is their salinity tolerance?

Although lionfish were previously renowned as being a typically salt-water species, recent studies have revealed they are capable of withstanding a great range of salinities (Jud et al. 2011; Jud and Layman 2012; 2014). Salinity stratification is believed to be responsible for such a feat since the formation of a salt wedge creates a stable high salinity refuge; thereby allowing lionfish to avoid lower salinity waters, even during high freshwater inflows (Jud et al. 2011). Despite not being renowned as a euryhaline species, Jud and Layman (2014) revealed that lionfish without any change to their behavioural, feeding or growth activities could withstand a salinity of 7 p.s.u. but have the potential to survive brief exposure to salinities as low as 1 p.s.u. Salinity tolerance will be essential in determining the future southward spread of the invasion to the Atlantic coast of South America and whether the Amazon-Orinoco plume serves as a sufficient obstacle (Jud and Layman 2014).

1.13 What is their thermal tolerance?

Thermal tolerance limits have been suggested as an important factor determining the distribution along the East coast of the United States (Kimball et al. 2004). This factor is likely to affect the survival, reproduction and dispersal of *P. volitans* especially since its temperature tolerance may be affected by faster decline rates experienced during fall and winter (Whitfield et al. 2002; Kimball et al. 2004). The predicted winter water temperature on the North-East coast of the United States is possibly too cold to allow overwintering (Whitfield et al. 2002), especially due to their sedentary nature. Hence juveniles are likely to perish when water temperatures decline to below their critical thermal minimum (Ruiz-Carus et al. 2006). Lionfish possess a mean lethal temperature minimum of 10.0^{0}C and a mean temperature at feeding cessation of 16.1^{0}C (Kimball et al. 2004; Ruiz-Carus et al. 2006; Freshwater et al. 2009). It has been suggested that juveniles should be able to survive the summer period in surrounding areas of New York and New Jersey, but there is need for migration further offshore or southwards to settle in areas above their lower tolerance limits during winter (Ruiz-Carus et al. 2006; Freshwater et al. 2009).

A phenomenon that makes it challenging to predict the future spread and impacts of invasive species is climate change (Côté and Green 2012). The pelagic larval duration and dispersal is likely to be affected by climate change as these processes are temperature dependent (Côté and Green 2012). Based on modelling, it is predicted that with increasing temperatures, larval duration will decrease but potential larval dispersal distance will also decrease (Côté and Green 2012). A shorter planktonic duration may increase larval retention rates whilst a reduced dispersal distance may affect connectivity between distinct sites, thereby affecting the success of management efforts in other sites (Côté and Green 2012). Nonetheless given the generalist and flexible nature of lionfish, how they will actually respond to a changing climate remains unknown. Additionally it remains unknown how climate change may affect the overall functioning of lionfish. Changes in temperature are likely to affect physiological and mechanical processes which can potentially influence how lionfish perform as well as their resilience and resistance to changes (Turingan and Sloan 2016).

1.14 How do they feed?

According to the theory of optimal foraging (Charnov 1976), the efficiency of food utilization and the ability to fast are important factors when understanding the expenditure and conservation of energy (Pyke et al. 1977; Fishelson 1997; Green and Côté 2014). Lionfish are nocturnal and usually most active during crepuscular periods (dawn and dusk), which coincides with the peak activity on reefs where diurnal crustaceans are retreating and smaller nocturnal fishes are becoming active (Syngajewski et al. 2004). They employ a diverse range of feeding strategies which makes them well suited for feeding on benthic and cryptic prey (Morris 2009). Prey species in the Atlantic region are naïve to the novel predation strategies of lionfish, resulting in lionfish having higher predation efficiencies in the invaded range compared to that of their native range (Albins and Hixon 2008). They are opportunistic predators consuming fish, shrimps and crabs (Whitfield et al. 2007) and possess a variety of feeding strategies (Table 1.5). As prey species found on Caribbean reefs are not adapted to the way they hunt and native predators cannot compete due to their own already established hunting strategies, lionfish have the potential to decimate populations of both prey and predator species (Bervoets 2009).

1.15 What do they eat?

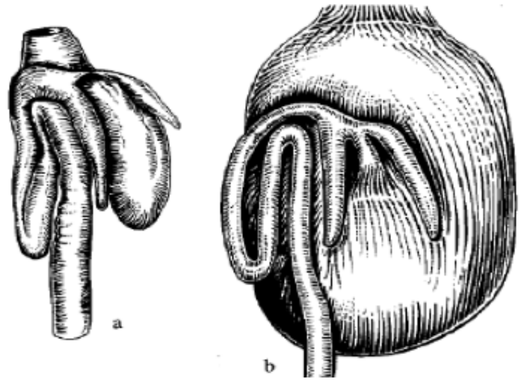


Figure 1.7. Lionfish stomach (a) empty; (b) containing prey (Fishelson 1997)

Lionfish are principally piscivorous, but are known to also feed on a number of invertebrates (Morris 2009) and in their native range, they tend to occupy the higher levels of the food chain (Hare and Whitfield 2003; Bervoets 2009). In the introduced range, lionfish have been reported to feed based on a size dependent relationship whereby larger individuals fed on teleosts, and smaller ones fed more heavily on crustaceans (Morris and Akins 2009). Morris (2009) has proposed they have the ability to consume 2.5 to 6.0% of their body weight per day at 25-26^{0}C. Additionally, their stomachs can expand to more than 30 times in volume (Freshwater et al. 2009), allowing for large meals to be consumed (Figure 1.6). This further supports Fishelson's (1997) hypothesis that lionfish were adept in undergoing periods of starvation of over 12 weeks without mortality due to their capability of long-term fasting (Morris 2009). Nonetheless, lionfish do not possess uniform diets throughout their introduced range. Based on the pioneer feeding ecology study in the Bahamian archipelago, lionfish were found to have a very generalist diet with 21 families of teleost, 4 families of crustacean and 1 family of molluscs being recorded within lionfish diets (Morris and Akins 2009). However in Bermuda, lionfish diets are dominated by crustaceans, particularly *Cinetorhynchus rigens* (red night shrimp) (Eddy et al. 2014).

Table 1.5. Lionfish feeding strategies

Feeding Strategy	Description	References
Suction feeding	A common teleostan feeding technique consisting of swift expansion of the buccal and opercular cavities. The lionfish's ability to stretch its mouth and expand its stomach up to 30 times its original size enhances this strategy	Freshwater et al. 2009; Morris 2009
Ambush predation	By remaining motionless and waiting for their prey to come within striking distance lionfish can successfully prey upon small fish and invertebrates	Whitfield et al. 2002
Use of pectoral fins	Using large, outstretched, ornate pectoral fins to corral and corner prey and also to flush benthic invertebrates from the substrate	Ruiz-Carus et al. 2006; Albins and Hixon 2008
Alteration of centre of gravity using bilateral swim bladder muscles	This allows for novel control of their pitch in the water column, and allows them to orient and hover upside down under ledges or on lateral faces of structures	Morris 2009
Jet assisted predatory behaviour	Using water jets enhance the predation efficiency of lionfish since it can potentially disorient prey, leaving them vulnerable to predation. Jets also increase the incidence of head first capture	Nilsson and Bronmark 1999; Albins and Lyons 2012

1.16 What limits lionfish populations?

It is often suggested that lionfish, like other invasive species have successfully established and thrived within their introduced range since they have left behind their co-evolved natural enemies like parasites, predators or other forms of biotic control within their native range, a feat termed the enemy release hypothesis (also referred to as the ecological release hypothesis) (Shea and Chesson 2002; Colautti et al., 2004; Liu and Stiling 2006; Pusack et al., 2016). Furthermore, the biotic resistance hypothesis can be a potential reason for the establishment and subsequent spread of non-native species (Tuttle et al., 2016). According to this hypothesis, native areas with high levels of biodiversity and natural enemies tend to minimise the likelihood of a successful invasion (Stachowicz et al. 1999). When native communities do not successfully limit the establishment of non-native species, biotic resistance is low (Shea and Chesson 2002; Tuttle et al., 2016).

The apparent scarcity of predators both in the native and introduced range may be due to their defensive dorsal, anal and pelvic spines which have the ability to deliver venom that is potentially fatal to fishes (Albins and Hixon 2008; Tuttle et al., 2016). Within their native range, there have been reports of the Pacific cornetfish eating lionfish. Bernadsky and Goulet (1991) reported a captured cornetfish having the remains of *P. miles* in its stomach and displaying very little reaction to the venom (Hare and Whitfield 2003; Syngajewski et al. 2004). However, other than this report, there have been no other observed predation events of lionfish reported within their native range. However, Maljkovic and Leeuwen (2008) suggested that in the introduced range, lionfish were found in the stomachs of groupers yet Morris (2009) revealed that based on laboratory experiments, groupers actively avoid lionfish, even in periods of extreme starvation. Nonetheless, even if wild groupers actually predated on lionfish, they are systematically overfished throughout the Caribbean and are thus unlikely to control lionfish populations (Albins and Hixon 2008). Most recently, there was the first report of a confirmed natural predation event on lionfish by a moray eel (*Gymnothorax moringa*) (Muñoz 2017). Retrieved from a chevron trap set at 47 m depth at a site located 130 km from Florida in an area not frequented by divers, a 25 cm lionfish was regurgitated by a 90 cm moray eel (Muñoz 2017). This predation event lends some hope to potential biological control of lionfish within the invaded region especially since moray eels are renowned for their large size and high densities (Gilbert et al. 2005; Muñoz 2017). To best advise for future management of invasive species, there is a need to fully understand what limits lionfish populations, both in their native and invaded regions. In addition to predation, parasitism may be an additional but often overlooked means of population control.

In general, invasive species tend to have fewer parasites within their invaded range since they leave their native parasites behind (Torchin and Mitchell 2004). Although parasite loads within the invaded region are considerably lower than the native range (Sikkel et al. 2014), lionfish are not completely free from parasitism in the invaded range. Thus far, a total of 33 parasite species have been reported for lionfish within the western Atlantic region (Bullard et al., 2011; Sikkel et al., 2014; Ramos-Ascheri et al., 2015; Sellers et al., 2015). Most of the endoparasites recorded on lionfish were in their larval stages, thus suggesting that lionfish might represent an intermediate vector by serving as mesopredators for parasites (Simmons 2014). The venom contained within lionfish spines is systemic and it is unknown whether this deters parasitism (Wilcox and Hixon 2015) but this might account for why the majority of the ectoparasites did not appear to be highly attracted or able to successfully affect lionfish (Sikkel et al., 2014).

Although current research suggests that parasitism is unlikely to be a major limiting factor to lionfish populations, there is still need to investigate this relationship in the future. Factors such as the number of individuals released, time since introduction, vector of introduction, distance from native range as well as host susceptibility may affect parasite diversity and abundance in invasive species (Blakeslee et al., 2009; Simmons 2014). The larger sizes and higher growth rates attained by lionfish within the invaded range are likely to be due to a combination of low biotic resistance in the invaded region, prey naivete and a general release from biotic controls such as predators, parasites and competitors (Pusack et al. 2016).

1.17 How are they managed?

Considering the swift growth and expansion of their invasion, total eradication of lionfish has been deemed highly unlikely (Morris and Whitfield 2009; Muñoz et al. 2011; Cure et al. 2012; Frazer et al. 2012; Diller et al. 2014; Trotta 2014) especially with existing technology (Côté et al. 2014). Throughout the invaded range, the most successful strategies applied to reducing lionfish populations involve dedicated spearfishing by divers (snorkelling and scuba) either independently or in small groups (Frazer et al. 2012; de Leon et al. 2013) or via organised events such as lionfish tournaments/derbies (Barbour et al. 2011; Biggs and Olden 2011; Ali et al. 2013; Green et al. 2013; Trotta 2014). Capture via trapping and hook and line has been reported but is extremely rare (Henderson and Côté 2011; Lee et al. 2011; Morris et al. 2011; Curtis-Quick et al. 2013). Furthermore, lionfish consumption and the development of a commercial fishery is being increasingly promoted in order to sustain fishing pressure on populations (Morris et al. 2011; Muñoz et al. 2011; Frazer et al. 2012; Albins and Hixon 2013; de Leon et al. 2013; Lopez-Gomez et al. 2014; Wilcox and Hixon 2015). Morris (2009) suggested that the scale of ecological and economic impacts of lionfish predation remains unknown and that multiple scenarios are conceivable (Figure 1.8).

1.18 What are their likely impacts?

An effective larval dispersal mechanism coupled with a generalist diet is likely to have favoured the successful invasion of lionfish (Whitfield et al. 2007). Lionfish can directly reduce prey through consumption and indirectly influence other non-prey species by competition for resources or through trophic cascades (Palmer et al. 2016). The theory behind trophic cascades assesses how predators influence ecosystems through their reduction of prey density (Wallach et al. 2015). Defined as the indirect effect of predators on primary producer biomass (Shears and Babcock 2003; Borer et al. 2005), trophic cascades have been reported in most systems, reinforcing the fact that they are not limited by ecosystem type, habitat complexity, diversity or constituent predator and consumer communities (Pace et al. 1999). Lionfish have proven efficient in exploiting juvenile herbivorous fish populations which have potentially detrimental indirect effects on corals (Albins and Hixon 2011). In addition to reductions in species richness, biomass and recruitment, these trophic cascades can lead to phase shifts from coral dominated to algal dominated reefs which can have severe subsequent ecological and economical impacts (Palmer et al. 2016).

Impacts can especially be intensified in systems where trophic cascades occur due to overfishing of top predators which allows for mesopredator release where smaller predators become the dominant controlling force (Prugh et al. 2009; Albins and Hixon 2011). Evidence has suggested that lionfish are capable of removing significant proportions (78%) of prey communities (Albins and Hixon 2008) on isolated patch reefs and their diet may shift over time if there is an alteration or reduction in the abundance of prey fish (Morris 2009). This reduction in recruitment implies that they may possibly compete with native piscivores by monopolizing the food resource (Albins and Hixon 2008). However, continuous mortality of native predators though overfishing may open niche space, and subsequently increase available resources for lionfish (Whitfield et al. 2007).

Unlike other native species, lionfish experience little/no fishing mortality, and natural mortality is lowered due to their venomous spines. These factors combined are expected to give them a competitive advantage over native species (Whitfield et al. 2007). As top-level reef predators, they may compete with native reef fishes of the snapper-grouper complex, which is potentially challenging since this group is already heavily overexploited (Morris et al. 2010). Thus, lionfish represent a major threat to reef communities by reducing the survival of a wide range of native species through predation and competition (Bervoets 2009). Also due to their toxic spines, and the amino acid secreted, there are few predators that are able to actively prey on lionfish in the Atlantic (Bervoets 2009). Furthermore, due to lionfish feeding on juvenile reef grazers, an increase in algal growth on coral reefs may occur, causing additional stress to coral, which can result in coral mortality and also negative economic effects to a potential decrease in dive tourism (Bervoets 2009).

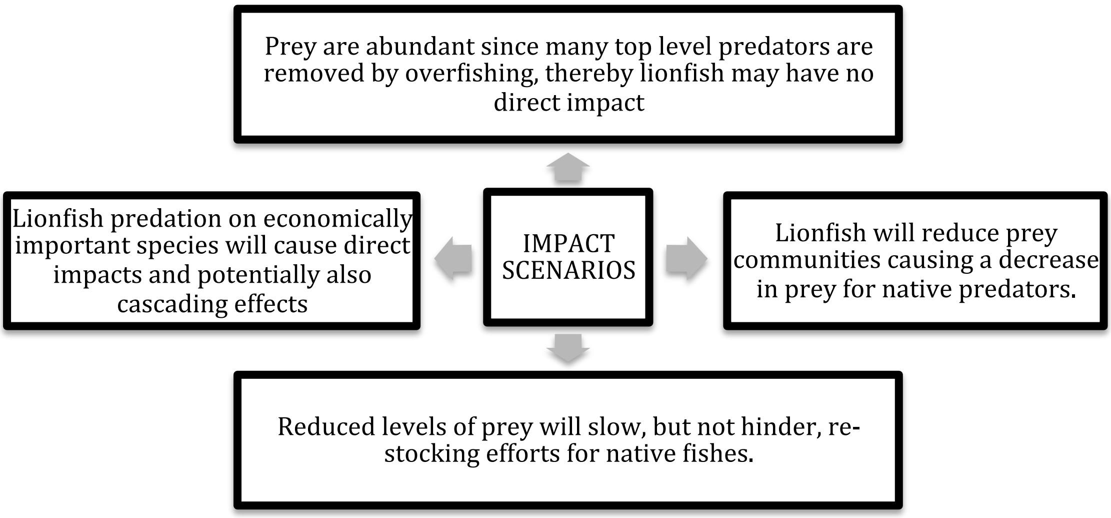


Figure 1.8. Potential scenarios of lionfish predation impact.

1.19 Introduction to study sites

Bonaire and Curacao are two of the 6 islands that comprise the Dutch Caribbean (formerly known as the Netherlands Antilles) and together with Aruba, these islands form a row off the northeastern Venezuelan coast (Stoffers 1956). These islands are volcanic in origin and all possess limestone dominated and very steep coasts (Zaneveld 1962).

Bonaire (12°10'N, 68°15'W) located in the La Blanquilla-Aruba island chain, is approximately 40 km east of Curaçao and 85 km north of Venezuela (Figure 2.1) and is separated from South America's continental shelf by the 1700m deep Bonaire Trench (Stokes et al. 2010). Lyons et al. (2015) described the typical reef in Bonaire as consisting of a sand, rubble or hard-pan shelf at ~5m and extends 50-150m from the shore with a reef slope of 45°. Klein Bonaire, a flat uninhabited 6km islet lies about 800m off the west coast of Bonaire and is included within the Bonaire National Marine Park (BNMP) boundaries. Bonaire is renowned as a top diving destination (Parsons and Thur 2008; Uyarra et al. 2009; Thur 2010; Lyons et al. 2015) and is recognised for its well-developed fringing reefs, high fish biomass and overall high biodiversity (Scatterday 1974; Ginsburg 1994; Hawkins et al. 1999; Parsons and Thur 2008; Sandin et al. 2008; Uyarra et al. 2009; Stokes et al. 2010; Jackson et al. 2014). This is testament to Bonaire being one of the first Caribbean countries to become designated as a National Marine Park in 1979 and protect its waters from high tide mark down to 60m depth (Dixon et al. 1995; Green and Donnelly 2003; Uyarra et al. 2005; Parsons and Thur 2008; Uyarra et al. 2009; STINAPA 2010).

Figure 1.9. Location of Bonaire and Curaçao within the wider Caribbean
(Image modified from Google Earth)

Bonaire is renowned as a marine park due to its prioritization of nature conservation at the forefront of its economic plan (CIEE Research Station Bonaire 2010a). Within the BNMP there is restricted fishing as well as prohibitions on boat anchoring, spear fishing and collection or removal of anything within the marine park (STINAPA 2010a; Uyarra et al. 2009; STINAPA 2010b). Furthermore, upon purchasing a marine park tag (USD$25) divers are allowed anywhere within park boundaries with the exception of two reserves where only scientific diving is permitted (Uyarra et al. 2009; STINAPA 2010b). These regulations along with dedicated marine park personnel help to maximise compliance with regulations, and thus minimize damage to the reefs by tourist activities (Kramer and Bischof 2003; Hawkins and Roberts 2004; Stokes et al. 2010). Within Bonaire, the main types of ecosystems include fringing coral reefs, seagrass beds, sandy beaches, mangroves, lagoons, bacterial mats and karstic systems (Uyarra et al. 2009; STINAPA 2010a). Lionfish were first confirmed in Bonaire on October 26th, 2009 (de Leon et al. 2013).

Curaçao is situated in the southern Caribbean (12^{o}10'N, 69^{o}15'W) about 80km off the coast of Venezuela (Diekmann et al. 2002). The coast of the leeward side of Curaçao is characterized by a continuous fringing coral reef, consisting of a small surf zone and a reef flat which gradually slopes down to a drop off at 7-12m (Bak 1977; Dorenbosch et al. 2009). The Curaçao Underwater Park was established in 1983, covering 20km of south coast coral reefs, starting at the eastern tip and extending to the west. Curaçao is located south of the Atlantic hurricane belt accounting for infrequent strong winds and rough seas (Bak and Lockhurst 1980). Nonetheless, tropical storms pass within 200km of the island every 4-5 years (Pors and Nagelkerken 1998) and have had serious negative impacts on shallow *Acropora* spp. (Bak and Lockhurst 1980). Curaçao is completely surrounded by fringing reefs, situated at a distance from the coast ranging from 20 - 250m (Van Duyl, 1985). Lionfish were confirmed in Curaçao on October 28th, 2009.

1.20 Training and workshops

Throughout Bonaire, under the guidance of STINAPA, interested certified divers, both recreational and professional were trained in the art of lionfish capture and removal. The first lionfish workshop was held in April 2009 and attendance was focused more towards dive operators and seasoned volunteers who had previously assisted STINAPA with other projects. This workshop introduced participants to background lionfish ecology and what has been done elsewhere in the Caribbean to manage their population growth. The practical aspects of this workshop involved training in lionfish capture using hand nets along with the use of lionfish markers. Additionally, to help mitigate the recognised costs and boost lionfish removal, a partnership was created between STINAPA and the local dive shops at the beginning of the invasion in Bonaire, whereby lionfish volunteers would receive free tank fills upon presenting their lionfish removal certification badge and showing proof of their lionfish removal equipment. Furthermore, STINAPA chartered dive boats once or twice a year for removal in targeted areas whilst other dive operators give dedicated volunteers discounted prices on tank fills and boat diving.

Since Bonaire is renowned as a marine park with limitations on spearing, the use of nets for lionfish removal remained the only legal option for removal. However, in December 2010, a provision in the Marine Ordinance allowed for special allowances to be made, leading to the introduction of the Eliminating Lionfish Tool (ELF Tool) to specific volunteers under a contract with the Marine Park Manager (Morris et al. 2012). The ELF tool is a hand held spearing device and is similar to a Hawaiian sling except it works via stretching of a spring rather than rubber tubing. Approximately 300 ELF Tools have been issued to volunteers thus far but it was revealed that only about 50 volunteers are active and dive at least once a week (de Leon, pers. comm.). The ELF Tool was designed specifically for lionfish removal and is thought of as presenting less damage to the reef. The introduction of the ELF Tool was warranted as the resident lionfish within Bonaire became too large and also too numerous to be effectively controlled by hand nets. However, in Curaçao the polespear was widely used since lionfish removal began in July 2011 (de Leon et al 2013).

1.21 Introduction to thesis

Knowledge of how the lionfish invasion proceeds is invaluable to tailoring management strategies in other countries still in the early invasion stages. The overall aim of this research was to conduct an analysis of the ecological and socio-economic impacts of the lionfish invasion in Bonaire, Klein Bonaire and Curacao in order to make recommendations for management. Following the Introduction in Chapter 1, Chapter 2 of this thesis assesses whether management has a significant role to play in the spread and/or growth of lionfish and if/how the success of control is affected by delaying management. Following on from this, Chapter 3 goes on to to evaluate the magnitude of ecological impacts based on their diet, assess for local scale variation in feeding ecology and identify which traits make prey species more vulnerable to predation. Chapter 4 examines the effectiveness of management strategies to identify the most efficient and successful strategy; the best time for removal and the most suitable tools/equipment for successful control. Finally Chapter 5 takes into account the socio-economic aspects of the invasion; looking at the use of volunteers for removal, their attitudes, motivations and means for reinforcement and recruitment as well as a cost benefit analysis of the lionfish invasion. Chapter 6 summarizes and links together all facets of the research to present an optimal lionfish response strategy as a final product. The components of this thesis and how they fit together are summarised in Figure 1.10.

The main novelty of this work lies in the fact that it combines both an ecological and socio-economic assessment of the impacts of the lionfish invasion and how these factors affect and interact with one another. Furthermore, aspects of this study examined the response of lionfish between islands where there were varying responses to management, but also within a single island where there was different hierarchies of hunting pressure. This research also represents the first direct comparison of lionfish diets within distinctly different habitats and also stages of the invasion timeline. This work contributes to new knowledge by identifying which lionfish should be removed, what is the most effective depth, which tools and education strategies should be applied as well as the value of a dedicated volunteer response effort as well as their motivations and means for recruitment and reinforcement.

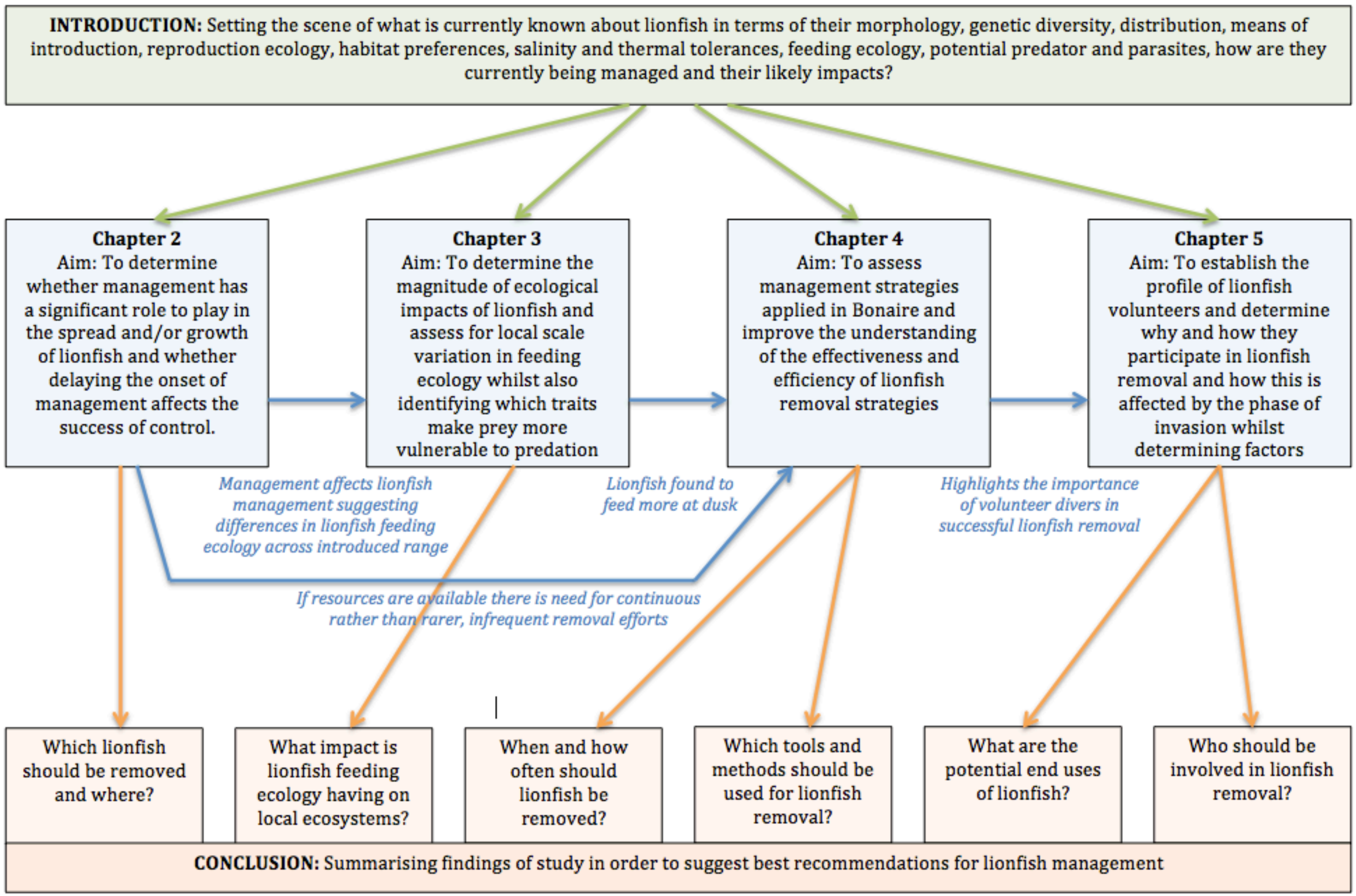


Figure 1.10. Summary of thesis components and the interactions between chapters

Chapter 2: THE EFFECT OF MANAGEMENT STRATEGIES AND THEIR IMPLEMENTATION ON LIONFISH POPULATIONS IN THE SOUTHERN CARIBBEAN

2.1 Abstract

In the space of approximately 30 years in their invasive range, lionfish have infiltrated a diverse array of habitats, inhabited a depth range of > 300 m and exceeded the size and density reported in the native range, demonstrating the difficulty of effective lionfish management. If left unmanaged, lionfish pose a significant, but still uncertain, threat to Caribbean ecosystems thereby warranting the need for effective and efficient, tailored management schemes based on their ecology within invaded habitats. During a monitoring period between 2009 - 2013, 11,161 lionfish specimens from Bonaire, Klein Bonaire, and Curaçao were documented, measured and weighed, with their population dynamics, size-class distributions and densities analysed in relation to local management strategies and timing. This research reinforced the importance of an early detection and rapid response strategy when managing invasive species but revealed the importance of considering the intricacies and variations in factors affecting lionfish removal. Thus, rather than having a one size fits all response to lionfish management, there is need to consider the invaded area in terms of access, ease of entry and popularity of sites and thus refocus removal efforts accordingly. Areas with a less frequent or delayed removal effort were found to harbour lionfish that were on average larger than those in areas with a more frequent hunting pressure. These findings also suggest that if resources are available, there is need for continual removal of lionfish which is more effective than larger, rarer removal events.

2.2 Introduction

Invasive species are considered to be the one of the most important causes of global biodiversity loss (Vitousek et al. 1996; Stachowicz et al. 2002; Altman and Whitlach 2007) except on islands where they are considered to be the greatest threat (Clout and Veitch 2002; Clavero and Garcia-Berthou 2005). Species invasions are increasing in frequency and this has caused great concern globally (Rosecchi et al. 2001; Garcia-Berthou 2007; Blackburn et al. 2011). Regarding an introduction event, the number of initial colonisers and the amount of genetic variance set the precedence for later invasions (Parker et al. 2003). Physiological tolerance limits set the thresholds beyond which an organism cannot grow, reproduce or survive, and ecological interactions such as competition, predation and mutualism help to modify these limits (Rilov and Crooks 2009). Progression towards a biological invasion can be split into four phases. introduction; establishment; naturalization and invasion (Perrings 2002; Emerton and Howard 2008). The stages between introduction and full invasion; knowing which ecosystems will be invaded; and what the consequent impacts will be in these ecosystems, generally remains unknown (Born et al. 2005).

Lionfish possess many characteristics (see Table 1.2) which enhances their potential as an invasive species. Firstly their generalist diet and range of feeding behaviours allows it to fully exploit and capitalise on available prey, at rates sometimes more efficient than native predators. In addition to a generalist diet, they also exhibit great plasticity in terms of their habitat choice (Cure et al. 2014; Raymond et al. 2015). Lionfish have been found anywhere from <1 to >300m (Whitfield et al. 2007; Muñoz et al. 2011; Côté et al. 2013) in habitats ranging from ship wrecks and other man-made structures (Ruiz-Carus et al. 2006; Nuttall et al. 2014), coral reefs (Biggs and Olden 2011; Lesser and Slattery 2011; Côté 2013), mangroves (Barbour et al. 2010), sea-grass (Claydon et al. 2012) and have most recently been discovered within estuaries (Jud et al. 2011). Their generalist behaviours are complemented by an efficient reproductive and dispersal system that has accounted for the effective colonisation of their invasive range within two decades (Morris et al. 2011) and explain why they are viewed as one of the worst marine invaders in history (Albins and Hixon 2011; Kulbicki et al. 2012).

Lionfish were first confirmed in Bonaire and Curaçao between October 26 - 28, 2009 (de Leon et al. 2013). Both of these islands are renowned globally for snorkeling and shore diving (Uyarra et al. 2009; Thur 2010), which make lionfish removal exceptionally feasible. Although lionfish were first confirmed within days of each other in Bonaire and Curaçao, the strategies implemented varied tremendously (de Leon et al. 2013). Bonaire adopted an early and rapid response approach where, prior to lionfish arrival, preparation begun for the lionfish invasion via education and training of divers, especially those within the diving industry from a top-down approach, i.e. headed by the nature management entity on Bonaire (STINAPA). On arrival, lionfish were reported, removed and submitted to the on-island research facility (CIEE Research Station Bonaire) for the invasion ecology to be monitored. Thus there were partnerships formed between nature management agency, dive operators and a research facility. However, in Curaçao, there was a delayed response, and removal was eventually initiated in July 2011 by the Ministry of Health, Nature and Environment (de Leon et al. 2013).

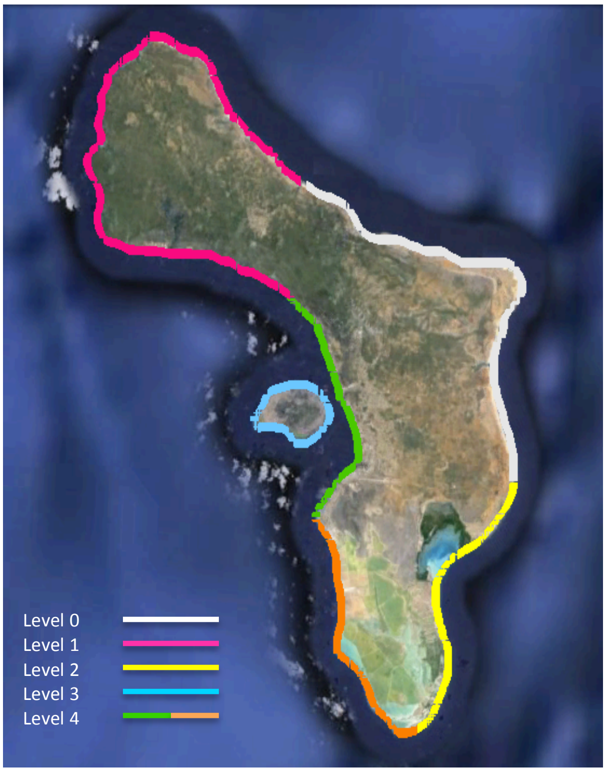


Figure 2.1. Variation in lionfish hunting pressure in Bonaire. Where the white sector (level 0) represents an area where no hunting occurs due to extremely rough seas and lack of access for diving; the pink sector (level 1) indicates infrequent hunting due to the presence of no-diving reserves and the oil refinery; the yellow sector (level 2) represents the East coast of Bonaire where infrequent hunting takes place due to unfavourable dive conditions; the blue sector (level 3) represents Klein Bonaire where infrequent hunting takes place as it is only accessible by boat and finally level four which represents the most heavily hunted area due to the proximity to hotels (green sector), house reefs and popular dive sites (orange sector)

Although an early and rapid response to lionfish was enacted within Bonaire, hunting pressure was not uniform (Figure 2.1). The leeward coast of Bonaire is sheltered and calm allowing for easy access throughout the year whereas the windward shores tend to have stronger wave action and less favourable conditions making dive sites less accessible (de Leon et al. 2013; Lyons et al. 2015). As a result, there is a hierarchy in lionfish hunting pressure with the level 0 area experiencing no hunting due to the extremely rough sea conditions and a lack of access to sites. The level 1 sector experienced infrequent removal due to the presence of areas where diving is restricted permanently (with the exception of special hunting events organized by STINAPA) such as Playa Frans and Karpata no-diving reserves and the BOPEC oil refinery. Additionally within this area is the Washington Slagbaai National Park (WSNP), which is a considerable distance from the capital Kralendijk, and also where diving is limited to the park's opening hours and volunteers must complete all dives by 15.30

in order to exit by 17.00. The level 2 sector also receives infrequent hunting due to difficult access and advanced dive conditions and diving mostly occurs in the event of a wind reversal. The level 3 sector represents Klein Bonaire which also receives infrequent hunting due to the fact that it is only accessible via boat. Finally the most heavily hunted sector (level 4) represents areas where most hotels and popular dive sites with easy shore access are located.

Since their introduction to the Caribbean 30 years ago, lionfish have continually increased in size, exceeding densities and sizes from the native range (Morris 2009) (see Table 1.3 and Table 1.4). Although in some islands considerable achievements have been made with limiting their population growth thus far (Frazer et al. 2012; de Leon et al. 2013), with existing management tools and techniques, complete eradication of lionfish seems to be an impossible task (Muñoz et al. 2011; Cure et al. 2012; Côté et al. 2014). Throughout the invaded range, various management schemes have been applied, but with varying success (Morris 2012). Currently, many countries are still struggling to reduce lionfish densities, whilst others have achieved considerable success in controlling local populations. These management strategies throughout the invaded region vary in the promptness of their response, education and awareness schemes enacted as well as the tools and groups of individuals utilised for removal.

An indication of a successful invasive species management strategy is a general reduction in the average body size of individuals over time (Frazer et al. 2012; Côté et al. 2013; de Leon et al. 2013). What makes this work different is that this study not only looks at the response of lionfish between islands where there are varying responses to management (Bonaire, Klein Bonaire and Curaçao), but also within a single island (Bonaire) where there are different hierarchies of lionfish hunting pressure. Therefore the main aim of this work was to determine whether management had a significant role in the spread or growth of lionfish and also whether delaying the onset of management affects the success of controlling local populations. Within this study, the success of lionfish control will be measured by a reduction in lionfish size class distribution, weight, biomass and density. Studying the dynamics and response of an invasive species to management helps to assess the effectiveness of current strategies and gain knowledge to enhance future control. Thus the following hypotheses were presented.

H_1. Management has a positive impact on the control of lionfish populations

H_2. Impacts of management are affected by the promptness of initiation

2.3 Methods

In order to assess the impact of management on lionfish populations, lionfish of various sizes were captured, measured and analysed in Bonaire, Klein Bonaire and Curacao where there were varying responses to management

2.3.1 Collections

A total of 11,161 lionfish ranging between 21 to 455 mm TL were collected by divers and analysed by the author and trained staff at CIEE Research Station Bonaire between October 26, 2009 and November 24, 2013 in Bonaire (6288), Klein Bonaire (2743) and Curaçao (2130). Lionfish were collected every month of the year, with the smallest sample sizes occurring during December (n = 221) and the largest sample sizes in March (n = 2696). Collections were achieved between 07.00 and 22.00 with the majority (48%) taking place between 14.00 and 18.00. All specimens were obtained opportunistically from trained lionfish volunteers who collected all specimens using scuba gear at the dive sites surrounding Bonaire, Klein Bonaire and Curaçao. These sites consisted of high profile coral reefs and patch reefs, ranging in depth from 0.3 to 91.5m. Within Curaçao, the majority of the specimens were obtained from annual lionfish tournaments (March 2012 and April 2013) where local lionfish volunteers dove throughout the island and submitted their catch to be judged for the tournament. Prizes were awarded for the largest, smallest and most lionfish caught. Collections were achieved using hand nets, pole spears or the use of the Eradicating Lionfish Tool (ELF Tool) which is similar to a Hawaiian sling except it works via spring rather than rubber. The ELF Tool was designed specifically for lionfish removal and is thought of as presenting less damage to the reef. Caught specimens were stored in containment devices such as dry bags or the Zookeeper which is a plastic PVC tube with a funnel that allows for safe storage of lionfish after collection. (See Appendix A for images of all collection tools).

2.3.2 Measurements

Upon capture or submission of specimens, data were collected on the date, time, location and depth of capture. All caught lionfish (N = 11,161) if not already dead were euthanized and measured according to their standard length (snout to beginning of tail), total length (snout to end of tail) (Figure 2.2) and wet weight when possible. The head length (HL) was also measured. All measurements were conducted either by the author or trained staff at CIEE Research Station Bonaire.

Figure 2.2. Demonstration of the measurement of lionfish head length (HL), standard length (SL) and total length (TL)

2.3.3 Data analysis

Using the statistics program R (version 3.01), a one-way ANOVA was used to compare differences in mean total length of lionfish in Bonaire, Klein Bonaire and Curaçao. Trends in lionfish mean total length were examined over a 50 month time scale using a linear least squares regression with a LOESS smoother (previously known as LOWESS. Locally Weighted Scatterplot Smoothing). Finally a General Linear Model with a binomial distribution was used to investigate the relationship between lionfish total length and depth.

2.4 Results

2.4.1 Size distribution

Lionfish caught within Bonaire, Curaçao and Klein Bonaire ranged in size from 21 – 446 mm. Lionfish in Bonaire were on average smaller (190mm TL [±68 SD] and 130g WW [±155 SD]) when compared to Klein Bonaire (228mm TL [±70 SD] and 210g WW [±208 SD]) and Curaçao (250mm TL [±64 SD] and 276g WW [±215 SD]) (one-way ANOVA, p <0.0001, df=2,10304). In Bonaire, the size of lionfish increased gradually over the 4 year time period, growing from a mean TL of 152mm [±71 SD] in 2009/10 to 207mm [±74 SD] in 2012/13. The size distributions changed from a more negatively skewed population in Bonaire towards a more normally distributed population in Curaçao (Figure 2.3). In Bonaire the majority of lionfish were in the 101-200mm size class (46%) whereas in Klein Bonaire and Curaçao the majority (45% and 52% respectively) were found in the 201-300mm size class (Figure 2.3).

In areas of Bonaire with higher hunting pressure (fished), lionfish biomass was 2.76 fold lower when compared to other areas of Bonaire with minimal/no hunting pressure (unfished) and 4.14 fold lower than unfished areas of Curaçao. Within fished locations on Bonaire, the average weight of lionfish was 1.83 fold lower in unfished sites in Bonaire and 2.24 fold less than unfished areas of Curaçao (Figure 2.4). Over the four year monitoring period in Bonaire, the size class distribution changed from being dominated by fish <200mm in 2009/10, to a majority 101-200mm size class in 2010/11, to 100-300mm size class in 2011/12 to a more equally spread distribution between 101-400mm in 2012/13 (Figure 2.5). These differences in mean TL over each of the four sampling years was found to be statistically significant (One-way ANOVA, df = 5176, $p < 0.0001$). Lionfish TL in Bonaire was on average lower in areas of high hunting pressure as compared to areas with lower hunting pressure (Figure 2.6).

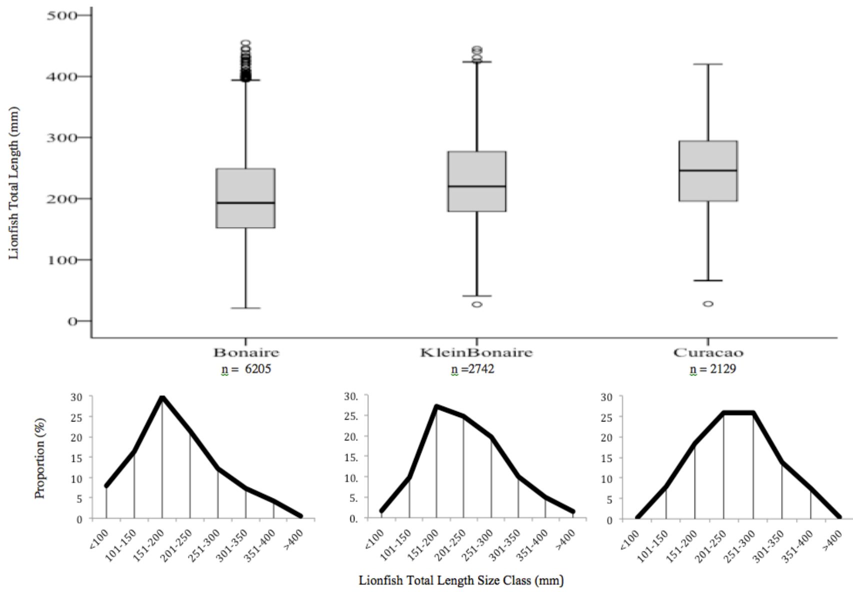


Figure 2.3. Size class distribution of lionfish within Bonaire, Klein Bonaire and Curaçao based on total length (TL) measurements Number of specimens per each sampling site indicated below boxes. Box plots display the interquartile range (box), median (center line in box), 10th and 90th percentiles (whiskers), and minimum and maximum outliers (o)

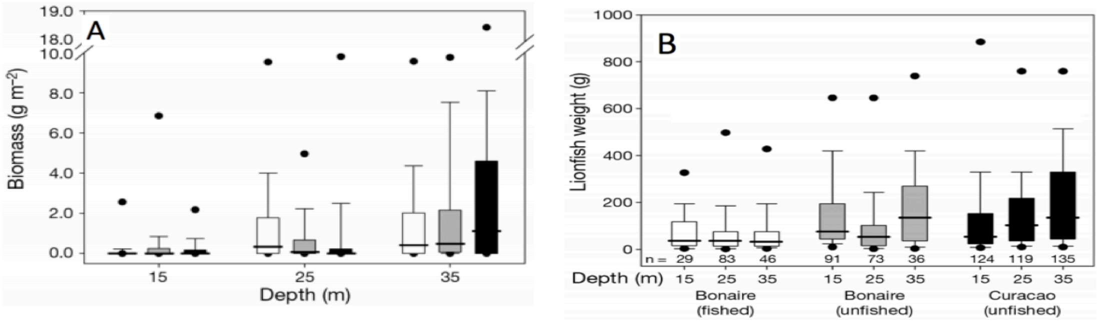


Figure 2.4 (A) Lionfish *Pterois* spp. biomass in fished locations on Bonaire (white) and unfished locations on Bonaire and Curaçao (grey and black, respectively) for 3 different depths. Figure 2.5 (B) Influence of depth and hunting pressure (fishing) on lionfish weight. Number of sites surveyed per each combination of factors indicated below boxes. Box plots display the interquartile range (box), median (center line in box), 10th and 90th percentiles (whiskers) and minimum and maximum values (black dots). Figures modified from de Leon et al. (2013).

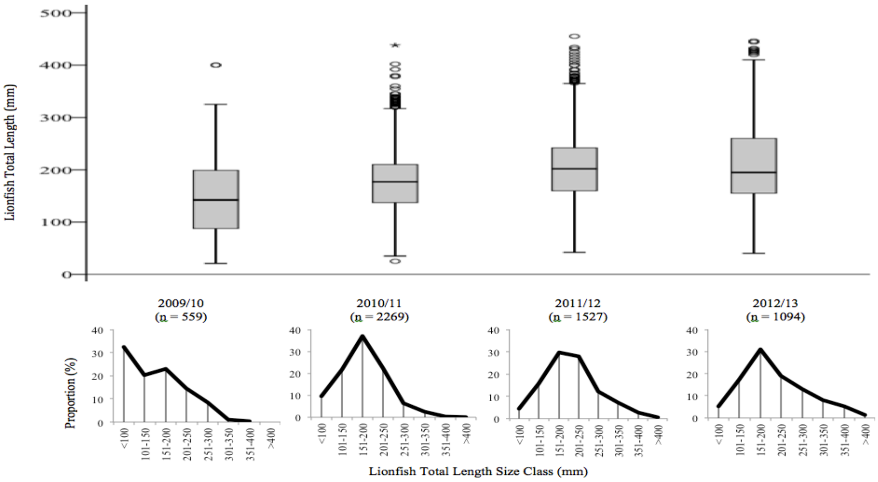


Figure 2.5. Lionfish size class distribution within Bonaire over a four-year sampling period (October 26th 2009 – November 24th, 2013) based on total length (TL) measurements. Number of specimens per each sampling year indicated below boxes. Box plots display the interquartile range (box), median (center line in box), 10th and 90th percentiles (whiskers), and minimum and maximum outliers (o)

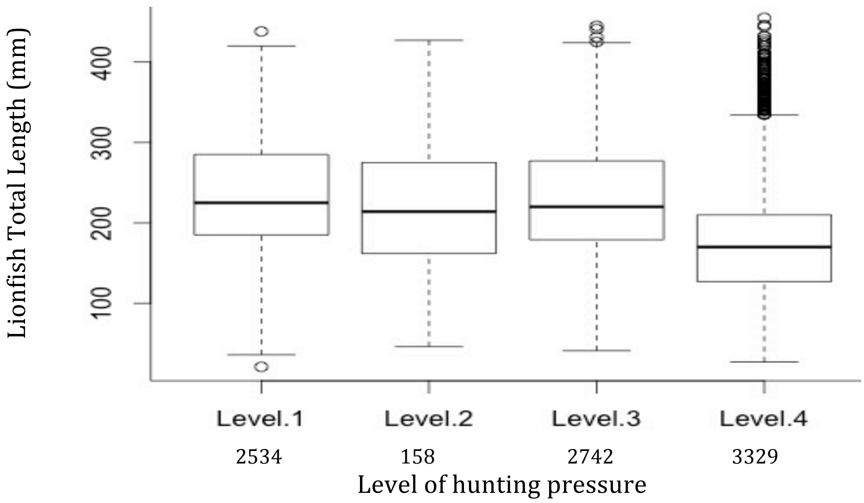
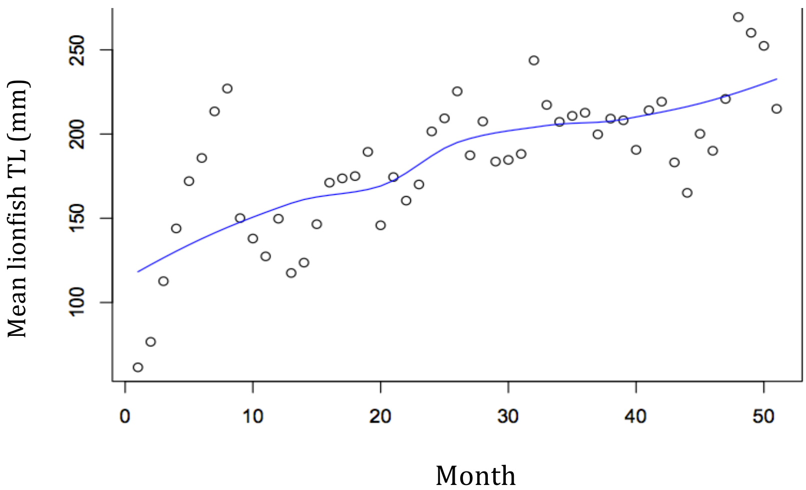


Figure 2.6. Lionfish size under different levels of lionfish management in Bonaire where Level 1 indicates infrequent removal due to presence of no-dive reserves, Level 2 indicates infrequent removal due to adverse conditions; Level 3 indicates infrequent removal due to boat access and Level 4 indicates frequent removal due to shore access and proximity to dive operators. Number of specimens per each sampling year indicated below boxes. Box plots display the interquartile range (box), median (center line in box), 10th and 90th percentiles (whiskers), and minimum and maximum outliers (o)

2.4.2 Lionfish size as a function of time in Bonaire

When examined on a 50-month time-series scale rather than a 12-month scale (Figure 2.7a), the overall increasing size trend is apparent, with superimposed fluctuations. Shorter temporal fluctuations were identified by taking residuals from a loess smoother linking mean TL and month (Figure 2.7b). The largest residual (i.e. highest size anomaly) occurred in June 2010. After this time a semi-regular pattern of positive and negative size anomalies is seen, typically with a relatively gradual increase in size anomaly to a local maximum, followed by a rapid reduction to local minimum values. This trend continued until May 2012, where there was a continuous decline in mean size for 12 months, at which point lionfish attained a size of 50mm below the long term expected TL, where there was a sudden peak in September 2013, followed by another decline.



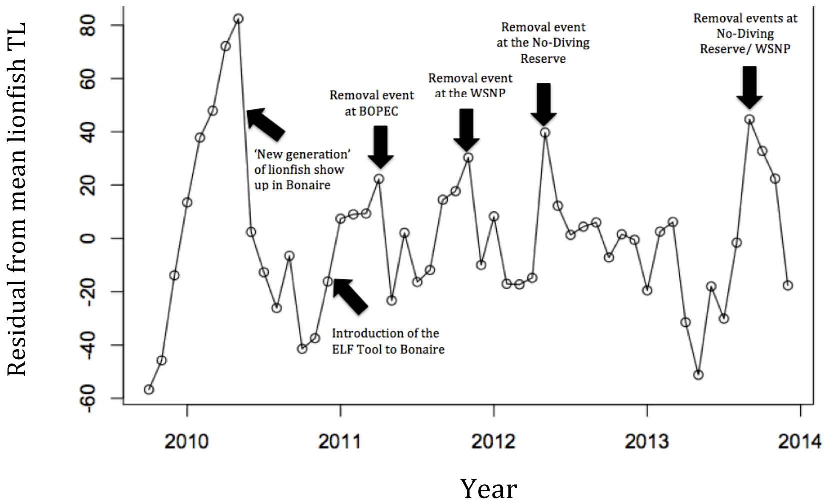


Figure 2.7a. Mean lionfish size based on total length (TL) measurements over a 50 month time-series scale with blue line representing loess smoother. The loess smoother fits a curve to a dataset rather than plotting a line of best fit. Figure 2.7b. Temporal fluctuations in lionfish size based on residuals from a loess smoother, linking mean TL and month. Black arrows indicate specific events within the lionfish invasion of Bonaire including larger-scale lionfish removal events.

2.4.3 Lionfish depth distribution

Lionfish in Bonaire were caught at depths ranging from 0.3 to 91.5m (Figure 2.8). A General Linear Model (GLM) with a binomial distribution found that the general size of lionfish increased with depth and that there was a significantly greater proportion of fish within the size class 101 – 200 mm occupying the 15 – 25 m depth range ($P = 0.0473$). Results from the GLM also found that the year of invasion did not affect the relationship between lionfish total length and depth.

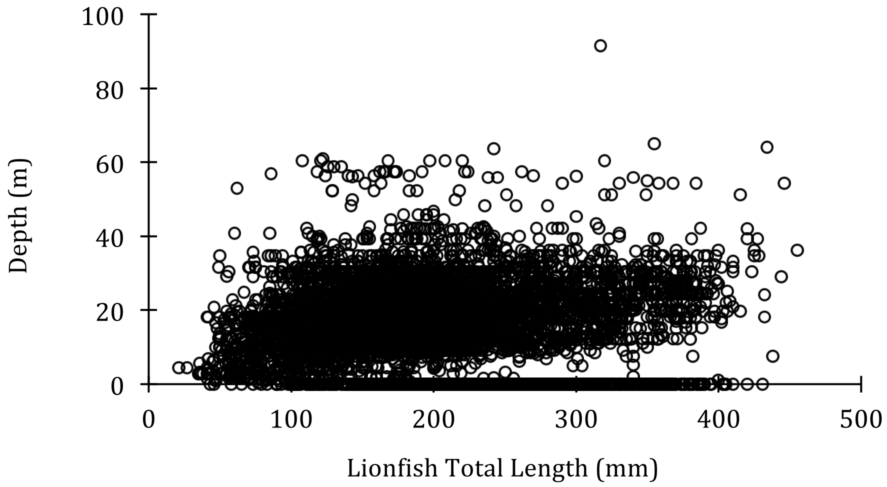


Figure 2.8. Lionfish depth association according to size

2.5 Discussion

A consequence of a successful invasive species management programme is a reduction in mean size over time (Frazer et al. 2012; Côté et al. 2013; de Leon et al. 2013). The almost two year delay in implementing management strategies can account for the observed size difference between Bonaire and Curaçao, where lionfish were on average larger in Curaçao than Bonaire. For invasive species, failing prevention, an early detection and rapid response (EDRR) management scheme has proven more successful because the options available to eradicate invasives drastically decreases over time (Bax et al. 2001; 2003) and it has proven efficient in reducing growth of invasive species (Culver and Kuris 2000; Secord 2003; de Leon et al. 2013). This is because the longer the delay in implementing action, the greater the magnitude of individuals needing removal and also the treatment area (Simberloff 2000). Furthermore, with growing numbers of individuals, resources can become limited and competition occurs, resulting in lionfish being forced to extend their range. This is especially worsened when no action is taken or if there is a delay in response. By delaying management of an invasive species, not only is it given time to increase in size, their density also increases as a reproductive population establishes. Thus this research highlights the need for and recommends an EDRR management scheme for any territory early in their lionfish invasion timeline or facing an invasion of a new species.

De Leon et al. (2013) found similar results where lionfish density, biomass and body mass were significantly lower in areas with a more immediate and greater hunting pressure (Bonaire) than areas with delayed and reduced hunting pressure (Curaçao). The early and prepared response in Bonaire where approximately 300 divers were trained to remove lionfish prior to their confirmation was suggested as the reason why lionfish biomass and density was lower (de Leon et al. 2013). Thus, an imperative factor in EDRR is education and awareness since a more educated population is more likely to assist, encourage and even help finance the removal of invasive species.

Where possible, education of key stakeholders and provision of sufficient skills to detect, report, remove and monitor target species should be done before confirmation of the invasive species within the territory, or if not, as immediately as possible. Thus for countries still early within their invasion timeline or those yet to be invaded by lionfish, it is imperative to apply this EDRR strategy as this has proven very successful in not only reducing lionfish density, but also their size (de Leon et al. 2013). Furthermore a continued and constant hunting pressure helps to deter the average size of lionfish from increasing and thereby helps to mitigate against potential subsequent ecological impacts. Lionfish have been reported to attain sexual maturity at ~100 mm TL length for males and ~180mm for females (Morris 2009), thus removing lionfish before they have had a chance to reproduce should be beneficial in alleviating their further spread.

Within Bonaire, even though an EDRR strategy was applied, there were still variations in hunting pressure within the island due to differences in access and proximity to dive operators. Within Bonaire, the majority of diving is concentrated on the more sheltered west coast, thus hunting on the east coast is significantly reduced and only occurs during wind reversal events or by very advanced divers due to harsh conditions and difficult entries. Since Klein Bonaire is only accessible by boat, it also receives reduced hunting pressure. The more popular dive sites or the ones which are closer to dive operators and house reefs receive a much higher hunting pressure which accounts for the reduced average size of lionfish compared to areas with lower hunting pressure. Therefore given this non-uniformity in hunting pressure, it warrants the need for increased efforts in these areas with less frequent hunting. This also highlights the fact that a 'one size fits all' approach to lionfish management is not recommended. Instead the intricacies of the factors that affect the success of removal activities need to be thoroughly understood. Furthermore this research has also revealed how active management (and the lack of) can affect the size structuring of an invasive population and thus their consequent impacts.

Lionfish removal within Bonaire is achieved by a variety of individuals including STINAPA personnel, dive operators and volunteer divers. Volunteer divers are responsible for a considerable proportion of the lionfish removed within Bonaire (de Leon et al. 2013), and these volunteers supplied the majority of the specimens analysed for the purposes of this research. Thus there is need for the volunteer effort to remain relatively consistent; otherwise seasonality in effort could potentially lead to a boom and bust fluctuation in lionfish population (Green and Cote 2014). Due to adverse conditions and entries in some areas there might be a need to recruit a specialist group of more experienced divers to focus removal efforts in these areas. Within Bonaire, STINAPA enlisted some of the more skilled lionfish volunteers aboard chartered dive boats destined for focused removal activities on less hunted areas such as the East coast, the No-Diving Reserves and Klein Bonaire. These actions should be replicated in other countries where there there can be identification of not only the individuals who can be recruited but also the areas where removal efforts should be focused.

A cyclical relationship was observed whereby it took lionfish 5-6 months to recover from one peak in maximum size anomaly to the next. After being confirmed in late October 2009, lionfish began to continually increase in size until June 2010 where a ‘new generation’ of lionfish (i.e. juvenile fish ~50mm TL) began showing up, thereby lowering the mean TL and accounting for the first sharp decline in size anomaly. Subsequent to this, the peaks in lionfish size coincided with targeted removal efforts at areas not as regularly controlled. The ‘No-diving Area’ (Karpata Reserve) prohibits diving of any kind throughout the year, even for hunting lionfish. STINAPA has opened the Reserve to a select number of volunteers once or twice a year and have also chartered boat trips to the WSNP with lionfish removal being the sole purpose. Due to the reduced frequency of hunting, the individuals caught during these events tend to be larger and of a higher density thus raising the mean TL and accounting for the observed peaks. These findings suggest that if resources are available, there is need for continual removal of lionfish which is more effective than larger, rarer removal events (such as annual or bi-annual removal events), a recommendation echoed by Frazer et al. (2012) and Green and Côté. (2014).

Lionfish within Bonaire, regardless of their size, occupied a wide depth range. Although the literature has reported lionfish occupying depths as great as 300m (Albins and Hixon 2011; Lesser and Slattery 2011; Côté et al. 2013; Johnston and Purkis 2014), the shallower depth range reported in this study was a result of captures being conducted primarily by recreational divers. A general trend was observed whereby larger lionfish were associated with greater depths and this has been linked to ontogenetic shifts from shallow to deep reefs once fish mature (Barbour et al. 2010; Biggs and Olden 2011; Claydon et al. 2012). There have been limited studies on the association and behaviour of lionfish at mesophotic depths (Nuttall et al. 2014; Switzer et al. 2015), but this needs to be a priority for future research and management, as very little is known of this relationship. This may also be an indication of a refuge at greater depths and could potentially account for the increasing mean size of individuals within this study over the 4-year sampling period. Nonetheless, this shift of lionfish to greater depths highlights one of the limitations of lionfish control. With larger, and more fecund individuals shifting to depths which exceed the limits of divers, complete removal is unlikely since larvae from these inaccessible populations will continuously and permanently offset the effectiveness of removal activities. Thus there may be the need to recruit or even hire a team of technical divers to concentrate removal efforts at depths inaccessible to recreational divers. However, given the vastness of the ocean and the extent of the lionfish invasion, a recommendation will be for the development of a lionfish specific trap that can be deployed at depth may be one of the greatest priorities to combatting the lionfish invasion.

2.6 Conclusion

Generally, an indication of a successful invasive species management strategy is a general reduction in the average body size of individuals over time. The observed variation in lionfish size amongst islands and also within Bonaire likely reflects the management strategies instilled along with the ease of accessibility for removal**.** This research reinforced the importance of an early detection and rapid response strategy when managing invasive species but revealed the importance of considering the intricacies and variations in factors affecting lionfish removal. Thus, rather than having a one size fits all response to lionfish management, there is need to consider the invaded area in terms of access, ease of entry and popularity of sites and thus refocus removal efforts accordingly. Areas with a less frequent or delayed removal effort were found to harbour lionfish that were on average larger than those in areas with a more frequent hunting pressure. These findings also suggest that if resources are available, there is need for continual removal of lionfish which is more effective than larger, infrequent removal events.

Chapter 3: A COMPARISON OF LIONFISH FEEDING ECOLOGY WITHIN THE INVADED REGION

3.1 Abstract

Widely regarded as a generalist predator with a voracious appetite, lionfish are principally piscivorous and have been known to feed opportunistically on a wide range of taxa including invertebrates. Lionfish have been present throughout the invaded Atlantic-Caribbean region across different habitats and for varying time scales. If lionfish feeding ecology differs among islands, the consequent ecological impacts are likely to vary, cautioning against drawing inferences from studies in contrasting habitats and warranting control strategies to be tailored accordingly. To determine the feeding ecology of lionfish in the southern Caribbean, the stomach contents of 11,161 lionfish from Bonaire, Klein Bonaire and Curacao were analysed. Stomach contents were identified and feeding ecology analysed to assess whether feeding behaviours and preferences were uniform throughout the introduced range. Dietary preferences were assessed to determine whether any traits of prey increased vulnerabilty to lionfish predation, Results were compared to the only other equivalent-scale analyses of stomach contents of invasive lionfish, drawn from the Bahamas. This research revealed that although lionfish diets amongst Bahamas, Bonare, Klein Bonaire and Curacao were similar in terms of composition, there were considerable differences in rankings of dietary importance. When compared to fish from the Bahamas, lionfish in southern Caribbean island reefs consumed fewer prey items of increasingly larger size which may be due to the differences in reef structure and health. Lionfish also exhibited trait-based selection, showing a preference for prey with a slender, elongated body shape, within the yellow/orange colour spectrum. This research therefore confirms that the feeding behaviours and preferences of lionfish are not uniform throughout their introduced range and reveals the potentials implications for ecology if lionfish are not as ubiquitous as represented in the Bahamas

3.2 Introduction

The red lionfish (*Pterois volitans)* is typically viewed as a generalist predator with a cosmopolitan appetite due to its consumption of large amounts of prey species of various varieties (Morris and Akins 2009; Green et al. 2012; Layman and Allegeier 2012; Benkwitt 2013; Côté et al. 2013). Although renowned for being principally piscivorous, lionfish have been known to feed on invertebrates (Morris 2009) and in their native range, they occupy higher trophic levels than seen in the invaded range (Hare and Whitfield 2003; Bervoets 2009). Lionfish are visual (Côté and Malkovic 2010; Green et al. 2011; Green and Côté 2014), opportunistic predators (Whitfield et al. 2007) and employ a diverse range of feeding strategies (see Table 1.5) making them well suited for feeding on benthic and cryptic prey (Morris 2009; Albins and Lyons 2012) . Thus, a variation in feeding behaviours in different habitats is likely, and as a result relying on studies from only one habitat type can be misleading when predicting lionfish impacts. Furthermore, if lionfish feeding ecology varies between regions (especially amongst islands in the invaded regions), then the consequent ecological impacts are likely to vary, and control or eradication strategies will need to be tailored for each regional area.

Within the introduced region, the majority of published research on lionfish feeding ecology has taken place in the Bahamas, which is characterised by discontinuous patch reef habitats. Many of these studies portray lionfish as having the potential to cause great ecological harm to local ecosystems (Whitfield et al. 2007 Albins and Hixon 2011; Kulbicki et al. 2012) whilst others present lionfish as gluttonous individuals, consuming as much as 20 small fish in a single 30 minute period (Albins and Hixon 2008) or anywhere between 4-10% of their own body weight daily (Fishelson 1997; Morris et al. 2008; Frazer et al. 2012) (Table 3.1). Others suggest that lionfish are renowned for preying upon more than half of potential prey species (Côté et al. 2013) and reducing juvenile fish abundance by 79% (Albins and Hixon 2008) or removing 230kg of small fish per year (Fishelson 1997; Muñoz et al. 2011). As a result, determining whether this gluttonous diet is uniform throughout the invaded region will be important in predicting future impacts of lionfish, and also in tailoring management schemes

Table 3.1. Reported feeding behaviours of lionfish

Statement	Location of study	Reference
…consuming as much as 20 small fish in a single 30 minute period…	Bahamas	Albins & Hixon (2008)
…consuming between 4-10% of their own body weight daily…	Gulf of Aqaba, Red Sea	Fishelson (1997)
…predating on more than half of potential prey species…	Bahamas	Côté et al. (2013)
…reducing juvenile fish abundance by 79%...	Bahamas	Albins & Hixon (2008)
…removing 230kg of small fish per year…	Gulf of Aqaba, Red Sea	Fishelson (1997)

Lionfish stomachs can expand to more than 30 times in volume (Freshwater et al. 2009) which accounts for their adeptness in undergoing periods of starvation of over 12 weeks without mortality, due to their capability of long-term fasting (Fishelson 1997; Morris 2009). Lionfish are nocturnal and most active during dawn and dusk (Green et al. 2011), which coincides with the peak activity of reefs where diurnal crustaceans are retreating and smaller nocturnal fishes are becoming active (Syngajewski 2004). Prey species in the Atlantic region are regarded as being naïve to lionfish predation strategies, resulting in lionfish having higher predation efficiencies in the invaded range (Albins and Hixon 2008).

Understanding how predators select prey can provide important knowledge on community structure and function. According to the optimal foraging theory (OFT), predators try to maximise the ratio between benefits gained and costs incurred (to locate, handle and process prey items) (Hambright 1991; Green and Cote 2014). Thus if all prey items are deemed equally profitable, it is expected that predators would consume prey in proportion to their abundance within the environment. However, more often this is not the case and prey are be consumed dispropotionately compared to their relative abundance. When selective predation occurs, it is thought to be a result of variation in morphological or behavioural characteristics of prey that subsequently affect encounter rates and handling time. Since prey assemblages vary within the invaded region, identifying which traits make prey more susceptible to predation can be integral when predicting the impacts of the lionfish invasion on native prey (Green and Cote 2014).

To determine the magnitude of ecological impacts of an invasive predator like a lionfish, it is essential to understand their interaction and effect on the native community and also how their arrival, establishment and dietary choices consequently affect the native community structure (Rilov and Crooks 2009; Muñoz et al 2011). However, it is also important to determine whether feeding behaviours and preferences are uniform throughout an introduced range so that further ecological impacts can be more accurately predicted and managed.

In this study I provide the first comprehensive assessment of lionfish diets in the southern Caribbean range, and compare lionfish diets between local reef environments, and with comparable analyses conducted in the Baahamas. Thus, the novelty of this study lies in the fact that it provides the first direct comparison of lionfish diets between islands within distinctly different habitats and also stages of the invasion timeline. Lionfish were first confirmed in 2005 within the Bahamas and in 2009 in Bonaire and Curacao. Understanding whether any traits of prey make them more vulnerable to lionfish predation will assist in predicting potential declines of local species and consequent impacts of the invasion. In order to accurately assess the impact on potential prey or competitors there is need for detailed knowledge of lionfish behaviour and feeding preferences (Meister et al. 2005, Ruiz-Carus et al. 2006; Muñoz et al. 2011) and how feeding may vary in different habitat types. Given that Bonaire, Klein Bonaire and Curacao are characterised by continuous fringing reef rather than discontinuous patch reef like the Bahamas, regional differences in lionfish feeding behaviour might be expected. Thus assessing whether lionfish feeding behaviour is similar across the invaded range was the main aim of this work and were assessed through the following hypotheses

H_1. The environmental differences that exist between the Bahamas and Bonaire are sufficient to induce systematic differences in lionfish diet.

H_2. The prey selectivity of lionfish in the Bahamas is different to Bonaire

H_3. Specific traits of prey increase their vulnerability of predation by lionfish

3.3 Methods

To assess whether lionfish feeding behaviour was similar throughout the invaded range, lionfish were collected within Bonaire, Klein Bonaire and Curacao. Subsequent to collection, all specimen were measured and weighed with stomach content and volumetric analysis being performed. To compare this study to other research within the invaded region, further dietary analyses (Index of Relative Importance, Index of Importance and Index of Preponderance) were performed. Furthermore, in order to make predictions on prey vulnerability, a trait based analysis was implemented and combined with REEF surveys to make predictions on the impact of lionfish to local populations.

3.3.1 Collections

Between October 26, 2009 and November 24, 2013, 11,161 lionfish ranging between 21 to 455 mm total length (TL) were collected and analysed in Bonaire (6,288), Klein Bonaire (2,743) and Curacao (2,130), making this one of the largest and most representative surveys of lionfish diets in their invaded habitat. Trained volunteer lionfish hunters collected all specimens using scuba gear at the dive sites surrounding Bonaire, Klein Bonaire and Curacao. Collections were achieved using hand nets, pole spears or the use of the Eradicating Lionfish Tool (ELF Tool) and caught specimens were stored in containment devices such as dry bags or the Zookeeper. Lionfish were collected every month of the year, with the smallest sample sizes occurring during December (n = 221) and the largest sample sizes in March (n = 2696). Collections were achieved between 07.00 to 22.00 with the majority (48%) taking place between 14.00 to 18.00.

3.3.2 Measurements

Upon capture or submission of specimens, data was collected on the date, time, location and depth of capture. All caught lionfish (N = 11,161) if not already dead were euthanized and then measured according to their standard length (snout to beginning of tail), total length (snout to end of tail) and wet weight when possible. All measurements were conducted either by the author or trained staff at CIEE Research Station Bonaire

3.3.3 Stomach content and volumetric analysis

Following visual analysis of the lionfish mouth area for regurgitation, specimens were dissected, the stomach severed and its contents examined. Stomach contents were gently rinsed in distilled water and identified to the lowest possible taxon using identification guides such as Humann and Deloach (2002a, 2002b), Victor (2006-15) and other identification software. After identification, individual prey items were counted and measured to the nearest mm, and relevant traits were assigned (Table 1). Prey length was converted to weight in grams using the allometric scaling function mass (g) = a * TL $(cm)^b$, where are and b are species specifc constants obtained from FishBase (www.fishbase.org). Volumetric analysis of prey by taxon was measured via water displacement and was determined for 4,658 lionfish stomachs. Prey specimens were first blotted dry on tissue paper and then inserted into a graduated cylinder where the water displaced was taken up via a graduated syringe for more accurate measure of their volume.

3.3.4 Dietary analysis

The contribution of individual prey taxa to the overall diet of lionfish was assessed via percent frequency of occurrence (%F); percent composition by number (%N) and percent composition by volume (%V). Such dietary measures like %F can give insight into population wide food habits (Cailliet 1977), whilst %N can provide valuable information on feeding behaviour (Macdonald and Green 1983) and %V can reflect nutritional value of diets (Macdonald and Green 1983). Although these measures can provide useful knowledge to understand diets (Assis 1996), when they are used individually, there can be biases. Generally numerical estimates such as %F or %N can overemphasize the importance of small, more abundant prey items which contribute very little to the bulk of the diet whilst %V tends to overemphasise larger, less abundant prey (Hynes 1950; Hyslop 1980; Gray et al. 1997).

As a result compound indices, which incorporate volume, number and frequency into a single measure, have been recommended since they can provide a more accurate representation of dietary importance whilst also enabling comparison (Cortes 1997). Thus for this study, in order to perform a robust assessment of prey importance and to be comparable with other studies on lionfish feeding ecology (e.g. Higgs 2009; Morris and Akins 2009; Layman and Allegeier 2012; Eddy et al. 2014), three indices of dietary importance were calculated. Index of Relative Importance (IRI), Index of Importance (IOI) and Index of Preponderance (IOP). The IRI is one of the commonly used indices for fish diet studies (Pinkas et al., 1971) since its method (IRI = %F x (%V + %N) seems to cancel out biases within individual components (Bigg and Perez 1985; Cortes 1997). The IOI is calculated based on %F and %W which means that biases in favour of heavier and less frequently found prey items are reduced (Hunt et al., 1998). The IOP uses %V and %F estimates to provide a more definite and measurable means for assessing diets since it gives a combined representation of occurrence and bulk in the diet (i.e. volume) (Natarajan and Jhingran 1961). The three indices are calculated as follows.

1. **Index of Relative Importance (IRI)**

$$IRI_a = F_a\,(N_a + V_a)$$

2. **Index of Importance (IOI)**

$$IOI_a = \frac{100 \cdot (F_a + V_a)}{\sum^{s}_{a=1} (F_a + V_a)}$$

3. **Index of Preponderance (IOP)**

$$IOP_a = \frac{F_a \cdot V_a}{\sum^{s}_{a=1} (F_a + V_a)}$$

Where:

a = species

s = number of prey species (in stomach)

F_a = the frequency of occurrence of species *a* *(in stomach)*

V_a = the proportion composition by volume of species *a*

N_a = the proportion composition by number of species

3.3.5 Trait based analysis

A functional or trait based approach has been recognised as a valuable means to make community ecology more predictable (Green and Cote 2014) by identifying particular traits which make prey more vulnerable to predation. Predictions were made by the author (Table 3.2) by investigating prey traits the author considered that would affect vulnerability to lionfish predation. These traits included body size, body shape, behaviour, armour, aggregrating behaviour and colour and some of these traits (body size, body shape and armour) were investigated in the study by Green and Cote (2014)

Table 3.2. Description of traits of prey consumed by lionfish

Trait	Description	Prediction
Body size	Length of prey item measured in cm	Prey items which are smaller in body size will be more vulnerable to predation
Body shape	Fusiform. Streamlined with pointed ends allowing fish to move through water quickly Compressiform. Laterally compressed with tall and thin body shape. Fish usually move with bursts of energy Filiform. Long and thin thread-like body structure Taeniform. Ribbon-like body structure Globiform. More irregularly-shaped body and fish is usually slow moving	Prey items with a shallower/more elongated body shape will be more vulnerable to predation
Behaviour	Bottom dwellers. Always associated with benthos Cryptic. Always partially hidden and associated with crevices and holes between coral heads and/or rocks Swimmers. Usually found within the water column or not specifically associated with the benthos and/or crevices and holes	Prey items not specifically associated with the benthos and/or crevices will be more vulnerable to predation
Armour	Presence or absence of defenses e.g. spines (dorsal, ventral, anal or pelvic), scalpels (on the base of tail) or other body deterrants	Prey items without physical or chemical defenses will be more vulnerable to predation
Aggregating behaviour	Are species found solitary, in pairs, in groups or in schools	Prey items which do not engage in schooling behaviour will be more vulnerable to predation
Colour	Whether the body colour is yellow, orange, red, blue, green, brown, black, silver or multicoloured	

3.3.6 REEF Surveys

Within the Tropical Western Atlantic Region, a Geographic Zone Report was generated for Bonaire (Geographic Zone Code 8503) between January 1, 1993 – 2014. During this time a total of 507 species were recorded within 166 sites where 19,841 surveys were conducted (11,080 Expert, 8761 Novice) and a total of 26,262 hours and 51 minutes spent underwater. Within REEF surveys, divers progress through 5 experience levels (Table 3.3) (Novice 1-3 and Expert 4-5) by continuous assessment through extensive species identification exams and based on the number of surveys completed (Pattengill-Semmens and Semmens 2003; Wolfe and Pattengill-Semmens 2013a). For the purpose of this research, only surveys conducted by experts were utilised.

Divers typically conduct these REEF surveys on their own or through organised field surveys. The Roving Diver Technique (RDT) is used whereby divers swim freely throughout the site whilst recording every observed fish species (Holt et al., 2013). At the end of each survey divers assign each recorded species one of four log10 abundance categories. single (1), few (2-10), many (11-100), abundant (>100) (SFMA) (Pattengill-Semmens and Semmens 2003; Wolfe and Pattengill-Semmens 2013a). According to Wolfe and Pattengill-Semmens (2013a), REEF summarises this data by reporting sighting frequency (SF) i.e. the fraction of dives when a specific species is observed, and log-density index (DEN) defined as.

$$DEN = \frac{S + 2F + 3M + 4A}{S + F + M + A}$$

Where, for a specific species, area and period,

S = Number of dives reporting Single (1)

F = Number of dives reporting Few (2-10)

M = Number of dives reporting Many (11-100)

A = Number of dives reporting Abundant (>100)

Table 3.3. Description of the five categories of REEF surveyors

Level	Designation	Description
1	Novice	This level includes all new REEF members who are learning the first X number of species
2	Novice	This level requires passing the Level 2 quiz (20-25 questions) with a minimum score of 80% and completion of 2 surveys
3	Novice	This level requires passing the Level 3 quiz (100 questions) with a minimum score of 80% and submission of 25 surveys prior to taking the test. Usually only includes adult stages of species and common species but no rare or cryptic species
4	Expert	This level requires passing the Level 4/5 quiz (200 questions) with a minimum score of 90% and submission of 35 surveys prior to taking the test. Requires general knowledge on life history phases of fishes along with rare and cryptic species
5	Expert	This level requires passing the Level 4/5 quiz (200 questions) with a minimum score of 95% and submission of 50 surveys prior to taking the test. Requires general knowledge on life history phases of fishes along with rare and cryptic species

This data along with other factors such as survey time, depth, temperature and any other environmental information are recorded on REEF datasheets to be returned to REEF headquarters (Pattengill-Semmens and Semmens 2003) where they are reviewed before the information is transferred to the permanent database and any obvious errors corrected and/or deleted and surveyors contacted if any irregular or unusual sightings were reported (Wolfe and Pattengill-Semmens 2013b).

3.4 Results

3.4.1 Diet composition

Lionfish across all study sites possessed a predominantly fish only diet (Bonaire. 63%, Klein Bonaire. 71% and Curacao. 71%), similar to reports from the Bahamas and other invaded Caribbean islands. A total of 10,945 prey items (7,383 fish and 3562 invertebrate) belonging to 29 families (11 invertebrate, 18 fish) were documented in the 11,161 lionfish stomachs examined within this study.

3.4.2 Prey composition

Eighteen families of teleosts, ten families of crustaceans, and one family of molluscs were represented in the diets of lionfish in this study. Teleost fish dominated the diets of lionfish within Bonaire, Curacao and Klein Bonaire (Figure 3.1). In Curacao, teleost fishes accounted for 97% by volume (%V), 72% by occurrence (%F) and 72% by number (%N) of lionfish diets whilst invertebrates accounted for 3%V, 28%F and 28%N. Within Bonaire, teleost fishes dominated lionfish diets comprising 92%V, 67%F and 59%N whilst invertebrates accounted for 7%V, 33%F and 41%N. Similarly in Klein Bonaire, teleost fishes dominated lionfish diets comprising 91%V, 56%F and 73%N whilst invertebrates accounted for 9%V, 40%F and 30%N.

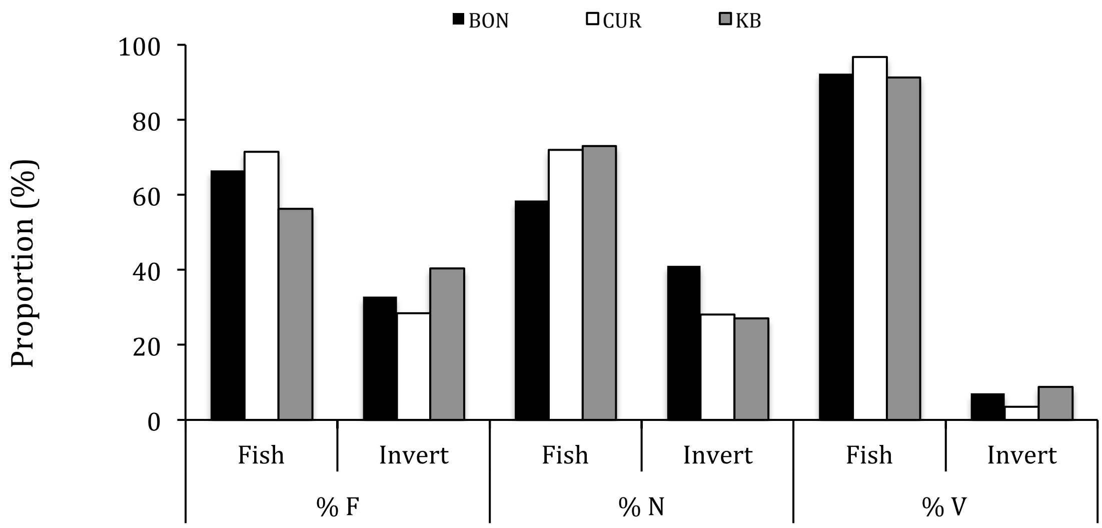


Figure 3.1. Comparison of the percent frequency, volume and occurrence of fish and invertebrates in lionfish diets

3.4.3 Diet vs size

Lionfish demonstrated clear size dependent feeding patterns. The importance of teleosts in the diet of lionfish increased with body size whilst the frequency of invertebrate-only and mixed diets decreased. The majority (61%) of lionfish larger than 400mm possessed empty stomachs (Figure 3.2). Taking into account the stomach content analysis of 8901 lionfish possessing prey within their stomach contents, 34% of the population had one prey item in their stomachs at the time of the capture, with 27% having empty stomachs and 20% having contents that were too digested for identification purposes.

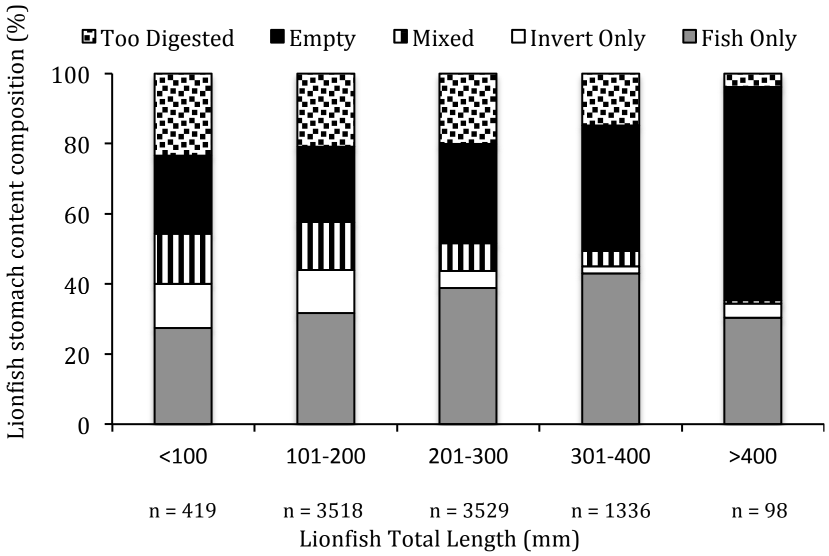


Figure 3.2. Lionfish diet composition at varying size classes

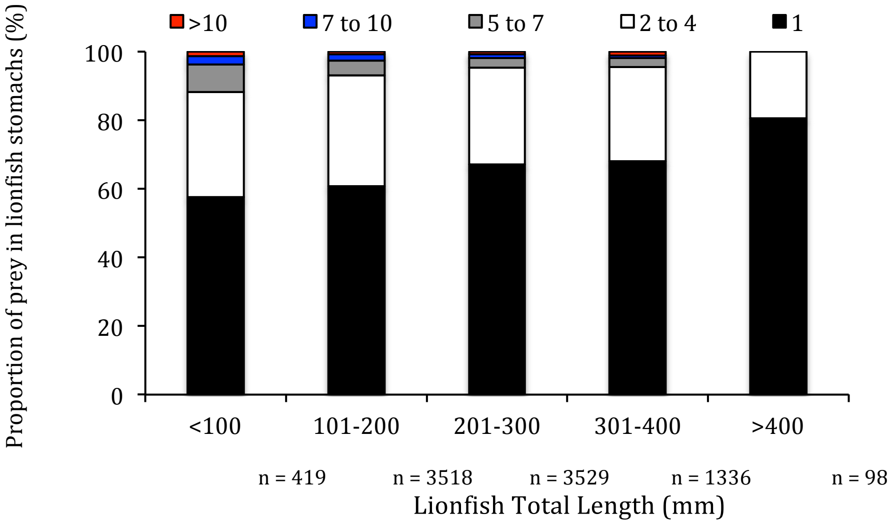


Figure 3.3. Number of prey items consumed at varying size classes

Just under 4% of the 8,901 lionfish analysed possessed >5 prey items within their stomach contents at the time of capture (Figure 3.3). Generally as lionfish increased in size, there was a decrease in the number of prey items consumed but a higher frequency of larger prey items in their diet (Figure 3.5). On an island basis, in Curacao there was a significant positive relationship between lionfish size and the number of prey the consumed (Zero-inflated Poisson regression, $P = <0.0001$), however the number of prey items consumed decreased as lionfish size increased in Bonaire (Zero-inflated Poisson regression, $P = <0.0001$) and Klein Bonaire (Zero-inflated Poisson regression, $P = 0.008$) (Figure 4.6). As lionfish increased in size, they consumed larger prey (GLM with Poisson distribution, $P=<0.0001$) (Table 3.5A). When the predator-prey mass ratio was taken into account, a positive relationship was found between lionfish mass and predator-prey mass ratio (Figure 3.4) (Table 3.5B).

The mean ratio of prey size (TL) to lionfish size (TL) was 0.132±0.004 standard error of the mean. The maximum prey size was 49.8% of the total length of lionfish, whereas the minimum prey size was 1.5%. Generally as lionfish increased in size (TL), the size of prey fish consumed also increased within diets in Bonaire, Klein Bonaire and Curacao. However, when examined taking body shape into account, this relationship was much stronger with the taeniform body shape (Linear Regression Model, $p < 0.0001$) (ribbon-like/elongated) as compared to fusiform and other (globiform and compressiform) body shapes (Figure 3.5C).

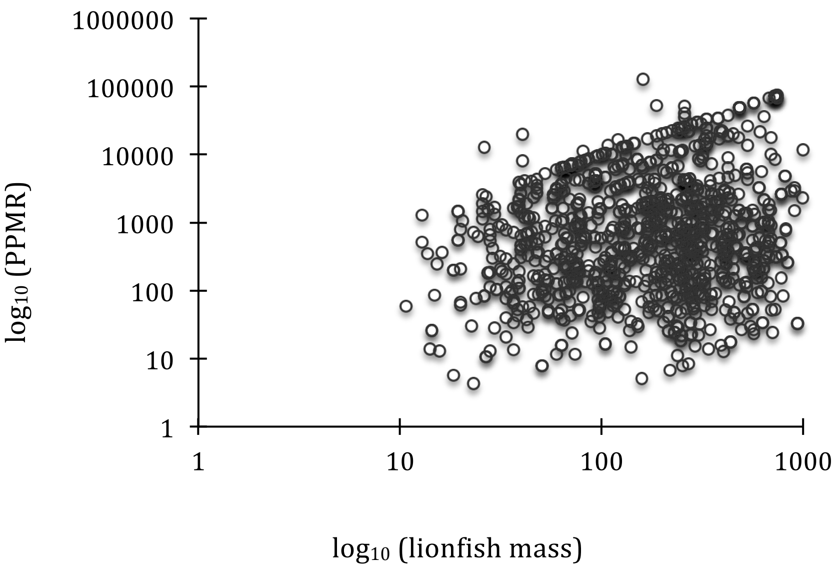


Figure 3.4. Predator-prey mass ratio (PPMR) of lionfish in Bonaire (n=1029). [Min PPMR = 4, Max PPMR = 127,791, Avg PPMR = 4118]. Mass measured in grams

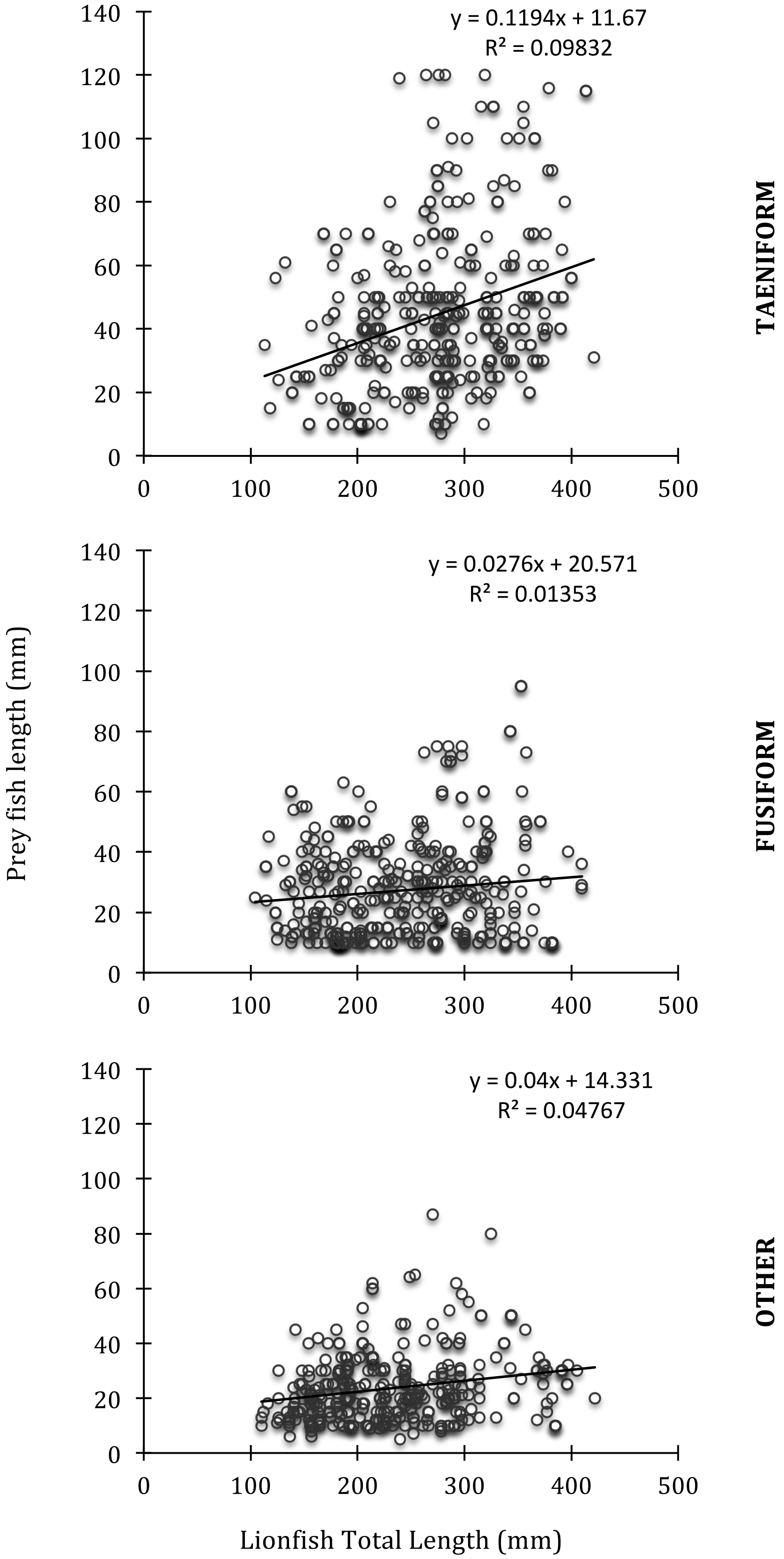


Figure 3.5. Size relationships based on the consumption of prey fish of varying body shapes by lionfish. Black line represents linear regression line. “Taeniform” refers to ribbon-like/elongated body shapes, “Fusiform” refers to body shapes that are streamlined with pointed ends whilst “Other” encompasses compressiform (laterally compressed with tall and thin body) and globiform (irregular shaped body) body shapes

Comparison to the Bahamas. Within this study, a total of 10,945 prey items were documented in the 11,161 lionfish stomachs examined in this study, an order of magnitude more than the 1,876 items documented from 1,069 stomachs examined in Bahamas (Morris and Akins 2009). Additionally, within this study, the maximum number of crustacean prey per lionfish was 29, whereas the maximum number of teleost prey was 42, compared to maximums of 50 invertebrates and 21 fishes reported in the Bahamas (Morris and Akins 2009). Within the Bahamas based on Morris and Akins (2009) the size of prey fish consumed increased very minimally as lionfish increased in size, with the mean total length of prey consumed fluctuating between 15 – 25 mm. However, within Bonaire, the minimum mean prey size consumed was larger and there was a greater increase in the size of prey fish consumed with the mean TL of prey consumed fluctuating between 24 – 65 mm (Figure 3.6). A significant positive relationship was found between lionfish total length and prey length (Linear Regression Model, df = 21, p <0.0001) (Table 3.5D) however the study location did not prove to be a significant factor (Linear Regression Model, df = 21, p = 0.07) (Table 3.5E).

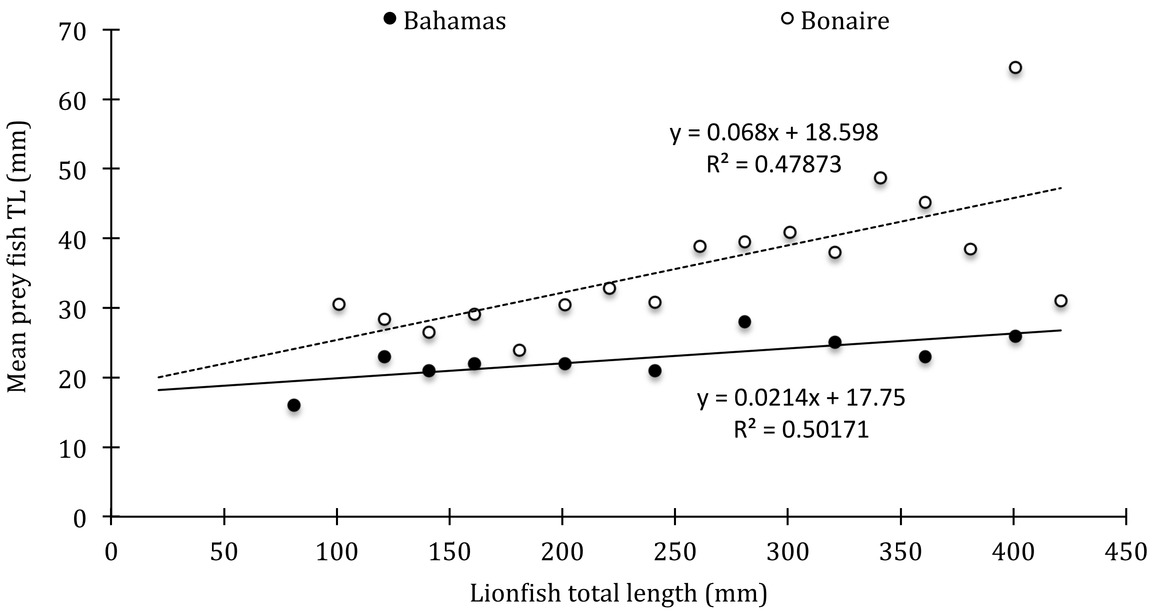


Figure 3.6. Mean fish prey size consumed by lionfish of varying sizes in Bonaire and Bahamas

Lionfish were captured between 07.00 – 22.00 in Bonaire and Bahamas, however there was considerable differences in stomach composition throughout the day within these two regions (Figure 3.7). Generally within Bonaire, between 07.00 – 16.00 (i.e. during daylight house); 70 - 85% of the lionfish caught had prey in their stomachs, but between 16.00 – 19.00 (twilight) this decreased to 57%. Furthermore at night, (19.00-22.00), 94% of lionfish caught contained prey in their stomachs. However within Morris and Akins' (2009) study, there was much higher fluctuation in the proportion of lionfish with prey in their stomachs. Between 08.00 – 12.00, there was a peak where 60 – 80% of the lionfish caught had prey in their stomachs, which was followed by the period of 12.00 - 13.00 where approximately only 10 – 20% of lionfish caught had prey in their stomachs. Furthermore after 18.00, there was a considerable decrease in the proportion of lionfish with prey in their stomachs, where

between 19.00 – 22.00 all lionfish caught had empty stomachs.

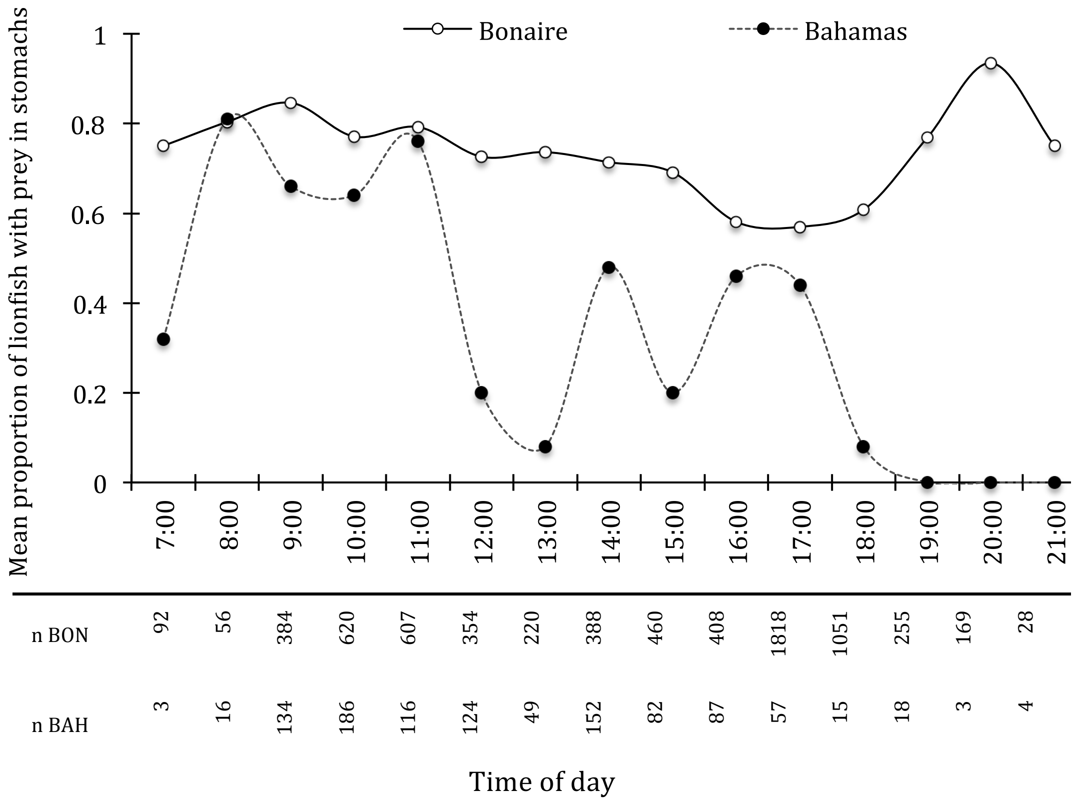


Figure 3.7. Proportion of lionfish stomachs containing prey throughout the day in Bonaire and Bahamas

3.4.4 Comparison of lionfish diet composition within the introduced range

Based on results from published research, lionfish generally possessed a fish dominated diet in terms of percentage frequency of occurrence (%F) and percentage composition by volume (%V) (Figure 3.8) however there were still differences amongst the different islands within the introduced range. In terms of %F, fish and invertebrates were more equally represented within lionfish diets in Bermuda, whereas within Curacao, Cuba, and the Bahamas, there was a greater disparity in representation. Similarly, like %F, Bermuda compared to the rest of the introduced region had a higher representation of invertebrates in terms of %V.

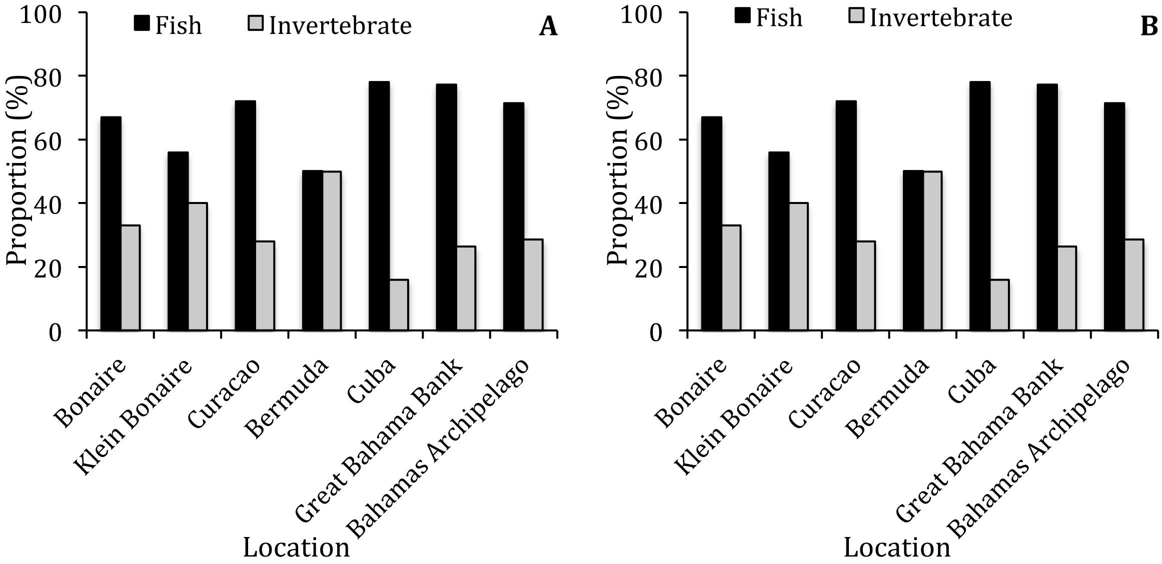


Figure 3.8. Comparison of lionfish diet composition within the introduced range according to (A) Percentage frequency of occurrence and (B) Percentage composition by volume. Black bars indicate the proportion of fish whilst grey bars indicate the proportion of invertebrates in lionfish diets.

3.4.5 Trait based selection

Lionfish fed on a wide array of prey items, of varying sizes and colours and possessing varying body shapes, traits and behaviours (Appendix B). Based on a GLM with a binomial distribution *[glm(formula = Freq.Diet ~ Freq.Reef, family = binomial, data = data)]* prey selection by lionfish appeared to be a negative density-dependent relationship whereby as the frequency on the reef increased, the frequency of these prey in lionfish diets decreased (Figure 3.9). However, this relationship was not statistically significant (GLM, df=50, p=0.206) (Table 3.5F). Since there was no clear pattern to lionfish dietary choices, the role of trait based selection was introduced, but based only on stomach content data, rather than both in situ and ex situ observations like Green and Côté (2014) where personal observations in the field were combined with stomach content analysis. This study found that specific characteristics (prey size, body shape, aggregation and cleaning behaviour) increased vulnerability to predation (Green and Côté (2014).

Within this study, traits like body shape, behaviour, presence of armour/defenses and aggregating behaviour did not have any statistically significant effect on selection, however prey colour did. By including prey's frequency on the reef in this analysis, the availability of prey colour was assumed to be uniform. Thus, with this influence of prey abundance in the environment being taken into consideration, *[glm(formula = Freq.Diet ~ Freq.Reef + Colour, family = binomial, data = data)]*; based on a GLM with a binomial distribution, there was negative selection occurring with considerably less prey within the multicoloured, blue and indigo colour spectrum being selected by lionfish (GLM, df=50, p = 0.00268) whilst those in the orange, red and yellow colour spectrum were positively more selected, however this was not significant at the 95% level (GLM, df=50, p = 0.07) (Table 3.5G). Within this study, lionfish were more likely to consume prey with a more elongated body shape rather than those with more dorso-ventrally flattened/irregular body shapes.

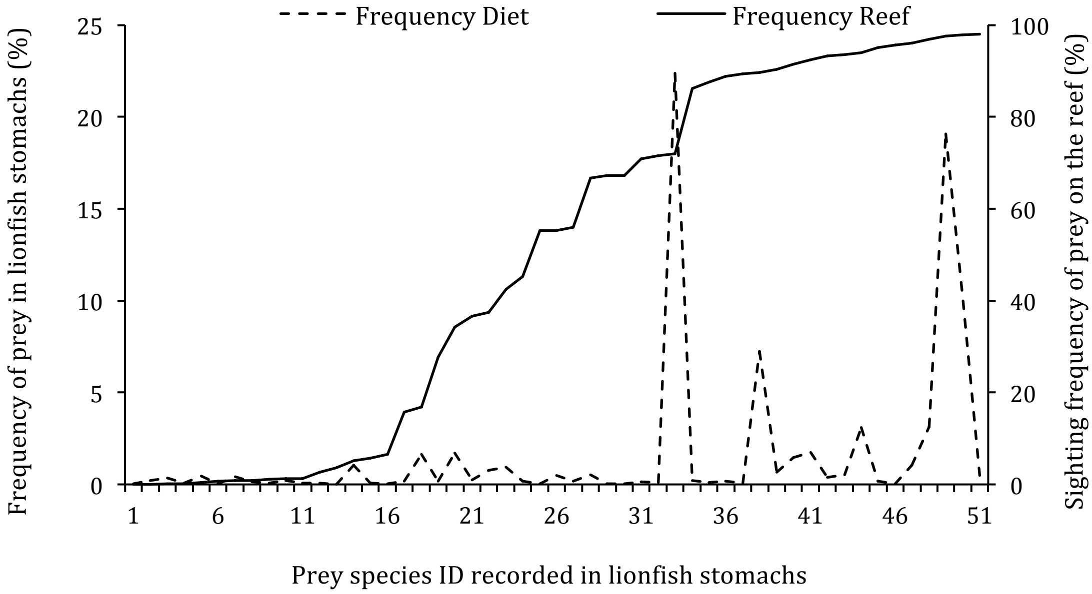


Figure 3.9. Comparison of the frequency of prey species recorded in lionfish stomachs to their frequency on the reef in Bonaire, Klein Bonaire and Curacao

ID	Scientific name	Common name	ID	Scientific name	Common name
1	*Centropristis ocyrus*	Bank sea bass	27	*Halichoeres maculipinna*	Clown wrasse
2	*Diplectrum formosum*	Sand perch	28	*Acanthurus chirurgus*	Doctorfish
3	*Coryphopterus punctipectophorus*	Spotted goby	29	*Neoniphon marianus*	Longjaw squirrelfish
4	*Tigrigobius macrodon*	Tiger goby	30	*Sargocentron coruscum*	Reef squirrelfish
5	*Synodus synodus*	Red lizardfish	31	*Cephalopholis fulva*	Coney
6	*Liopropoma mowbrayi*	Cave basslet	32	*Coryphopterus glaucofraenum*	Bridled goby
7	*Liopropoma carmabi*	Candy basslet	33	*Coryphopterus personatus*	Masked goby
8	Haemulonidae	Grunt	34	*Ocyurus chrysurus*	Yellowtail snapper
9	*Hypoplectrus randallorum*	Tan hamlet	35	*Halichoeres bivittatus*	Slippery dick
10	*Haemulon aurolineatum*	Tomtate	36	*Myripristis jacobus*	Blackbar soldier fish
11	*Haemulon striatum*	Striped grunt	37	*Stegastes diencaeus*	Longfin damselfish
12	*Ctenogobius saepepallens*	Dash goby	38	*Gramma loreto*	Fairy basslet
13	*Scorpaenodes caribbaeus*	Reef scorpionfish	39	*Serranus tigrinus*	Harlequinn bass
14	*Phaeoptyx pigmentaria*	Dusky cardinal	40	*Clepticus parrae*	Creole wrasse
15	*Apogon phenax*	Mimic cardinal	41	*Chromis cyanea*	Blue chromis
16	*Lutjanus analis*	Mutton snapper	42	*Stegastes planifrons*	Threespot damselfish
17	*Monacanthus tuckeri*	Slender filefish	43	*Acanthurus bahianus*	Ocean surgeonfish
18	*Liopropoma rubre*	Peppermint basslet	44	*Halichoeres garnoti*	Yellowhead wrasse
19	*Coryphopterus dicrus*	Colon goby	45	*Aulostomus maculatus*	Trumpetfish
20	*Malacoctenus triangulatus*	Saddled blenny	46	*Scarus taeniopterus*	Princess parrotfish
21	*Coryphopterus eidolon*	Pallid goby	47	*Sparisoma aurofrenatum*	Redband parrotfish
22	*Apogon binotatus*	Barred cardinal	48	*Thalassoma bifasciatum*	Bluehead wrasse
23	*Apogon maculatus*	Flamefish	49	*Stegastes partitus*	Bicolor damselfish
24	*Apogon townsendi*	Belted cardinal	50	*Chromis multilineata*	Brown chromis
25	*Gnatholepis thompsoni*	Goldspot goby	51	*Sparisoma viride*	Stoplight parrotfish
26	*Amblycirrhitus pinos*	Red-spotted hawkfish			

Table 3.4. Comparison of the top ten rankings of prey families in lionfish diets based on 3 indices of dietary importance in the Bahamas, Bonaire, Klein Bonaire and Curacao

RANK	BAHAMAS (n=706)	BONAIRE (n=1883)	KLEIN BONAIRE (n=1493)	CURACAO (n=1282)
		INDEX OF RELATIVE IMPORTANCE		
1	Gobiidae	Pomacentridae	Pomacentridae	Pomacentridae
2	Labridae	Labridae	Gobiidae	Gobiidae
3	Grammatidae	Grammatidae	Apogonidae	Labridae
4	Apogonidae	Apogonidae	Rhynchocinetidae	Rhynchocinetidae
5	Pomacentridae	Gobiidae	Labridae	Apogonidae
6	Serranidae	Serranidae	Serranidae	Serranidae
7	Blennidae	Blenniidae	Scaridae	Scaridae
8	Atherinidae	Rhynchocinetidae	Grammatidae	Grammatidae
9	Mullidae	Scaridae	Mysidae	Blenniidae
10	Monocanthidae	Lutjanidae	Palaemonidae	Stomatopodidae
		INDEX OF IMPORTANCE		
1	Labridae	Pomacentridae	Pomacentridae	Pomacentridae
2	Pomacentridae	Grammatidae	Gobiidae	Labridae
3	Gobiidae	Labridae	Apogonidae	Gobiidae
4	Grammatidae	Apogonidae	Rhynchocinetidae	Rhynchocinetidae
5	Mullidae	Serranidae	Labridae	Apogonidae
6	Serranidae	Gobiidae	Serranidae	Serranidae
7	Apogonidae	Blenniidae	Scaridae	Blenniidae
8	Blennidae	Lutjanidae	Grammatidae	Scaridae
9	Atherinidae	Scaridae	Mysidae	Grammatidae
10	Monacanthidae	Rhynchocinetidae	Blenniidae	Stomatopodidae
		INDEX OF PREPONDERANCE		
1	Gobiidae	Pomacentridae	Pomacentridae	Pomacentridae
2	Labridae	Labridae	Gobiidae	Gobiidae
3	Grammatidae	Grammatidae	Apogonidae	Labridae
4	Apogonidae	Apogonidae	Rhynchocinetidae	Rhynchocinetidae
5	Pomacentridae	Serranidae	Labridae	Apogonidae
6	Serranidae	Gobiidae	Serranidae	Serranidae
7	Blennidae	Blenniidae	Scaridae	Grammatidae
8	Atherinidae	Scaridae	Grammatidae	Scaridae
9	Mullidae	Lutjanidae	Mysidae	Blenniidae
10	Monacanthidae	Rhynchocinetidae	Blenniidae	Stomatopodidae

3.4.6 Comparison of prey family rankings of lionfish diets in Bahamas, Bonaire, Klein Bonaire and Curacao

Across islands, there was fluctuation in the ranking of the top families of teleost prey for all three indices (IRI, IOI, IOP) (Table 3.4). Since species ranking data was not available for the Bahamas, comparison of the overall ranking of families within Bahamas, Bonaire, Klein Bonaire and Curacao was conducted. (full species data for all families recorded in lionfish diets within this study are summarised in Appendix B). This revealed that the top seven families were similar in composition but different in ranking. Within the Bahamas, families such as Atherinidae and Mullidae featured within the top ten rankings, however these families were not represented in any lionfish diets within Bonaire, Klein Bonaire and Curacao. Across all three dietary indices, the highest-ranking teleost families in lionfish diets in the Bahamas, Bonaire, Klein Bonaire and Curacao were Pomacentridae, Gobiidae, Labridae, Apogonidae and Grammatidae.

Table 3.5. Summary of outputs from models performed for analysis of aspects of lionfish feeding ecology within this study. Significance codes are represented by. 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	Model script	Coefficients				
A	*model<-*		Estimate	Std. Error	z value	Pr(>|z|)
	zeroinfl(No.Prey~TL +	(Intercept)	0.7097098	0.0331444	21.413	< 2e-16 ***
	Island | Time.cat,	TL	-0.0016093	0.0001533	-10.500	< 2e-16 ***
	data=data)	IslandCUR	0.2278828	0.0409034	5.571	2.53e-08 ***
		IslandKB	-0.0698225	0.0264025	-2.645	0.00818 **
B	*glm(formula = Freq.Diet*		Estimate	Std. Error	z value	Pr(>|z|)
	~ Freq.Reef + PPMR,	(Intercept)	-2.864e+00	6.034e-01	-4.746	2.08e-06 ***
	family = binomial, data	Freq.Reef	8.980e-01	6.761e-01	1.328	0.184
	= data)	PPMR	5.003e-06	3.597e-06	1.391	0.164
C	*lm(formula = LF.TL ~*		Estimate	Std. Error	t value	Pr(>|t|)
	Prey.Length +	(Intercept)	246.3629	6.2781	39.242	< 2e-16 ***
	(Body.Shape), data =	Prey.Length	0.6628	0.1158	5.725	1.5e-08 ***
	data)	CodeOther	48.4482	17.4973	2.769	0.005763 **
		CodeTaeniform	-20.1546	5.2825	-3.815	0.00014***
D	*lm(formula = Avg.LF.TL*		Estimate	Std. Error	t value	Pr(>|t|)
	~ Avg.Prey.TL, data =	(Intercept)	74.687	53.081	1.407	0.17172
	data)	Avg.Prey.TL	5.599	1.612	3.474	0.00189 **
E	*lm(formula = Avg.LF.TL*		Estimate	Std. Error	t value	Pr(>|t|)
	~ Avg.Prey.TL + (Region),	(Intercept)	49.788	52.440	0.949	0.351867
	data = data)	Avg.Prey.TL	7.983	2.007	3.977	0.0005***
		RegionBON	-78.906	42.659	-1.850	0.076712 .
F	*[glm(formula = Freq.Diet*		Estimate	Std. Error	z value	Pr(>|z|)
	~ Freq.Reef, family =	(Intercept)	-2.7602	0.5827	-4.737	2.17e-06 ***
	binomial, data = data)	Freq.Reef	0.8297	0.6566	1.264	0.206
G	*glm(formula = Freq.Diet*		Estimate	Std. Error	z value	Pr(>|z|)
	~ Freq.Reef +	(Intercept)	-9.8090	4.5534 -	2.154	0.0312 *
	Main.Colour, family =	Freq.Reef	8.5074	4.6798	1.818	0.0691 .
	binomial, data = data)	Main.ColourBlue	-2.0794	1.4259	-1.458	0.1448
		Main.ColourBrown	-0.9304	0.3870	-2.404	0.0162 *
		Main.ColourIndigo	-0.5610	0.6060	-0.926	0.3546
		Main.ColourMulti	-1.6872	10.7135	-0.157	0.8749
		Main.ColourOrange	2.4196	1.2407	1.950	0.0512 .
		Main.ColourRed	4.3689	8.0941	0.540	0.5894
		Main.ColourWhite	-3.9282	16.3948	-0.240	0.8106
		Main.ColourYellow	-1.8774	0.9292	-2.020	0.0433 *

3.5 Discussion

The large number of prey families (11 invertebrate, 18 fish) and species (13 invertebrate, 55 fish) represented within lionfish stomach contents suggest a very generalist (Morris 2009, Morris and Akins 2009), but fish-dominated diet in Bonaire, Klein Bonaire and Curacao. Fish dominated diets are usually the most optimal because of the high-energy content and minimal waste due to the similarity of protein, lipid, mineral and vitamin composition (Weatherley and Gill 1987; Forseth and Jonsson 1994; Jonsson et al. 1999) and their larger size increases encounter rates (Persson 1987; Noakes and Godin 1988; Paradis et al. 2006).

When compared to Bonaire, it was found that lionfish in the Bahamas did not consume increasingly larger prey as their body size increased. This could explain the great differences in reported diet in the Bahamas as compared to Bonaire. Within the Bahamas, lionfish are reported to possess very gluttonous feeding habits (Table3.1), but within Bonaire, as lionfish increased in size, the general size of the prey they consumed also increased, whilst the number of individual prey items generally decreased. This meant that as lionfish increased in size, they were generally eating larger, more profitable prey but in smaller quantities, but within the Bahamas, since the prey items being consumed were on average smaller; there would be a need for consumption of larger quantities of smaller prey items. Usage of the predator-prey mass ratio (PPMR) has been long established in explaining the movement of energy within marine food webs (Sheldon et al. 1972; Moloney et al. 1991; Barnes et al. 2010). Thus, a finding where effective PPMR increased with body size suggests that predators may be feeding down the food chain on smaller prey that may lead to greater total production (Barnes et al. 2010). Food webs tend to be most stable when predators are bigger than their prey (Tucker and Rogers 2014).

Prey profitability depends on its total energy content when compared to the time and energy resources required for detection, pursuit and handling (Hart 1993; Jonsson et al. 1999). The higher proportion of bigger, more profitable prey in lionfish diets as body size increases is common amongst tropical piscivores (Kahilainen and Lehtonen 2003; Villaseñor-Derbezi and Herrera-Pérez 2014), where there are shifts from invertebrate-dominant diets by small juveniles to predominantly fish diets in sub-adult and adults (Winemiller 1989). As a fish increases in size, piscivorous rather than invertebrate diets are more energy efficient (Paradis et al. 2006). Furthermore, it has been established amongst invasive species that the size of prey consumed increases with predator body size (Grosholz and Ruiz 2003; Muñoz et al. 2011) since this allows for maximum growth to be attained (Wootton 1990; Jonsson et al. 1999). However within the Bahamas, prey profitability may not have been the factor governing lionfish dietary choices, but instead prey availability. The Bahamas, in addition to being characterised by discontinuous patchy reef habitats, also has ongoing intensive fishing and tourism. Reduced biodiversity in disturbed, less complex habitats could affect the variety of prey available and also the size (e.g. dominated by juveniles). Furthermore, the concept of feast vs famine feeding suggests that under fluctuating prey availability, predators feed excessively and store energy when food is abundant and then utilise these resources during times of scarcity (Wang et al. 2006; Armstrong and Schindler 2011). Lionfish are physiologically adapted to this feast vs famine feeding strategy since their stomachs can expand to more than 30 times in volume (Freshwater et al. 2009) and they are capable of long-term fasting and undergoing periods of starvation of about 12 weeks without mortality (Fishelson 1997; Morris 2009). Thus it could be hypothesized that within a less ecologically disturbed environment like Bonaire or Curacao, where there is a constant availability of prey of varying sizes, there is no need for this feast vs famine strategy.

Additionally there were considerable differences in the proportion of lionfish with prey in their stomachs in Bonaire and the Bahamas, which might be an indication of differences in foraging behaviours and also their peak feeding times. Based on reports from the Bahamas, lionfish are renowned for being inactive during the day especially in times of high sunlight (12.00 – 14.00) and also at night (Green et al. 2011), but have peak feeding bouts at dawn and dusk (Cure et al. 2012; Bernal et al. 2014). The feeding behaviours revealed in the Bahamas were considerably different to Bonaire, not only in terms of the time of peak and minimal activity but also in terms of the proportion of lionfish with prey in their stomachs which was generally higher in Bonaire as compared to the Bahamas. Based on first-hand observations with Bonaire, lionfish were most active at dusk, however lionfish captured at this time tended to have empty stomachs as they had just began feeding activities. As a result the majority of lionfish caught at night had recently consumed prey within their stomachs as a result of their high feeding activity at dusk.

The variation in lionfish feeding behaviour could potentially be a result of the differences between habitat structure in the Bahamas as compared to Bonaire. By inhabiting patchy, discontinuous reefs, lionfish in the Bahamas might have different foraging habits to those on continuous fringing reefs in Bonaire. Although lionfish are renowned as being sedentary (Fishelson 1975; Green et al. 2011) and having high site fidelity (Layman and Allegeir 2012; Bacheler et al. 2015), there have been many reports of extensive movements by lionfish (Claydon et al. 2012; Jud and Layman 2012). On continuous reefs lionfish movements of up to 50 m were recorded, but on patch reefs these movements extended to up to 800 m, with a maximum movement documented at 1.38 km (Tamburello and Côté 2014). Lionfish possess traits that enable them to withstand long-distance dispersal, such as their relatively large body size, and their morphology which enables occasional active swimming (Tamburello and Côté 2014).

Due to their highly adaptable nature and generalist feeding strategy, a wide array of prey items, of varying sizes, colours, body shapes, behaviours and ecological roles were represented within lionfish diets. Based on stomach content analysis, lionfish do not appear to have any strict feeding selectivity but exhibit weak negative density-dependent feeding and feed more on rarer rather than abundant species. Since there was no clear pattern to lionfish dietary choices, the role of trait-based selection was introduced to determine whether any attributes could make prey species more vulnerable to predation. A study by Green and Côté (2014) found that characteristics such as prey size, body shape, aggregation and cleaning behaviour made prey more vulnerable to predation.

Owing to gape limitation, it was not surprising that lionfish were more likely to consume prey with a more slender/elongated (taeniform, fusiform, filliform) body shape rather than those with more dorso-ventrally flattened/irregular body shapes (compressiform, globiform). For a gape-limited predator like lionfish, the costs expended with consuming prey, grow with prey body depth (Nilsson and Brönmark 2000; Green and Côté 2014). Thus it is beneficial for gape-limited predators to focus on prey considerably smaller than their maximum gape limit (Einfalt and Wahl 1997; Nilsson and Brönmark 2000; Green and Côté 2014). Furthermore, lionfish had the highest selectivity for prey within the orange, red and yellow colour spectrum, but the lowest for those in the blue and indigo colour spectrum. Within the ocean, red light is most preferentially absorbed, violet to a lesser extent and blue the least (Losey et al. 1999), but how this affects lionfish prey selection remains a mystery. Whether this observation is a result of lionfish exhibiting visual selectivity or rather is purely coincidental remains unknown, but further research into whether lionfish perceive colour or are visual predators is necessary.

Green and Côté (2014) suggested that small, non-cleaner, solitary and shallow-bodied species were more selectively consumed whereas this study suggested a preference for slender/elongated shaped fish within the orange, red and yellow colour spectrum. Based on findings from this research, species such as *Apogon townsendi, Apogon binotatus, Apogon phenax, Apogon maculatus, Halichoeres garnoti, Lipoproma mowbrayi, Thalassoma bifasciatum* and *Serranus tabacarius* appear to be potentially vulnerable, thus it would be wise to monitor these populations, but also consider these specific species attributes as bait for passive lionfish removal devices such as traps.

Cerino (2010) revealed that the diet composition of lionfish is variable and sometimes correlated with local species availability. Though there was some similarity to lionfish diets within the Bahamas based Morris and Akins' (2009) study in terms of prey composition and ranking, there were some noticeable differences. Firstly, Pomacentridae ranked at the top of diets from Bonaire, Klein Bonaire and Curacao, however ranked considerably lower (5) in the Bahamas. The abundances of species within this family are similar in both regions, thus there is no ecological jurisdiction for this selectivity. Furthermore families such as Atherinidae and Mullidae featured in the top 10 ranking in Bahamas, but not a single individual was recorded within the 11,161 lionfish examined during this study. Both of these families are abundant within Bonaire, Klein Bonaire and Curacao, but the reason for the lack of their selection, along with the differences in predation of Pomacentridae by lionfish in Bahamas remains a mystery. The selectivity observed within this study could simply be a random feat but these differences in lionfish feeding preferences throughout the invaded region can have important consequences.

The fact that lionfish possess a generalist diet can be a blessing and a curse at the same time. The lack of specialization on any individual or few species means there is limited risk that lionfish will drive an entire species to extinction immediately. However their generalist nature can be dangerous since it means that lionfish are able to exploit more prey species as compared to native predators. The lionfish's successful generalist diet is enabled by their wide repertoire of feeding strategies (Whitfield et al. 2007; Freshwater et al. 2009; Albins and Lyons 2012) coupled with the fact that local prey do not recognize them as predators (Albins and Hixon 2008; Maljkovic and Leeuwen 2008; Morris 2009). Studies have suggested that native prey are naïve to invasive lionfish possibly because of its distinct colouration and feathery pectoral fins and are not threatened as they may perceive it as a feather duster worm or a floating bit of algae (Albins and Hixon 2013; Kindinger 2014), thus allowing lionfish to have higher predation efficiencies in the invaded range compared to its native range (Albins and Hixon 2008).

3.6 Conclusion

Although lionfish are renowned throughout their invaded range for having a generalist, fish-dominated diet, there were still some important differences revealed when comparisons were made between this study and the Bahamas. Although the rankings of prey families within lionfish diets in the Bahamas, Bonaire, Klein Bonaire and Curacao were similar in terms of composition, there were some differences in ranking. Furthermore, lionfish within this study when compared to the Bahamas consumed fewer prey items, which was found to be related to prey selectivity of lionfish within the Bahamas. As lionfish increased in size within this study, they consumed increasingly larger prey items; however in the Bahamas the size of prey consumed generally remained constant even as lionfish grew in size. Furthermore lionfish in the Bahamas had greater fluctuations in their feeding activities that might be related to environmental conditions within the Bahamas and the need to forage between patches. Within this study, lionfish had a relatively constant diet, typical of any other native reef fish, whereas in the Bahamas there were more fluctuations in the quantity of prey consumed as well as the frequency leading to a perceived voracious and gluttonous type diet. Furthermore it was found that lionfish exhibited some form of trait based selection and that there was especially a preference for prey with a slender, elongated body shape, within the yellow/orange colour spectrum, and a lack of chemical or physical defences. This research revealed the need to consider the impacts of the lionfish invasion on a more local scale. This research also unveiled that the feeding behaviours and preferences of lionfish are not uniform throughout their introduced range and has also provided further insight into how to more accurately predict their impacts.

Chapter 4: AN ANALYSIS OF THE EFFICIENCY AND EFFECTIVENESS OF LIONFISH MANAGEMENT IN THE INVADED REGION

4.1 Abstract

Since their introduction to the Caribbean, lionfish have continually grown in size, exceeding densities and sizes from the native range. Although considerable achievements have been made with limiting their growth thus far, with existing management tools and techniques, it is unlikely that lionfish will be completely eradicated. Lionfish management strategies vary in the promptness of their response, education and awareness schemes enacted as well as the tools and groups utilised for removal. Within this study, through a literature review and recommendations made by managers, strategies applied throughout the Caribbean were evaluated based on their benefits and limitations in order to make recommendations for areas not yet/early in the invasion timeline. Additionally, the available methods and tools currently being used for lionfish removal were also assessed in terms of their advantages and disadvantages and considering cost-effectiveness. Finally removal activities were assessed by examining the number of lionfish removed according to the effort invested and evaluated in terms of its efficiency and suggestions were made on when and how often to remove lionfish. This study revealed that targeted removals by divers using hand held spears and zoo-keepers was the most efficient and effective method especially when focused at a crepuscular time like dusk when lionfish are most active and more removals can achieved before lionfish have had a chance to feed. This study also reinforced the importance of a top-down, prepared and rapid response whilst highlighting the value of education and social media to successful lionfish control.

4.2 Introduction

Invasive species have been regarded as growing contributors to global biodiversity loss (Carlton and Geller 1991; Carlton 1996a; Ruiz et al 1997; Grosholz et al. 2000; Biggs and Olden 2011; Lonnstedt and McCormick 2013; Thresher et al. 2014). By suppressing native species populations and further altering habitats and ecosystems, invasive species have contributed to the imperilment of nearly half of the plants and animals now considered rare, threatened or extinct (Chornesky and Randall 2003; Armon 2015; Montgomery et al. 2015). Invasive species can affect local ecosystems in a variety of ways, but the impacts are generally effected by a complex but intricate relationship between invader attributes and the receiving environment (Strayer et al. 2006; Ricciardi et al. 2013; Thomsen et al. 2011). Thus gaining this knowledge of which attributes makes an invader more successful as well as what makes environments more susceptible to invasion is key to successful management. Within the United States, the environmental damage and the associated economic losses caused by invasive species have been reported to exceed US$1.4 trillion annually (Pimental et al., 2001; Hoddle 2002; Strayer et al. 2006; Frazer et al. 2012) and this damage manifests itself via a reduction in biodiversity, modification of trophic structures, and the overall crippling of healthy ecosystems (Hoddle 2002).

Given the great costs associated with invasive species, effective management is essential (Caplat and Coutts 2011) and is underpinned by understanding which factors result in successful invasions (Garcia-Berthou 2007). Prevention is generally accepted as the most effective method of management; once a species is established, further control can be very costly, and is often less effective (Mehta et al. 2007; Gallardo and Aldridge 2013; Roy et al. 2014; Saxena 2015) (see Figure 1.2). However, if the introduction of an invasive species is not prevented, early detection and rapid response is the next best option (Simberloff et al. 2005). Within the United States, Caplat and Coutts (2011) suggested that for every USD $1 invested in early control and prevention; an average of USD $17 was returned in prevented expenditure.

As the invasion timeline proceeds, successful eradication becomes increasingly difficult and expensive (Simberloff et al. 2000; Simberloff 2003; Olson and Roy 2005; Figure 4.1). The costs of removing the final 1% of an invasive population is often much higher than the removal of the initial 99% (Simberloff 2003) since detection at low population levels is very challenging unless there is highly apparent damage (Mehta et al. 2007). Unlike terrestrial invasions, the available experience and techniques to handle marine invasions are limited (Bax et al 2001; Secord 2003; de Leon et al. 2013) thereby explaining why few marine invasive species have been completely eradicated from their non native range (Culver and Kuris 2000; Genovesi 2005; de Leon et al. 2013). Within marine systems, eradication is exceptionally challenging given the connected nature and vastness of the oceans (Bax et al. 2001; Simberloff et al. 2000; Thresher and Kuris 2004), which highlights the need for a more regional/global effort towards invasive species management (Bax et al. 2003; Hewitt et al. 2009; de Leon et al. 2013). The successful management of any invasive species is only as strong as its weakest point of control and should include a combination of strategies to detect, monitor and control populations (Mehta et al. 2007; Burgiel 2014).

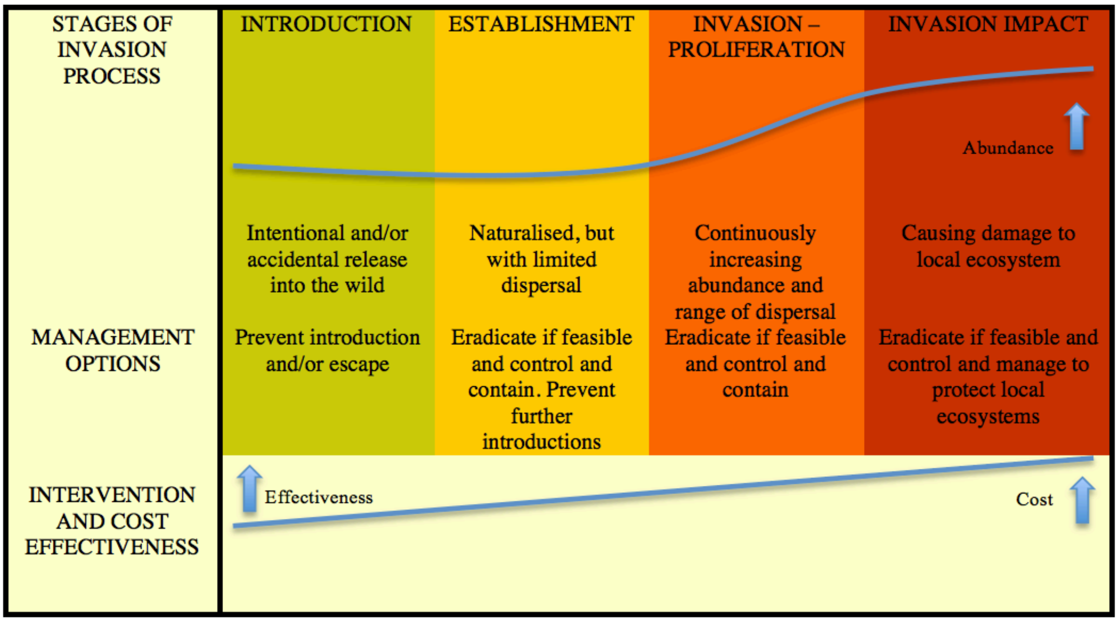


Figure 4.1. Management options during different stages of the invasion process (Invasive Species Council, 2014)

Lionfish were first introduced to the invaded region in the mid 1980s via unintentional and/or intentional releases from aquaria (Morris 2009). Capitalizing on an effective dispersal system whereby thousands of eggs are released in a gelatinous mass several times a month, lionfish have colonized approximately 2.8 million square kilometers within the invaded region (Betancur et al. 2011; Morris et al. 2012). Their generalist diet and habitat requirements, rapid growth rate and voracious appetite coupled, with their lack of natural enemies, have presented them with an opportunity to exert substantial impacts on the already fragile ecosystems within the Caribbean and invaded region (Albins and Hixon 2012; Green et al. 2012; Côté et al. 2014). Since their establishment, a variety of management strategies have been employed in an attempt to limit their spread (Arias-Gonzales et al. 2011; Morris 2012; Johnston and Purkis 2015). There have been diverse responses, education strategies, methods and tools applied to control lionfish, all with various success rates. Thus, there is need to assess, understand and determine which aspects of lionfish management have been the most effective and efficient in order to be successful in controlling future populations.

When managing invasive species, there is need to understand the area to be managed (Crooks and Soule 1999; Allendorf and Lundquist 2003). Within Bonaire and Curaçao there is great variability in lionfish removal with regards to the accessibility, ease, magnitude, frequency of and motivation for hunting. Bonaire and Curaçao are considered to be shore-diving paradises as the west coasts are well sheltered and generally offers much simpler and easier entries to dive sites, accounting for higher, and more regular hunting effort. However, the east coasts are considerably less sheltered; meaning that divers must either tolerate the adverse conditions or wait for a wind reversal that brings calmer conditions. Conditions on the east coasts thereby reduce the ease, accessibility, frequency and magnitude of diving. Klein Bonaire (located 400 m from Bonaire) and Klein Curaçao (located 24 km from Curaçao), are accessible only via boat, and therefore receives an infrequent and lower hunting effort. Furthermore, no diving is allowed in the Playa Frans Reserve and the Karpata Reserve areas in Bonaire and they remain closed to hunting for the majority of the year with the exception of annual or bi-annual events where approximately 20 volunteers are permitted between set hours and under guidance.

Understanding these differences in lionfish removal effort and the consequent impacts on the population can help to enhance the effectiveness of management strategies. The overall aims of this study were to assess the management strategy applied in Bonaire and improve the understanding of the effectiveness and efficiency of strategies for lionfish removal. More specifically, the purposes of this study were. (1) to determine what is the most efficient time for lionfish removal; (2) to determine which size and/or sex removal efforts should be best focused upon; (3) to determine how often to conduct lionfish removal efforts; (4) to examine which education and control strategies are most efficient and have proven most cost effective for lionfish management; and (5) to conduct a cost-benefit analysis on the tools used for lionfish removal.

4.3 Methods

4.3.1 Collections

Collections were achieved using hand nets, pole spears or the use of the Eradicating Lion Fish Tool (ELF Tool) and captured lionfish were stored in containment devices such dry bags or the Zookeeper. Within Bonaire, lionfish were collected and analysed every month of the year between October 26, 2009 and November 24, 2013 between the hours of 07.30 to 23.00. At Curaçao collections occurred between April 8th 2012 and September 13th, 2013, mostly from annual lionfish tournaments and opportunistic collections. Klein Bonaire, collections occurred between February 11th and May 6th 2012; February 9th – June 15th 2013 and August

21st - October 23rd 2013. Klein Bonaire represented an area with minimal hunting which allowed for uninterrupted studies on lionfish size, abundance and density to be conducted and compared to other areas of varying hunting pressure such as Curaçao and the No-Diving Reserves on Bonaire. Furthermore, conducting the study at dusk and night also offered important value as infrequent hunting occurs at this time but also because they are suggested to be most active at this time period (Fishelson 1975; Green and Côté 2011).

At Klein Bonaire, 9 dives were conducted at dusk (starting time ~17.15) with a further eight dives at night (starting time ~19.00). At dusk, a drift dive was completed, with buddy pairs being dropped off at various starting points between 2 dive sites so that a depth profile extending to 40m could be covered. Following a surface interval, the night dive was conducted with divers diving in opposite directions (north and south) of the moored boat. On either side, one buddy pair would cover the deeper profile whilst the other buddy pair covered the shallower profile. These dusk surveys were repeated in 2013 with 13 dives between February 9 – June 15 (2013A) and another 13 dives between August 21 – October 23 (2013B) with the aim being to determine the effectiveness of lionfish removal one year after removal (2013A), and then after a six- month period (2013B).

4.3.2 Catch Per Unit Effort (CPUE)

Following dives for collection of specimens, all divers were required to submit data regarding their maximum depth, general lionfish depth, total bottom time, number of lionfish seen, number of lionfish caught, number of shooters and number of spotters, in order to determine the catch per unit effort as in Frazer et al. (2012). Additional data on lionfish aggregation and behaviour was also collected. CPUE was calculated as the number of lionfish removed by divers, divided by divers' total bottom time (Frazer et al. 2012).

4.3.3 Measurements, visual examination and stomach content analysis

Upon capture or submission of specimens, data were collected on the date, time, location and depth of capture. All caught lionfish if not already dead were euthanized and then measured according to their standard length (snout to beginning of tail), total length (snout to end of tail) and wet weight when possible. All measurements were conducted either by The author or trained staff at CIEE Research Station Bonaire. Lionfish were then dissected by making an incision just above the anal fin, and cutting towards the throat (Green et al. 2012). The gonads were visually examined according to shape and colour as suggested by Green et al (2012). The sex of lionfish was recorded (Figure 4.2) as immature male (M1), spawning capable male (M2), early developing female (F1), developing female (F2), spawning capable female (F3), actively spawning female (F4) and unknown (X) which was either too young or too badly damaged for the sex to be determined. The stomach was severed from the lionfish and its contents examined. Stomach contents were gently rinsed in distilled water and identified to the lowest possible taxon by The author using identification guides such as Humann and Deloach (2002a, 2002b) and Victor (2006-15).

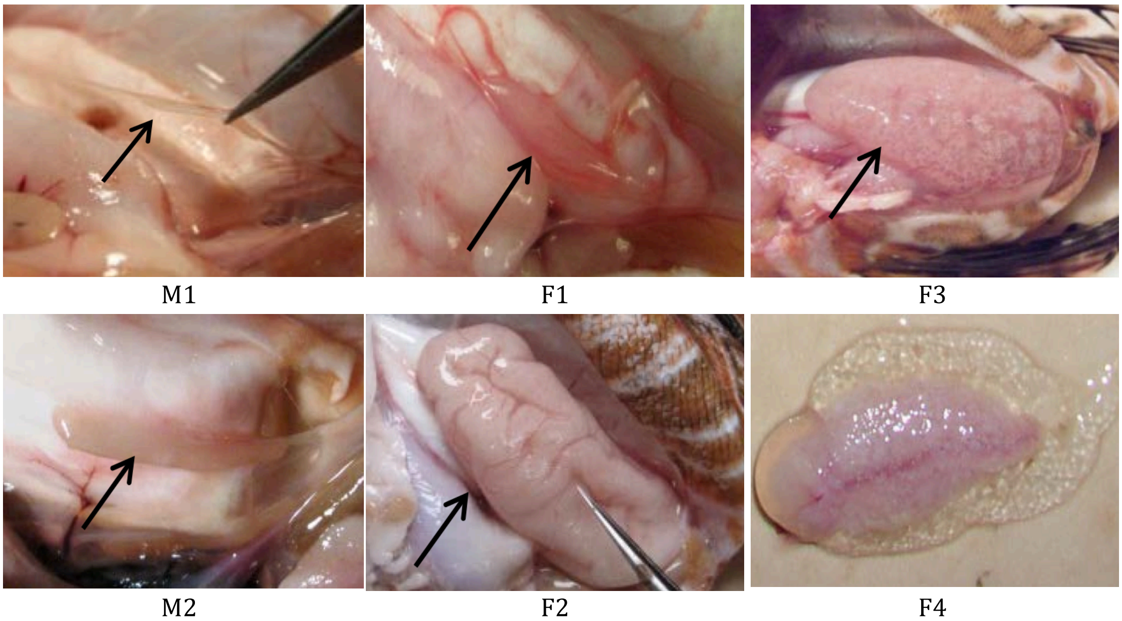


Figure 4.2. Classification of the reproductive condition of lionfish. immature male (M1), spawning capable male (M2), early developing female (F1), developing female (F2), spawning capable female (F3), actively spawning female (F4). Images modified from Green et al. (2012).

4.3.4 Assesment of the management of the lionfish invasion

This was conducted through analysis of lionfish management plans, manuals, websites, and personal communication with lionfish volunteers, marine park managers and lionfish scientists. Education and management strategies, lionfish collection methods and tools and efficiency of removal activities were assessed in order to make recommendations for areas not yet/early in the invasion timeline.

4.3.5 Data analysis

Using the statistical analysis package R (version 3.01), with all assumptions of parametric testing met the differences in mean lionfish total length at dusk and night was compared using a t-test. A t-test was also used to assess the differences in CPUE between 2012 and 2013 in terms of lionfish total length, the number of lionfish seen, the number of lionfish caught as well as the efficiency of capture.

4.4 Results

4.4.1 Dusk vs night

During the research at Klein Bonaire in 2012, a total of 1390 lionfish were seen by divers of which 893 were caught. At dusk, of the 856 lionfish seen, 535 were caught, whereas at night, of the 534 seen, 368 were caught. The largest number of lionfish seen (174) and caught (115) during a single dive occurred at dusk whist a dive at night accounted for the smallest number of lionfish seen (31) and caught (24). Lionfish caught at dusk were significantly larger than those caught at night (t-test, df = 92, p=0.0003). Stomach content analysis revealed that there was a higher proportion of empty stomachs at dusk (41%) compared to night (18%) (Figure 4.3). Generally, at dusk, there was a lower frequency of prey in lionfish stomach contents (60%), when compared to those at night (82%) where the majority of fish caught had prey in their stomachs.

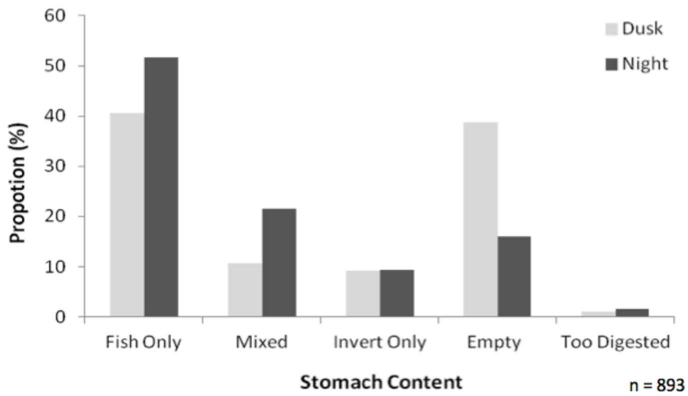


Figure 4.3. Comparison of the stomach content of lionfish caught at dusk and night

4.4.2 How often should removals be conducted?

There was a considerable decrease in the number of lionfish seen and caught when removals were conducted after one year. There was a decrease from a total of 2240 observed in 2012 to 876 in 2013 (Table 4.1). As a result there was also a decrease in the overall number of lionfish caught from 893 in 2012 to 536 in 2013 and this decrease in CPUE in terms of number of lionfish caught per hour was significant (t-test, df = 192, p = 0.00072). However there was a significant decrease in the number of lionfish being seen in 2013A (t-test, df = 192, p = <0.00001) and 2013B (t-test, df = 192, p = = 0.00003) when compared with 2012. The average size of lionfish increased from 2012 (227mm TL +/- SD) to 2013 (240mm TL +/- SD). Within a 6-month time frame, there was an increase in the number of lionfish being seen (t-test, df = 203, p = 0.997) and caught (t-test, df = 203, p = 0.438), however these increases were also not significant.

Table 4.1. Comparison of the number of lionfish seen and caught in Bonaire between 2012 and 2013 (where 2013A. February - June 2013; 2013B. August – October 2013

Year	No. Divers	Total Bottom Time	No.lionfish caught	No. lionfish seen but not caught	Total No. lionfish observed
2012	153	8211	893	1347	2240
2013A	159	8361	536	325	876
2013B	144	7564	665	377	1042
Total	456	24136	2094	2049	4158

The efficiency of lionfish capture improved significantly over time (t-test, df = 192 p = <0.00001), from an average of 38% in 2012 to an average of 60% in 2013 (Figure 4.2). A similar higher efficiency of capture was observed based on removal activities in the No-Diving Reserve in Bonaire, however these capture rates (average 80%) were higher when compared with Klein Bonaire.

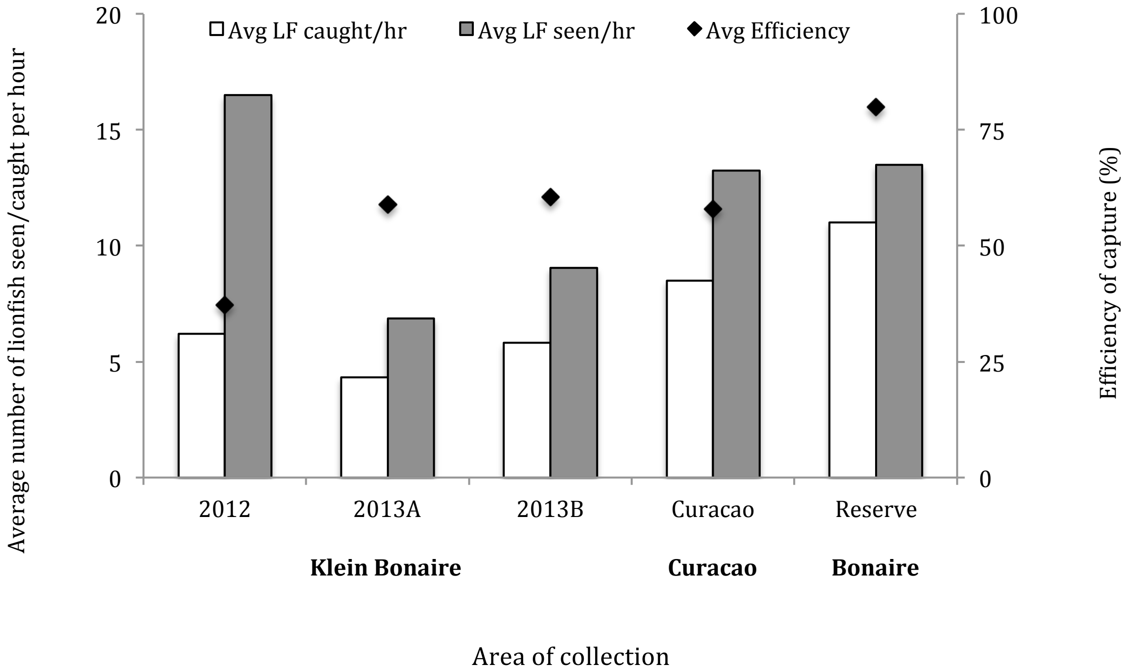


Figure 4.4. Comparison of the number of lionfish caught, seen and the efficiency of capture at Klein Bonaire (2012, 2013A. February - June 2013; 2013B. August – October 2013), Curaçao and Bonaire

4.4.3 Lionfish sex distribution

Within Bonaire, Curaçao and Klein Bonaire there was a generally male dominated lionfish population (42% male, 33% female and 25% unidentified) ranging in size from 41 – 446 mm (Figure 3.6). The largest female measured 410 mm whilst the largest male measured 446 mm.

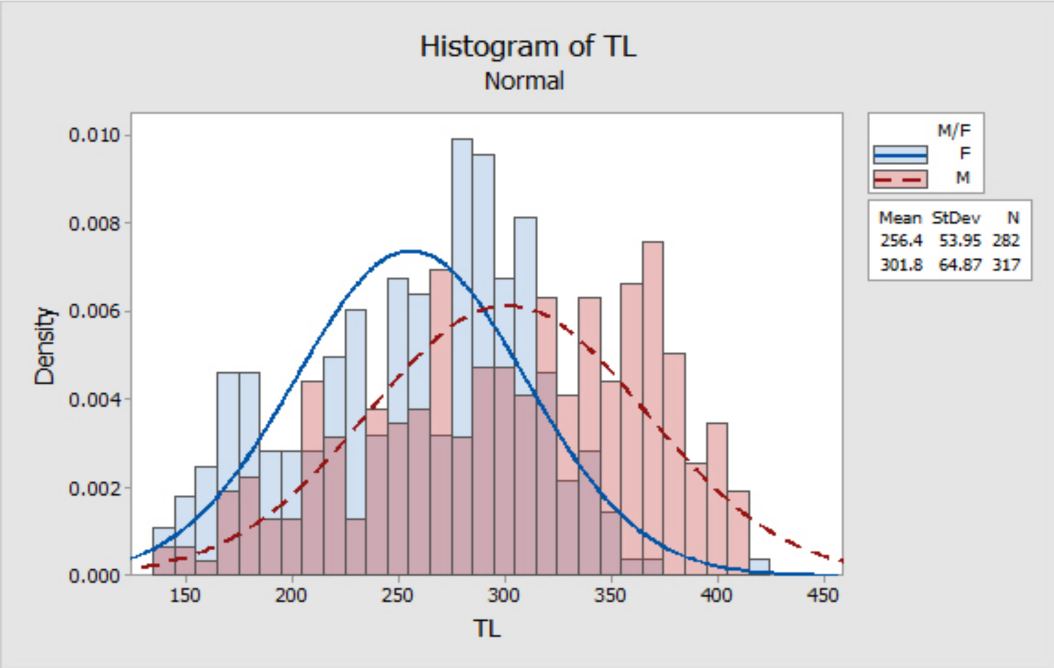


Figure 4.4. Distribution of male and female lionfish within Bonaire based on total length (TL)

In this study, only two females of the 4887 lionfish examined for sexual condition attained sizes greater than 400 mm. Regarding distribution of lionfish total length, male lionfish were on average bigger (301.8 mm) than females (256.4 mm), however this difference was not statistically significant (t-test, df = 3,343, p = 0.062,).

4.4.4 Assessment of lionfish management strategies

A variety of education types have been applied and range from broadcast materials such as TV and radio interviews; printed distributed types like newspapers, brochures and posters; web based materials such as social media, list-servs and websites and interactive informative sessions such as public forums. These media types differ in their effectiveness in terms of cost, ability to reach and target audiences and success in spreading the desired message (Table 4.2). Lionfish removal has been successfully achieved actively through diving (free-diving, recreational scuba diving and technical diving) and passively via fish traps and lobster pots. These methods vary in their effectiveness in terms of cost and ability to remove lionfish with minimal impact to other species and the local environment (Table 4.3). A range of devices have been designed, modified or repurposed for lionfish removal and containment. These tools vary in their effectiveness in terms of cost, applicability of use in protected areas and the ability to remove various sizes of lionfish with minimal impact to other species and the local environment (Table 4.4).

Table 4.2. Analysis of the effectiveness of various media types used for lionfish education and its applicability to various phases of the lionfish invasion

Type	Advantages	Disadvantages	Applicability to phase of invasion
TV Interviews	1) Low-cost & often free 2) Reaches wide audience 3) Can be visual 4) Can be repeated multiple times 5) Effective in areas with low literacy levels	1) Often very short with limited control over message	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Information spread via television is applicable at all phases of the invasion timeline. The messages disseminated will vary as the timeline progresses. In early stages and prior to introduction, messages should focus on making people aware of lionfish, why they are a problem and what to do if encountered. As the invasion progresses, the messages should focus more on encouraging removal and consumption and updates can be made as to advances in research and management. Periodic appearances on programs on local television or repeats of these interviews on television can be successful in sharing information.
Radio interviews	1) Low-cost & often free 2) Reaches wide audience 3) Effective in areas with low literacy levels	1) Often very short with limited control over message 2) Not visual	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Information spread via radio is applicable at all phases of the invasion timeline. The messages disseminated will vary as the timeline progresses. In early stages and prior to introduction, messages should focus on making people aware of lionfish, why it is a problem and what to do if encountered. As the invasion progresses, the messages should focus more on encouraging removal and consumption. Radio interviews are often more successful when there is an already established dedicated audience and also when there are very few radio stations which means that the probability of the message reaching a wide audience is greater.
Newspapers/ newsletters/ magazines	1) Low-cost & often free 2) Reaches wide audience 3) Can be very visual and appealing and increase interest	1) Not as effective in areas with low literacy levels	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Articles in newspaper, newsletters and magazines can be published periodically throughout the duration of the invasion timeline. Messages disseminated will evolve over time from more information based to updating, mitigating and disclosing of management strategies and their successes.
Printed: flyers/ brochures/ pamphlets	1) Can contain very detailed information 2) Can be targeted to specific audiences 3) Can be very visual and appealing and increase interest	1) Not as effective in areas with low literacy levels 2) Can easily be ignored/ discarded without reading 3) Limited audience	Introduction ✓ Establishment Proliferation Impact Printed materials are most effective for disseminating information periodically and spreading awareness of what lionfish are, why they are a problem and what should be done. Often for posters, once printed on durable materials such as canvas or poster board, they can last for considerable periods of time therefore there is a more long-term dissemination.
Social Media	1) Easy circulation with rapid and frequent sharing of information 2) Can reach a very wide audience 3) Allows for interaction, collaboration and reinforcement	1) Message can get lost especially in high volume media 2) Not everyone in desired audience may use social media 3) Not as effective in low literacy areas	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Social media is useful at all stages throughout the invasion timeline, not only for disseminating information but also for providing updates with a rapid turnover period. It is especially most effective when sharing concise messages especially with coupled with striking imagery. Additionally content can be updated more easily than a website and is a lot more user friendly thus social media is quickly becoming more popular as a means of circulating information.
Websites	1) Can contain very detailed information and/or links to relevant information 2) Reaches wide audience 3) Can be very visual & increase interest	1) Very time consuming to manage and maintain website 2) May require special skills/expertise to create and run	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Websites can be established as early in the invasion timeline as possible and thus be available throughout the duration of the invasion. Websites can serve as an important source of detailed information but requires significant investment to create, maintain and update content.
Emails/ Listservs	1) Shares short, important messages and can contain links to more detailed information 2) Can reach a wide audience	1) Can easily be ignored/discarded without reading 2) Message can get lost especially in high volume media 3) Not as effective in low literacy areas levels	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Emails and listservs are most useful in sharing updates throughout the duration of the invasion timeline. These messages that are disseminated should be quite concise and provide links to further information if the reader chooses to.
Public forum/ workshops	1) Opportunity to engage with the audience e.g. with Q&A session 2) Can be targeted to specific audiences and be very interactive 3) Effective in areas with low literacy levels	1) Requires effort to publicize event and encourage attendance, but still turn-out can be poor and is often erratic	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Public forums and/or workshops are especially integral at the start of the invasion timeline so that people are educated early on about what lionfish are, why they are a problem and what should be done if one is encountered. However as the timeline proceeds, the focus of the forums/workshops can be altered according to the audience. After lionfish have become established, specialist workshops can be held with groups such as divers and dive operators, fishermen, restaurants/chefs and other stakeholders with the information presented tailored to the relevant group.

Table 4.3. Analysis of the effectiveness of various methods used for lionfish removal and its applicability to various phases of the lionfish invasion

Method	Advantage	Disadvantage	Applicability to phase of invasion
Scuba diving	1) Allows for targeted removal with no by-catch. 2) A considerable amount of lionfish can be removed within a single dive (depends on hunter's skill) 3) Cost effective	1) Limits to length of dive 2) Limits to depths attained 3) Risk of injury to individuals through diving and/or handling lionfish	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Scuba diving has proven to be one of the most effective and efficient means of capture and it is recommended that this method be applied throughout the entire invasion period.
Technical diving	1) Allows for removal at depths not accessible by recreational divers 2) Allows for targeted removal with no by-catch. 3) A considerable amount of lionfish can be removed within a single dives	1) Very costly 2) Requires a considerable amount of training 3) Higher risk of injury to individuals through diving and/or handling lionfish	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Given the pattern of the lionfish invasion where they venture into depth later in their invasion timeline, it will be best to focus technical diving efforts after lionfish have become established.
Free driving	1) Allows for targeted removal with no by-catch.	1) Limits to breath-hold ability 2) Limits to depths attained 3) Risk of injury to individuals through diving and/or handling lionfish 4) Less lionfish can be removed within a single dive/immersion	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Since free diving is a targeted form of removal, it can be successfully applied at all stages of the lionfish invasion, however it has proven to be less efficient and effective when compared to scuba. Thus free diving is recommended for when scuba is not possible or at opportunistic moments.
Lionfish tournaments	1) Allows for large amounts of lionfish to be removed within a short space of time 2) Collected specimen can be used for research or taste-sessions 3) Good for education and raising awareness 4) Can utilise recreational scuba, technical and free divers	1) Requires incentives / prizes 2) Can have negative impacts on the reef if people are too financially motivated and will do anything to get big prize 3) Risk of injury to participants through diving and/or handling lionfish	Introduction; Establishment ✓ Proliferation ✓ Impact ✓ Lionfish tournaments are only efficient and effective following establishment of lionfish. Divers will not be motivated to participate in future events if the number of lionfish to be caught are so low that it is not worth their effort
Fish traps/lobster pots	1) Already being used for other species, therefore no additional cost for trap creation 2) Allows for removal at depths not accessible by recreational divers 3) A considerable amount of lionfish can be removed within a single immersion 4) No risk of injury to individuals through diving	1) Catch-success can be erratic 2) By-catch is high	Introduction ✓ Establishment ✓ Proliferation ✓ Impact ✓ Since this is an on-going method of fishing where lionfish is by-catch, they can be employed throughout the invasion period. Lionfish specific traps are especially effective once lionfish have become established and have started to proliferate
Hook & line	1) Allows for removal at depths not accessible by recreational divers e.g. 100-200m 2) No risk of injury to individuals through diving 3) Already being used for other species, therefore no additional cost for materials	1) Catch-success can be erratic 2) By-catch often occurs	Introduction; Establishment; Proliferation; Impact Hook and line has proven very ineffective at removing lionfish and is therefore not recommended as a primary means for control.

Table 4.4. Comparison of tools and devices utilised for lionfish removal throughout the invaded region

Device	Advantages	Disadvantages	Average Cost (USD)
Modified Eradicating LionFish Tool (ELF Tool)	1) The modified ELF with thicker, longer shaft and trigger is effective against lionfish of all size classes 2) Can be easily modified underwater with an O-ring to be effective against smaller lionfish. 3) Device does not leave divers control at any point in time, thereby reducing negative impact on reef 4) Modified ELF with longer shaft keep lionfish at distance from collector and when coupled with the Zookeeper allows for rapid removal 5) Modified ELF is effective for removing lionfish in deep crevices and holes 6) Not powerful enough to be used on other fish e.g. snappers/groupers	1) The original ELF is not as effective with larger lionfish 2) May still be ineffective for very large lionfish 3) Initial expense can be high 4) Some spearing devices may be prohibited in some areas or restricted to free-diving only.	70 - 160
Hawaiian Sling/Pole Spear	1) Affordable and effective at removing lionfish, especially larger ones. 2) Keeps fish at distance from collector and when coupled with Zookeeper, it allows for rapid captures 3) Effective for removing lionfish in deep crevices and holes	1) Not as effective on smaller fish 2) Spear leaves control of diver and can cause significant damage to reef and be used for other fish. 3) Does not fold up, so can affect a dive operation (e.g. if teaching). 4) Some spearing devices may be prohibited or restricted to free-diving only.	25 -85
Travel Pole Spear	1) Affordable and effective at removing lionfish, especially larger ones. 2) Folds up and can be attached to the diver, so does not interfere with dive operation.	1) Not as effective on smaller fish 2) Has the power to cause damage to coral and be used to catch other larger fish. 3) Some spearing devices may be prohibited or restricted to free-diving only.	50
Fold Spear	1) Affordable and effective at removing lionfish, especially larger ones. 2) Folds up and can be attached to the diver, so does not interfere with dive operation. 3) Keeps fish at distance from collector and when coupled with Zookeeper, it allows for rapid captures 4) Effective for removing lionfish in deep crevices and holes	1) Not as effective on smaller fish 2) Has the power to cause damage to coral and be used to catch other larger fish. 3) Some spearing devices may be prohibited in some areas or restricted to free-diving only. 4) Initial expense can be high	150
Frapper	1) Effective for removing lionfish of various sizes 2) Safe for the coral and does not have the power to kill other larger fish	1) Not as effective with larger lionfish. 2) Spear is not attached making it hard to recover when dislodged. 3) Not as effective for removing lionfish in deep crevices and holes	65
Speargun	1) Powerful and successful especially against large lionfish	1) Spear leaves control of diver and can cause significant damage to reef and be used for other fish. 2) Removing fish and then reloading spear can be a laborious process. 3) Some spearing devices may be prohibited in some areas or restricted to free-diving only. 4) Initial expense can be high	150 - 300

Device	Advantages	Disadvantages	Average Cost (USD)
Vinyl hand net	1) Very effective for small, naïve fish and live captures 2) Easy removal of fish after capture due to no entanglement 3) Can be useful in areas where spearing is banned	1) Capture requires patience and skill and can be time consuming 2) Not as effective for larger fish or capture on areas with high rugosity or where lionfish are not as accessible 3) Can be bulky to carry	35
Mesh hand net	1) Very effective for small, naïve fish 3) Can be useful in areas where spearing is banned	1) Capture requires patience and skill and can be time consuming 2) Not as effective for capture of large fish or areas with high rugosity or where lionfish are not as accessible 3) Entanglement common during removal of fish after capture	5 - 15
Zookeeper	1) Safest way to remove and contain lionfish, especially in highly infested areas. 2) Time efficient since there is no need to kill the lionfish completely before putting in the zookeeper	1) Can be a bit bulky especially for novice divers 2) Initial expense can be high	85 - 100
Collection Bag	1) Cost effective and can be rolled up and clipped to the diver, thus reducing drag	1) Not as effective for lionfish removal as it is not puncture proof	25 - 35
Hex Armour Gloves	1) Protects diver from lionfish envenomations	1) Can be difficult to handle tools whilst wearing gloves, thereby making diver more prone to accidents 2) Still exists some potential for the diver to be hurt by the spines	50

4.5 Discussion

When trying to manage a new species, in addition to understanding the species' ecology and its mode of dispersal it is also very important to understand the area you are trying to protect. Bonaire and Curaçao are a mere 41 km apart, possess comparable reef community composition and structure (van Duyl 1985; Sandin et al. 2008; de Leon et al. 2013) and according to Chollett et al. (2012) they exist in the same physicochemical province

(de Leon et al. 2013). These factors coupled with the identical confirmed introduction of lionfish to these islands suggest that varying fishing pressure is the main factor to affect lionfish density and biomass (de Leon et al. 2013).

However, within these islands there are disparities in hunting effort due to abiotic factors. The leeward coasts of both Bonaire and Curaçao are sheltered and calm allowing for easy access throughout the year whilst the windward shores tend to have stronger wave action and less favourable conditions making dive sites less accessible (de Leon et al. 2013; Lyons et al. 2015) accounting for disparities in lionfish hunting pressures. Furthermore, despite both islands being mostly shore diving locations, Klein Bonaire and Klein Curaçao are only accessible via boat making removal efforts even more infrequent. Additionally within Bonaire the No-Diving Reserve receives limited hunting pressure (unfished site) since no diving is allowed. STINAPA has hosted events where the Reserve was opened to a limited number of volunteers annually and more recently biannually. However due to the infrequency of hunting, the size and density of lionfish are considerably greater in unfished sites as compared to more regularly fished sites in Bonaire (de Leon et al. 2013). More constant and frequent removal efforts have proven most successful in reducing lionfish size and density therefore it is recommended for removal activities to occur as often as resources allow.

Despite their reported cryptic behaviour in their native range (Fishelson 1997), lionfish were observed and also captured at all times of the day ranging from 5.00-23.00. This study along with others (Fishelson 1975; Green and Côté 2011) suggested that their peak activity coincides with crepuscular periods of dawn and dusk. This knowledge can enlighten lionfish volunteers as to the best time to go hunting, however, because of practicality, more divers tend to hunt at dusk rather than dawn. Moreover, based on findings from this study, dusk is an effective time to focus removal efforts. Not only can more lionfish be seen and captured; but they can be removed before they have a chance to make their impact, i.e. start feeding.

At Klein Bonaire, surveys conducted in 2012 revealed that lionfish were most active at dusk, similar to other studies in the Caribbean (Morris and Akins 2009; Green et al. 2011; Cure et al. 2012; Bernal et al. 2014; Côté et al. 2014; Bejarano et al. 2015). Not only were more lionfish caught, but they were removed before they had a chance to have an impact, since at night 80% had prey in their stomachs, making dusk the more efficient and effective time for removal. Lionfish tend to be inactive and sheltered in crevices and under ledges during the day and most active during crepuscular times (i.e. at dawn and dusk) with their peak activity being accompanied with a high prey density (Fishelson 1975; Green and Côté 2011). However, it is important to note that stomach contents represent the lionfish's last meal and is not necessarily a representation of what lionfish eat, since it is expected that a lionfish will not intentionally choose to have an empty stomach (Hyslop 1980). Thus the large proportion of empty stomachs at dusk might suggest that that these lionfish were caught before they had a chance to feed. This has important implications for lionfish control, because by concentrating removal activities at dusk, not only can more lionfish be removed, but also they can be removed before they have had a chance to feed.

Lionfish may be capitalizing on the crepuscular periods due to their high success rate of hunting at lower light levels. Lionfish might either have exceptional visual perception or alternatively, the prey fish have poor abilities to detect incoming predators during these lower light levels (Green and Côté 2011). Many prey items are diurnal meaning that they retreat at night to escape predation. Similarly, lionfish may be coinciding their foraging activities in order to escape detection by other visually oriented predators (Green and Côté 2011) themselves. However the evident lack of natural predators in the invaded range along with lionfish possessing venomous dorsal, ventral and anal spines makes this an unlikely reason (Allen and Eschmeyer 1973; Albins and Hixon 2008).

The fluctuations in the number of lionfish seen and caught at Klein Bonaire between 2012 and 2013 cannot be explicitly accounted for but a few suggestions can be offered. Firstly, the drastic decrease between 2012 and 2013A in terms of the number of lionfish seen can potentially be explained by the fact that 2012 represented the first real removal attempt at this island accounting for why as much as 2240 lionfish were seen. The lionfish volunteers although experienced, were not as skilled as they were in 2013 which accounted for the large discrepancy between the number of lionfish seen and those that were actually caught. Furthermore, due to the sheer number of lionfish being observed, due to time and depth related limitations, it was impossible to remove every single one.

However, one year later, there was a smaller margin between the number of lionfish seen and caught. Over time, the lionfish volunteers became better at not only finding lionfish, but also at successfully catching them. This increase in successful removal rate is very promising since Barbour et al. (2011) proposed that a 35 – 65% removal rate of adult lionfish biomass per year was essential in significantly reducing further population renewal (Morris et al. 2011b; de Leon et al. 2013). As with 2012, there was never complete removal of lionfish as a result of time and depth restrictions but also due to the fact that the lionfish themselves were also learning. Côté et al. (2014) suggested that animal's behaviour is often changed as a result of being hunted and cause these individuals to become more vigilant, flee more readily and often modify the location and timing of their activities to avoid volunteers. As a result, successful survivors are possibly less prone to being confronted or captured in future attempts (Côté et al. 2014). This proposed learning behaviour in lionfish can also account for the increase in the number of lionfish caught between 2013A and B. There was an increase in the frequency of smaller individuals (i.e. those <200mm) which are possibly naïve to hunting, and were thus easily caught.

Furthermore, of the lionfish caught within Bonaire, Curaçao and Klein Bonaire ranging in total length from 21 – 446 mm, only two females of the 4887 specimens examined for sexual condition exceeded 400 mm. This suggests that female lionfish appear to have reached their maximum size whereas the males continue growing, with reports suggesting that lionfish as large as 485 mm have been recorded (Akins pers. comm.). The observed male-biased sexual size dimorphism could be explained by the difference in energetic requirements between the sexes. Female lionfish reproduce by releasing gelatinous egg masses multiple times per month. These egg masses presumably require substantial amounts of energy to be created and in some instances can account for as much as 15% of an individual's total body mass. Females need to invest more energy into gonad production especially since the size and weight of their gonads tend to greatly exceed those of males. Thus it can be hypothesised that males partition minimal resources towards gonads and can instead develop more fat whereas females, especially when gravid focus more on gonad development and as a result have minimal fat stores.

Determining whether sex-based differences exist within the behaviour, growth dynamics and preferences can be invaluable to management since any differences can inform on spatio-temporal dynamics, thus helping to tailor management strategies and increase efficiency (Sims et al. 2001). There appears to be a slightly more male dominated lionfish population within Bonaire, Curaçao and Klein Bonaire. The exact reason for this remains unknown but the following hypotheses can be offered. The specimens used in this study were obtained opportunistically, thus this was only a fraction of the overall population and it is nearly impossible to remove all lionfish. However, lionfish removals especially at derbies/tournaments may be biased to removing larger bodied fish. Since males are generally bigger than females, this could account for the more male-dominated sex ratio. Additionally there could be a behavioural difference between the two sexes (Magurran 1986). For example females may act more cryptically to conserve on resources whereas males may spend more time swimming and searching for food, an activity which puts them at greater risk of being caught. This risk aversion strategy is common in females of other species such as dogfish *Scyliorhinus canicula* (Sims 2001), bluehead wrasse *Thalassoma bifasciatum* (Warner 1998) and the Trinidadian guppy *Poecilia reticulata* (Piyapong et al. 2009).

After gaining an understanding of the most effective time for removal as well as the frequency that these activities should occur, there is also need to assess the effectiveness and efficiency of other essential components such as education schemes and media used, removal methods as well as the tools used for capture. Like management, education schemes are constantly evolving and are usually not a one type fits all model (Nunez and Pauchard 2010; Perrault and Muffet 2002) and need to be tailored according to the particular stakeholders group to achieve optimum success (Simberloff 2000). Often, invasive species are vilified in a means to encourage the urgency of their removal (Davis et al. 2011), but sometimes this backfires and has negative consequences on the success of the strategy (Landers 2012). Throughout the Caribbean, lionfish education schemes range from simple, local means via posters, brochures and newspapers to television and radio announcements to more regional and international means through social media and the internet. However, these schemes have had varying success rates since the message portrayed, the type of media utilised, the target audience and their literacy levels and reinforcement are instrumental factors that are often overlooked (Ali 2014a).

TV and radio interviews are advantageous since they have the ability to reach wide audiences and are effective in areas with low literacy levels and are very cost effective and sometimes free. However there is less control over the message to be distributed and interviews are often very short, thereby affecting the quantity and quality of disseminated information. Printed materials such as brochures and postures are also very effective as they are very visual and can create interest and be targeted to specific audiences and produced in multiple languages, but are less successful in low literacy areas and can also be discarded without reading. Web based media such as social media, websites and listservs are very effective at rapidly reaching a wide audience with very visually appealing material that can be detailed and targeted to desired audiences but is sometimes very time-consuming to manage and especially in the case of websites this can be very expensive.

The target audience and literacy levels are important factors when selecting the media to be utilized for the education strategy (Ali 2014a). The effectiveness of education media types are context based since invaded territories vary in their education and literacy levels, need for multilingual media and also the financial resources available to fund invasive species awareness schemes. Where possible, a combination of different media types with a strong visual content should be used and enacted as early as possible in the invasion timeline after carefully considering the message to be portrayed as well as the receiving audience. The messages disseminated often evolves as the invasion timeline proceeds. At the start of the invasion, messages should focus on awareness, i.e. what are lionfish, why are they a problem and what an individual should do if they happened to encounter lionfish. As lionfish become more established and begin proliferating, in addition to education type messages, messages related to what methods have been applied thus far to manage lionfish and their successes should be a priority. Furthermore where appropriate, messages should be disseminated on how to become involved, whether it be through lionfish tournaments, volunteering or simply utilising lionfish as a food fish.

Social media is often overlooked, but has proven to be a valuable platform for invasive species education, co-ordination and collaboration. Throughout the invaded range, Facebook has been utilized as the main platform for sharing information and updates on control activities occurring in respective countries or by individual lionfish removal teams. Within Bonaire, a lot of control activities are organized through the Bonaire Lionfish Hunters Facebook group. Here volunteers can report sightings, get buddies and share information and tips. STINAPA also uses this group to share information on their activities such as lionfish tournaments, chartered removal trips, opening of the no-diving reserve etc. Also this group also acts as a means of reinforcement and sharing findings on the success of these lionfish volunteers's removal efforts. Facebook also acts as a platform for collaboration and sharing experiences amongst neighboring territories and individual groups and volunteers. Since management of the lionfish invasion requires a regional, co-operative effort, having a means to share information in such a manner is especially beneficial.

Handheld pole spears and Hawaiian slings have proven most cost-effective and efficient at removing larger numbers of lionfish, however their power can have damaging effects on the reef and other species. The modified Eliminating Lionfish Tool has proven very effective at removing lionfish with minimal impact on the reef and environment, but is more expensive than hand held pole spears and slings. The Zookeeper has been established as the most effective containment device as it allows for large quantities of lionfish to be safely stored without harm to the diver. Also since lionfish do not need to be killed before storing in the Zookeeper, this allows for more time-efficient capture as compared to dry-bags or other home-made lionfish containment devices. Within recreational dive limits, targeted removals via diving have proven more effective at removing larger numbers of lionfish with minimal by-catch as compared to trapping. But, at depths exceeding recreational dive limits, lionfish removal via diving requires more skill and becomes more, dangerous, expensive and less effective. Throughout the invaded region, volunteer divers have been integral to the success of localised lionfish removal efforts in shallow coral reef habitats (de Leon et al. 2013) and usage of this group is highly recommended. Thus gaining knowledge of how to reinforce and amplify volunteers' inputs and actions can be used to encourage further lionfish control and be invaluable towards tailoring future management schemes.

4.6 Conclusion

In the 30 years since the confirmation of lionfish within the Caribbean and Atlantic region, their populations have grown in size and surpassed reported densities and sizes from the native range. Throughout the invaded range, individual countries have been successful at limiting their growth however it is still very unlikely that lionfish will be completely eradicated from the Caribbean and Atlantic. Nonetheless, an assortment of management schemes have been applied, but with varying success due to disparities in the promptness of their response, education and awareness schemes enacted as well as the tools and groups utilised for removal. This study revealed that targeted removals by divers using hand held spears and zoo-keepers is currently the most efficient and effective method for lionfish removal. Furthermore when these removal efforts are focused at crepuscular times such as dawn and dusk when lionfish are most active, larger numbers can be removed whilst also minimising the impact since at this time period the majority of lionfish had empty stomachs.

This study also reinforces the importance of a top-down, prepared and rapid response whilst highlighting the value of education and social media to successful lionfish control. Throughout the invaded region, there is still debate over whether an inclusive or selective strategy towards lionfish removal activities is more beneficial, but this study recommends that selective strategies should be applied in marine protected areas.

Chapter 5: THE ROLE OF VOLUNTEER DIVERS IN LIONFISH MANAGEMENT

5.1 Abstract

Since their introduction to the Caribbean, lionfish have continually grown in size and density. Although considerable achievements have been made with limiting their growth, it is unlikely that lionfish will ever be completely eradicated. Throughout the invaded range, various management schemes have been applied with varying success and they have been continuously evolving in terms of the tools used and the schemes implemented. At the beginning of the invasion, management initiatives involved primarily scientists and government or state department officials. However, due to the invasion characteristics of lionfish, a need was identified for a larger removal effort, warranting the involvement of dive operators and volunteer divers. Socio-economic questionnaires were conducted throughout the invaded range to determine the profile of the typical lionfish volunteers, the motivations for their involvement and a cost-benefit-analysis was performed to assess what economic effect the invasion was having. Knowledge gained from this research will be beneficial in tailoring future management schemes utilising volunteers by understanding people's motivations, factors key to recruitment and also which groups to target. This research revealed that lionfish volunteers were typically relatively experienced, male divers within the 40-60 year age group. Furthermore this research also identified that the majority of volunteers were not financially motivated and instead reinforcement that their actions were having positive impacts was the major motivating factor. This research also reveals how valuable and successful a dedicated volunteer removal effort is to controlling the lionfish population in the future.

5.2 Introduction

Lionfish are a major concern within their invaded range (Côté et al. 2013; Cure et al. 2014) and their establishment is due to generalist diet and habitat requirements (Morris and Akins 2009), high reproductive, feeding and growth rates (Green and Côté 2014), early maturation and year round reproduction (Ahrenholz and Morris 2010), and a lack of natural enemies (Darling et al. 2011). Various lionfish management measures have been initiated (Morris et al. 2010; de Leon et al. 2013) and their control has been an evolving process in terms of the schemes established, the tools used, the means to increase and enhance removal efforts as well as the groups of individuals involved in removal activities (de Leon et al. 2011). Knowledge of how the lionfish invasion proceeds is invaluable to tailoring management strategies in other countries still in the early invasion stages. Central to the lionfish management initiatives applied throughout the invaded region has been the use of volunteers. Volunteers may contribute not only to monitoring, but also through direct actions such as culling and lionfish removal. Divers in particular can help to raise awareness of lionfish-related issues by participating in citizen science activities (Darwal & Dulvy 1996, Harborne et al. 2000, Goffredo et al. 2004, Hammerton et al. 2012).

The term "citizen science" refers to the involvement of non-specialist volunteers in scientifically focused studies (Carr 2004, Cohn 2008, Gallo and Waitt 2011). Citizen scientists can assist in the early detection of invasive non-native species (INNS) (Delaney et al. 2008) since increased surveying effort leads to higher likelihood of detection, especially when organisms are present at lower abundance (Mehta et al. 2007, Lopez-Gomez et al. 2014). Since research and conservation efforts in marine systems are often restrained by monetary, spatial and temporal constraints as well as the availability of human resources (Danielsen et al. 2005, Crall et al. 2010), there has been increased utilization of citizen science in both data collection and management (Lopez-Gomez et al. 2014). Given the spatial scale of marine ecosystems, the capacity to monitor effectively the distributions of INNS such as lionfish is severely limited, resulting in their consequent impacts being under-recorded temporally and spatially (Delaney et al. 2008, Azzurro et al. 2013). More generally, citizen science can also contribute to monitoring, surveying and removal activities, and provide data on the structure, distribution, behaviour and dynamics of invasive species and their populations (Conrad and Hilchey 2011, Bodilis et al. 2014, Lopez-Gomez et al. 2014).

At the beginning of the lionfish invasion in the Caribbean, removal initiatives involved mostly scientists and government or state department officials. Due to the invasion characteristics of lionfish, a need was subsequently identified for a larger, community effort (Morris 2012), warranting the extension of removal activities to dive operators and volunteer divers. Divers are commonly sensitive to environmental issues from early on in their dive training since this helps to reduce diver impacts, and produce more environmental consciousness among divers (Cater & Cater 2007, Worachananant et al. 2008, Hammerton et al. 2012). In addition to removing lionfish, specimens can be made available for research; sightings and catch data are often submitted to government or research agencies to contribute to monitoring.

In order to understand how best to motivate individuals to participate in initiatives to deal with the problems of INNS, it is instructive to consider how and why individuals undertake actions. The theory of planned behaviour (TPB) (Azjen 1985) and the norm activation model (Schwartz 1977), for example, highlight the intricate relationship between environmental concern and environmental participation (Harvey 2015). Azjen (1988) refined the theory of reasoned action (TRA), originally proposed by Fishbein and Azjen (1975), to form the TPB which states that an individual's behaviour is determined by their intention as well as their perceived behavioural control (Hankins et al. 2000; Bamberg et al. 2003; Cookes and French 2008; McEachan et al. 2011).

Such work has explored how cognition (beliefs and attitudes) interacts with personality traits, emotions, personal norms, and situational factors and thereby influences intentions and subsequent behaviour (Hines et al. 1987; Kollmus and Agyeman 2002; Bamberg and Moser 2007; Harvey 2015). A person's reason for engaging in voluntary activities can vary, but it tends to stem from personal motivation and empathy, commitment to a greater cause and the expansion of knowledge (Batson et al. 2002; Preece and Schneiderman 2009; Hammerton et al. 2012; Rotman et al. 2014). By volunteering, people can become empowered since they believe their contributions make a positive difference, simultaneously helping them to feel good about themselves (Mirowsky and Ross 1989; Measham and Barnett 2007).

Understanding what might influence individuals' behaviours can help to determine motives for more selfless or altruistic behaviour. Kollmuss and Agyeman (2002) suggested that knowledge, attitude, commitment and the ability to initiate change through behaviour are factors that encourage individuals' more altruistic environmental actions; these factors are likely to apply to the voluntary participation of individuals in lionfish-related activities. The success to date of lionfish removal at the local level has been underpinned by the involvement of volunteers, due primarily to their efforts leading to increased detection of specimens which provides the impetus for higher removal rates (de Leon et al. 2013, Lopez-Gomez et al. 2014). Thus, knowledge of how to reinforce and amplify volunteers' inputs and actions may potentially be used to encourage them and others to do more in terms of lionfish control.

The main aims of this research were to (1) establish the profile of the individuals voluntarily participating in lionfish related activities within the invaded region; (2) to determine why and how these individuals participate in lionfish removal and how this was affected by the phase of the invasion, and (3) to investigate what needs to be done in the future to enhance volunteer usage and also the means to retain and reinforce current volunteers or even recruit new ones. Gaining this knowledge will be beneficial in tailoring future management schemes utilising volunteers by understanding people's motivations and which groups to target.

5.3 Methods

This study focused on individuals who have and continue to contribute as volunteers in lionfish management and control activities by participating in activities to detect, catch and remove lionfish from affected locations throughout the invaded region. For the purpose of this research, these individuals will be referred to as "lionfish volunteers" and this group was considered to present an opportunity to establish factors leading to both engagement with and continuation in lionfish control efforts. A questionnaire was created and disseminated in 2013 after piloting in 2010-2012 with stakeholder groups in Bonaire, Anguilla and Trinidad and Tobago. The target of this questionnaire was to involve individuals voluntarily participating in lionfish related activities within the invaded region (North, South and Central America and the Caribbean region). Additionally since lionfish have been confirmed within the invaded area for varying periods of time, by seeking a wide geographic range it was expected that responses would cover varying phases of the lionfish invasion. Thus the aim was to achieve responses from at least 50% of the countries within each individual phase category. These phases were assigned based on the time since lionfish had been confirmed within the country in relation to the time this research was conducted (recent. <2 years; early 2-5 years; mid. 5-10 years; late >10 years). As the lionfish invasion proceeded it can be expected that there may be changes in the groups of people involved, the frequency at which removal activities occurred as well as opinions and attitudes towards lionfish removal.

The questionnaire consisted of a mix of Likert scale and open questions and focused on three key themes. respondents' awareness, experience and motivation for hunting lionfish, (respondents' opinions on financial costs/benefits incurred by lionfish, and information, such as age, gender and dive experience (Appendix C). These themes align with the theory of planned behaviour (Azjen 1985) and the theory of reasoned action (Fishbein and Azjen 1975) since an individual's knowledge, attitudes, commitment and ability to initiate change can affect their participation in lionfish related activities. The questionnaire applied Contingent Valuation Methods (CVM) to conduct a perceived cost-benefit analysis of lionfish removal. CVM has been established by academics and policy makers as one of the best tools for valuing environmental goods, services and resources (Whittington 2002; Wang et al 2006) and participants are asked, for example, to express their willingness to pay (WTP) in response to a hypothetical situation (Carson 2000; Han et al. 2011).

The questionnaires were distributed electronically, primarily through social media in order to extend to a greater geographic reach than could be achieved via face-to-face interviews. In particular, social media platforms have recently become established as a means of disseminating information, sharing experiences and for the lionfish hunting community in general it has succeeding in creating a sense of community throughout the Caribbean and the Americas. Within Bonaire, the majority of lionfish control activities are co-ordinated via Facebook through the 'Bonaire Lionfish Hunters' Facebook group (BLH 2015), thus sharing the questionnaire via this group was a way of reaching lionfish volunteers. Furthermore, distribution via Facebook pages such as the 'World Lionfish Hunters Association' (WLHA 2015) and 'Lionfish University' (Lionfish University 2015) allowed for the questionnaire to reach a larger geographic group due to their online following.

The quantitative data acquired were analysed using the statistical package SPSS (IBM – Version 21) to assess whether differences existed amongst the respondents in terms of gender, age and location of diving. Responses from the questionnaire were also divided geographically in order to assess whether the experiences, opinions and practices of lionfish volunteers within the study area of this thesis, i.e. Bonaire and Curaçao differed to other countries within the invaded region. Respondents from Aruba, Bonaire and Curaçao were assigned to the group 'ABC' whilst those from the United States and other Caribbean and Central American countries were assigned as 'CAR'. This study hypothesised that respondents within the ABC islands group would not only be knowledgeable of the lionfish invasion but also stood to financially benefit more from the lionfish invasion due to established markets.

5.4 Results

5.4.1 Establishing the profile of individuals involved in lionfish removal

A total of 112 lionfish volunteer questionnaires were completed by respondents who primarily conduct their hunting within Antigua and Barbuda (1), Aruba (2), Bahamas (3), Barbados (2), Bermuda (6), Belize (10), Bonaire (37), Cayman Islands (1), Curaçao (16), Dominica (1), Grenada (5), Guatemala (1), Honduras (4), Jamaica (3), Mexico (2), Panama (2), Puerto Rico (2), Trinidad and Tobago (1) the United States of America (11) and undisclosed (3). This sample met the ambitions of this research as there were respondents from North, South and Central America as well as various Caribbean islands as well as at least 50% response rate was achieved from the various stages of the invasion (recent, early, mid, late) (Table 5.1). Of these territories, islands within the Lesser Antilles (Barbados, Dominica, Grenada and Trinidad and Tobago are in the earlier phase of the invasion since lionfish had only been confirmed <2 years at the time of the study. Of the 112 individuals who participated in this study, the majority of respondents were male (73%), in the 40-60 years age group (54%) and did not/ had never previously worked in the dive industry (61%) (Table 5.1). The level and frequency of diving experience varied amongst respondents but the majority were relatively experienced divers, with 53% completing >500 dives in their lifetime and many diving multiple times per week to remove lionfish (23%) (Table 5.2).

Table 5.1. Summary of the lionfish invasion throughout the invaded region and the composition of the respondents participating in this survey conducted in 2013. The year lionfish were confirmed within the country are indicated in parentheses () whilst the number of respondents participating are indicated via braces {}. An asterisk * highlights countries that were represented within this study.

Recent (<2 years)	**Early (2-5 years)**	**Mid (5-10 years)**	**Late (>10 years)**
Antigua (2011)*	Aruba (2009) {2}*	Bahamas (2005) {3}*	USA (1985) {11}*
Barbados (2012) {2}*	Bonaire (2009) {37}*	Belize (2008) {10}*	
Dominica (2011) {1}*	Cayman Islands (2009) {1}*	Bermuda (2004) {6}*	
Grenada (2012) {5}*	Curaçao (2009) {16}*	Jamaica (2008) {3}*	
Guatemala (2012) {1}*	Honduras (2009) {4}*	British Virgin Islands (2008)	
Trinidad & Tobago (2012) {1}*	Mexico (2009) {2}*	Colombia (2008)	
Martinique (2011)	Panama (2009) {2}*	Cuba (2007)	
St Lucia (2011)	Puerto Rico (2009) {2}*	Hispaniola (2008)	
St Vincent (2011)	Anguilla (2010)		
	Costa Rica (2009)		
	Guadeloupe (2010)		
	Nicaragupe (2009)		
	St Kitts (2010)		
	St Martin/Maarten (2010)		
	USVI (2010)		
	Venezuela (2009)		

Table 5.2. Composition of survey respondents, their dive experience and engagement in lionfish control (N=112)

Question	**Responses**			
Gender	Male (73%)	Female (25%)	Undisclosed (2%)	
Age	18-25 (9%)	25-40 (25%)	40-60 (54%)	>60 (12%)
Geographic Origin	North America (44%)	Caribbean Island (21%)	European Union (29%)	Central & South America (6%)
Worked in dive industry	Yes (37%)	No (61%)	No response (2%)	
How many dives in their lifetime	<100 (18%)	100-500 (29%)	500-2500 (31%)	>2500 (22%)
How often to they hunt lionfish	Many times per week (23%)	1 - 4 times per month (39%)	1 - 5 times per year (23%)	Other (15%)
How many lionfish caught in their lifetime	<25 (26%)	25 - 100 (26%)	100 - 1000 (30%)	>1000 (18%)
Where do they hunt lionfish	North America (9%)	Caribbean Island (23%)	ABC Islands (50%)	Other (8%)

When responses were examined according to the phase of invasion, the 40-60 age group dominated across all categories (recent. 45%, early. 59%, mid. 46%, late. 64%). Furthermore, as the lionfish invasion proceeded (from recent to late stages), although there was an overall domination of male lionfish volunteers, there was an increase in the involvement of female lionfish volunteers (Fig. 5.1). Additionally, the frequency at which lionfish volunteers engaged in lionfish removal activities decreased as the invasion proceeded. During the recent and early phases, volunteers were often involved in removal activities multiple times a week whereas during the mid and later phases, this became more infrequent (Fig. 5.2).

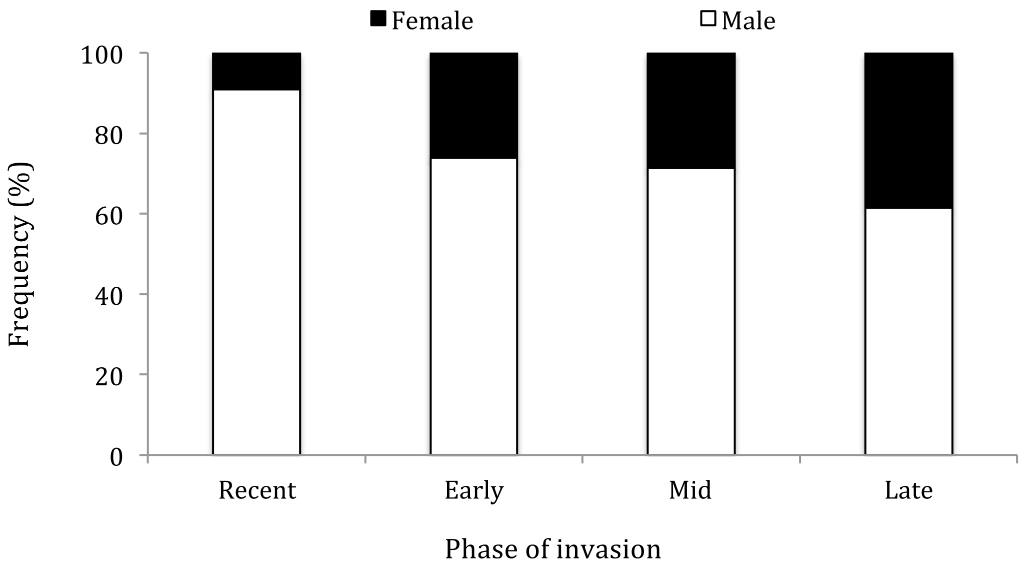


Figure 5.1. Distribution of male and female lionfish volunteers at varying phases of the invasion

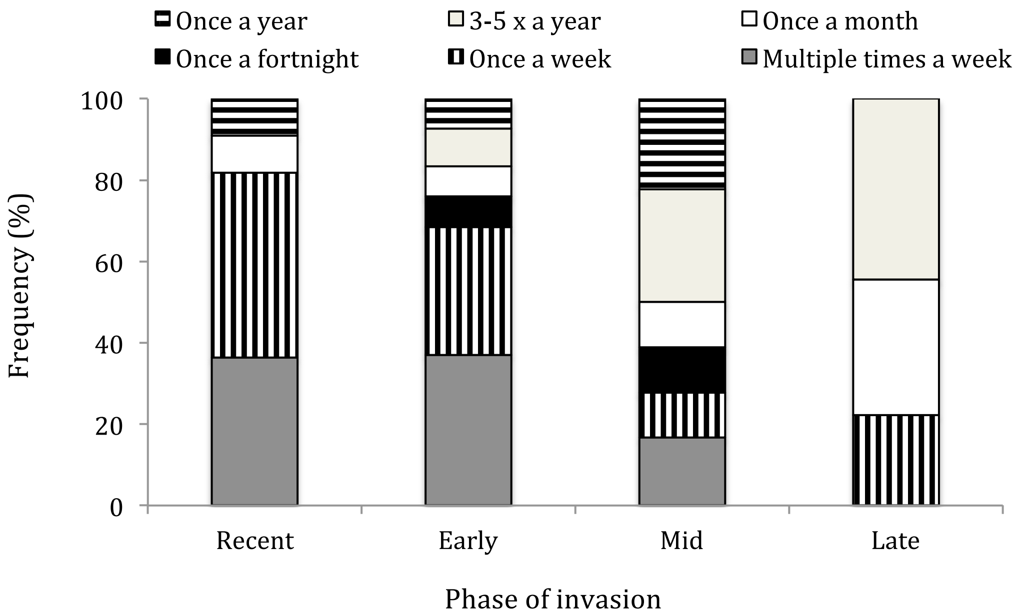


Figure 5.2. Frequency at which lionfish volunteers engaged in removal activities at varying phases of the invasion

Respondents' perceived impacts of lionfish and their reasons for removal. Of the 112 respondents, 89% believed that lionfish were having an impact in the Caribbean/invaded region. All respondents stated that they were aware of the impacts of lionfish, with the reduction in native fish populations (45%), damage to the ecosystem (37%) and the effect on local livelihoods (12%) being the main categories of impacts that were perceived by the questionnaire respondents (Fig. 3a). Results from all completed questionnaires suggest that knowledge of the negative impacts of lionfish (Fig. 5.3a) is the principal reason why people remove lionfish (36%) with the desire to protect the reef (31%), wanting to help (17%) and personal enjoyment (14.3%) being the other main reasons (Fig. 5.3b). Only 1% of the respondents identified financial benefit as their main incentive for removing lionfish.

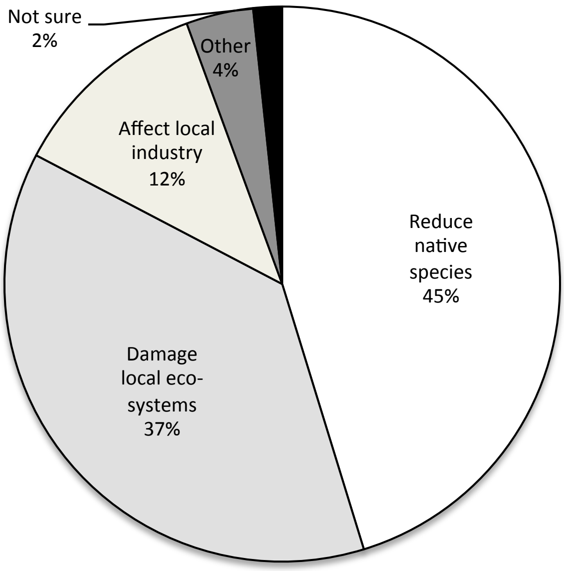


Figure 5.3a. Perceived impacts of lionfish reported by lionfish volunteers [N=112]

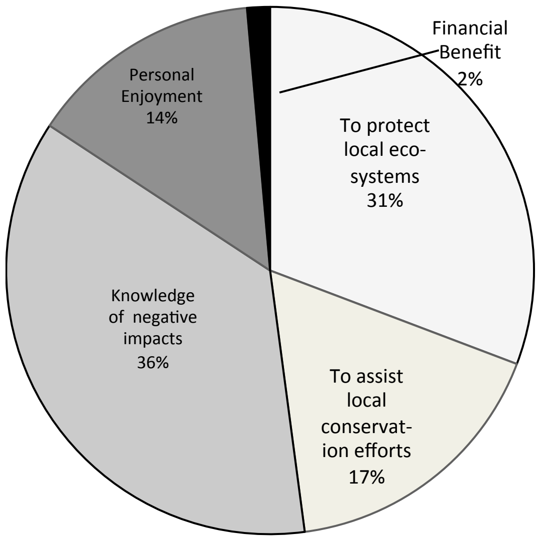


Figure 5.3b. Respondents' reported reasons for removing lionfish [N=112]

5.4.2 Suggested end uses of lionfish

Once a volunteer catches a lionfish there are a variety of possible destinations for the fish. When all respondents' data were pooled, the majority of respondents used the lionfish they caught for personal consumption (43%) or gave them to family or friends for consumption (21%). A smaller portion or respondents sold them to local restaurants/hotels (15%), and the minority either left them on the reef (10%) or fed the caught lionfish to other reef fish (5%) (Fig. 5.4). It was more common for respondents in the rest of the Caribbean to feed lionfish to other fish than those in the ABC islands. Based on pooled respondent data, 6% suggested "Other" means of lionfish utilisation which ranged from making lionfish jewellery, donating specimens to research, or using them for education and awareness purposes (Fig. 5.4).

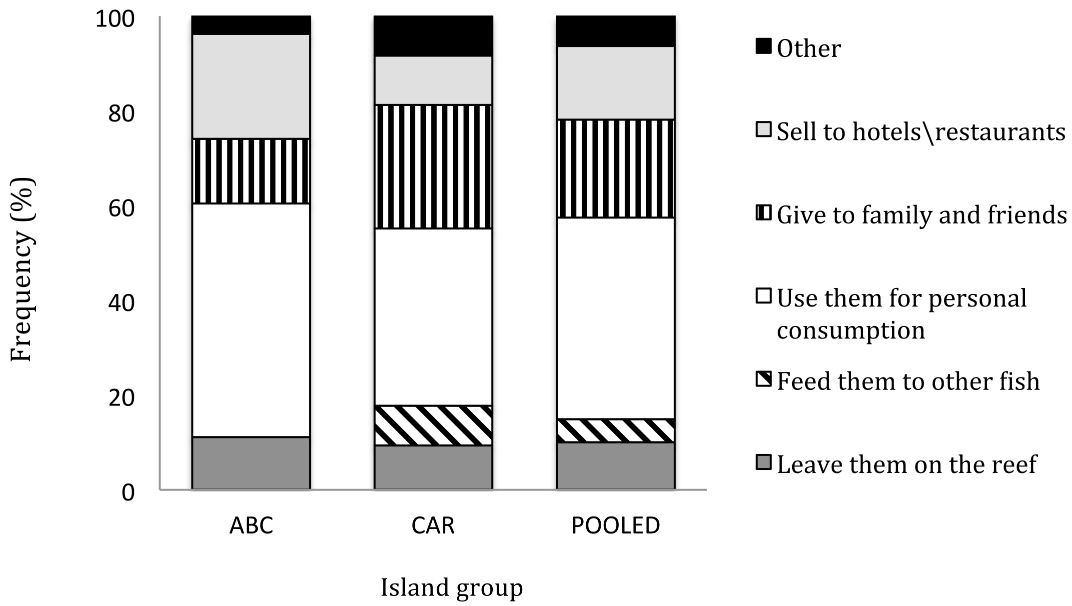


Figure 5.4. Reported end use of lionfish caught by volunteers [N = 112] (Where, ABC= Aruba, Bonaire, Curaçao; CAR = Rest of the Caribbean, i.e. North, Central, South America and Caribbean Islands)

Table 5.3. Summary of questionnaire responses reflecting perceived incurred financial costs and benefits of lionfish removal

Question	Responses				
Has catching lionfish (or the presence of lionfish) been responsible for incurring any financial costs or benefits to you thus far?	Yes (55%)	No (37%)	Not sure (8%)		
Can you suggest approximately how much money per month lionfish may be costing you?	$0 (36%)	$1 – 50 (36%)	$50 - 250 (19%)	$250 - 500 (4%)	>$500 (5%)
Can you suggest approximately how much money per month lionfish may be benefitting you?	$0 (56%)	$1 - 50 (22%)	$50 - 250 (14%)	$250 - 500 (4%)	>$500 (4%)

5.4.3 Cost-Benefit Analysis

A cost benefit analysis was conducted using respondents' answers to provide estimates of their perceived expenditure and earnings per month as a result of lionfish removal. Of the 112 volunteers interviewed, 55% suggested that the removal of lionfish involved some form of personal financial cost or benefit (Table 5.3). When results of the survey were treated as a whole, pooled geographic group, there was generally a greater perceived cost than benefit amongst respondents. However, when respondents were divided according to geographic group, i.e. where they conducted the majority of their lionfish hunting (ABC vs. CAR), there were considerable differences in the cost-benefit profile (Fig. 5.5). In the ABC islands there was a net perceived benefit ranging between US$30 - 60 per person per month whilst in the rest of the region the net cost ranged between US$50 - 100 per person per month. In the ABC islands, in the greater price range categories (i.e. >$50) there were a greater proportion of benefits (26%) whereas in the rest of the Caribbean there were a greater proportion of costs (36%) in this price range (Fig. 5.5).

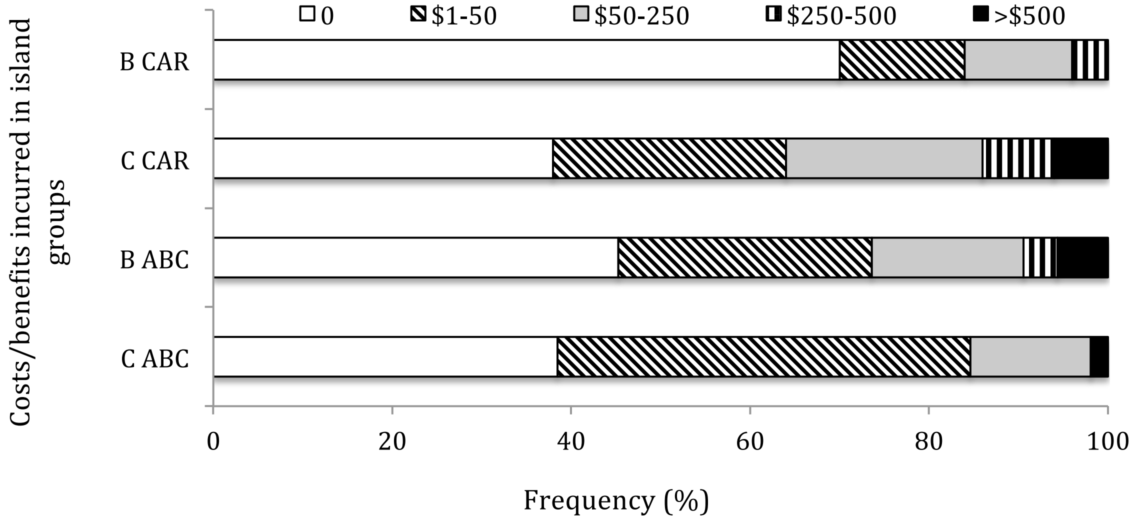


Figure 5.5. Reported monthly financial costs and benefits (in US$) incurred by lionfish volunteers as a result of the lionfish invasion [CAR. N = 57; ABC. N = 55] (Where B= Financial benefit incurred; C= Financial cost incurred; ABC= Aruba, Bonaire, Curaçao; CAR = Rest of the Caribbean, i.e. North, Central, South America and Caribbean Islands).

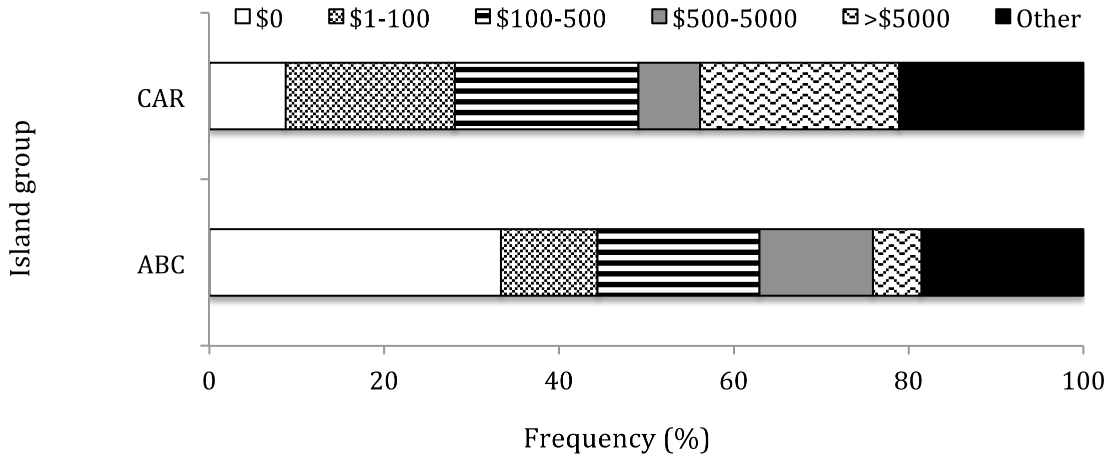


Figure 5.6. Reported willingness of lionfish volunteers to pay for total removal of lionfish (one off payment) [N = 104] (Where ABC= Aruba, Bonaire, Curaçao; CAR = Rest of the Caribbean, i.e. North, Central, South America and Caribbean Islands). The category 'Other' represents respondents who chose not to answer this question or provided responses that did not fit into the pre-listed category.

Willingness to pay evaluation. There was some variation in respondents' willingness to make a one-off payment for the total eradication of lionfish. When respondents' data were pooled, of the 90 respondents who participated in the WTP assessment, 25% were not willing to pay anything; 9% were willing to pay between US$1-50, 41% between US$51-1000 and 25% willing to pay >US$1000 for the total eradication of lionfish. However, when the responses were separated according to geographic group there were statistically significant differences (P=0.0001) with many respondents in the ABC islands (33%) willing to pay nothing (Fig. 5.6). In the rest of the Caribbean, a minority (9%) of respondents were willing to pay nothing, but 72% were willing to pay >US$100 for total eradication of lionfish (Fig. 5). Within the pooled dataset, the reported WTP per person for total eradication of lionfish ranged between US$1741 to $2,304. In general, as the invasion proceeded (from recent to late), respondents were willing to pay more for there to be total eradication of lionfish (Fig. 5.7). The responses that did not fit into the pre-listed categories were grouped into the category "Other". Within this group, the majority (50%) did not assign a monetary value because they believed that it was simply "not possible" for there to be total eradication of lionfish whilst 6% suggested that they would be willing to pay "millions and billions". The remaining respondents simply stated that they were unsure or did not understand the question.

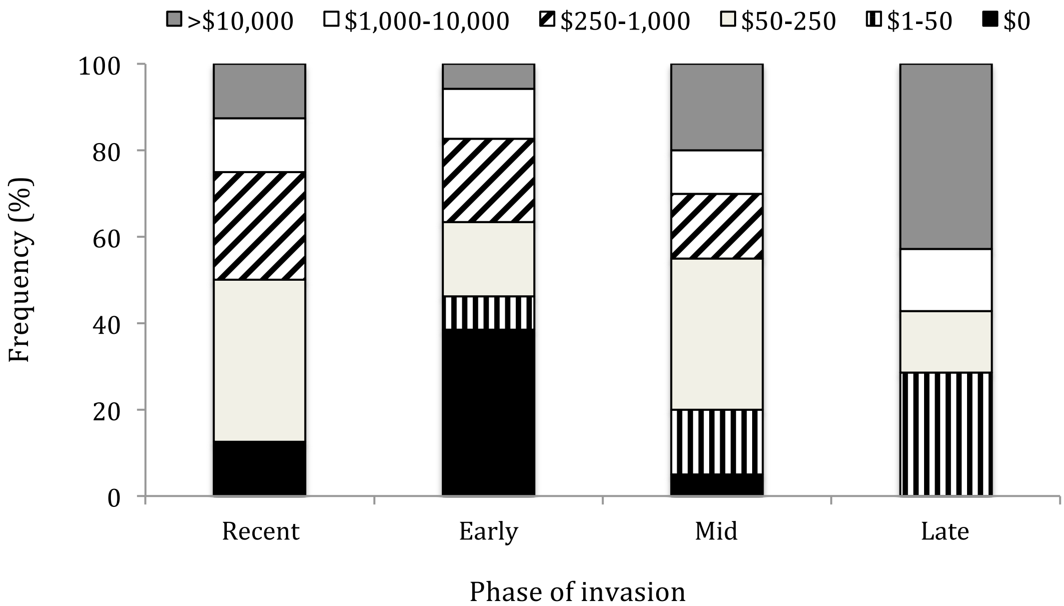


Figure 5.7. Reported willingness of lionfish volunteers to pay for total removal of lionfish (one off payment) at varying phases of the invasion [Recent. N = 8, Early. N = 52, Mid. N = 20, Late. N = 7)

5.5 Discussion

5.5.1 Establishing the lionfish volunteer profile

Lionfish hunting is developing as a popular past-time throughout the Caribbean and North America. Since the invasion of lionfish some two decades ago, their persistent growth and their potential to destroy native ecosystems (Anton et al. 2014; Cure et al. 2014; Layman et al. 2014) have caused alarm amongst scientists, fishermen, policy makers and also the concerned diving population. Divers are especially sensitive to environmental issues from early on in their dive training since this helps to produce more environmental consciousness among divers (Cater and Cater 2007, Worachananant et al. 2008, Hammerton et al. 2012).

Lionfish volunteers share a common goal, which is to eliminate lionfish. It was not surprising that this research revealed that lionfish volunteers tended to be relatively experienced divers, since pro-environmental diving behaviours tend to increase with diving experience (Todd et al. 2001; Worachananant et al. 2008; Hammerton et al. 2012). Lionfish hunting in Bonaire and Curaçao especially tends to be more male dominated which may be related to gender differences in risk-taking as well as attitudes towards hunting. Male divers are renowned for being for more adventurous and tend to enjoy deeper diving (Rouphael and Inglis 2001; Uyarra et al. 2009). Recreational hunting is also male-dominated (Herzog 2007; Kellert and Berry 1987); the United States Census Bureau, for example, reported a gender ratio of 6.5 men to every woman in 2004-2005 (Herzog 2007). Furthermore, globally, the highest rate of volunteering occurs during middle age (Churchman 1987; Dolnicar and Randlem 2004; Measham and Barnett 2007), which corresponds to the finding within this research that most volunteers tended to be in the 40-60 year age group.

Using this knowledge of which characteristics makes individuals more likely to volunteer in lionfish removal activities can be the first step to identifying and recruiting future lionfish volunteers. Relatively experienced male divers, within the 40-60 year age group were found to be the most common profile of lionfish volunteers. Similar trends regarding the profile of lionfish volunteers were found in research on lionfish tournaments within Bahamas and Florida (Trotta 2014). Furthermore, Trotta (2014) revealed that the majority of their respondents disclosed an annual household income of >10,000USD which suggests that these individuals participating in lionfish tournaments possess the financial ability to pursue activities like lionfish hunting. Although some attributes such as education (Yavas and Riecken 1985; McPherson and Rotolo 1996), employment (Curtis et al. 1992) and earning potential (Menchik and Weisbrod 1987; Smith 1994) have been previously linked with volunteering behaviour (Dolnicar and Randlem 2004), these attributes were not explicitly explored in this research in order to achieve greater questionnaire response rates. However it will be worthwhile to investigate these aspects further in future research.

5.5.2 Involvement of lionfish volunteers in removal activities

<u>The costs of removing lionfish</u>

Invasive species removal is no cheap task, especially in marine systems since there is need for specialist training and equipment which increase costs and limit the number of capable individuals. For lionfish hunting activities, there are two categories of costs involved. long-term one-off costs (purchasing dive equipment, lionfish removal tools and containment devices, gloves and other accessories) and short-term on-going costs (tank fills, and fuel for driving to dive sites). The cost of dive equipment may be negligible since, as avid divers, the majority of volunteers would have already owned personal gear, rather than investing in gear solely for lionfish removal purposes. In most countries, volunteers purchase their own tools such as pole spears or Hawaiian slings whereas in Bonaire, the ELF Tool is provided free of charge to volunteers (de Leon pers. comm.). As a result, lionfish containment devices such as the Zookeeper or homemade alternatives along with gloves or any other personal effects are the main additional cost for volunteers in Bonaire. These long-term investments may have additional on-going costs due to maintenance and upgrading of tools and containment devices over time.

Given the reported level of diving activity (47% of respondents dove at least once a week) these on-going costs undoubtedly accrue. For dive operators that possess their own compressors, tank fills are relatively cheap, but for the typical recreational diver a tank fill can cost on average \$10–30 USD if people are shore diving, but for boat dives the costs can range between \$50–150 USD depending on the location. Thus a question remains unanswered. why do lionfish volunteers invest so much into removal? Is there some sort of financial gain, or is it purely down to altruism, or is money simply not a material consideration?

However, within Bonaire, these costs were minimised since at the beginning of the invasion lionfish volunteers would receive free tank fills from specific dive shops upon presenting their lionfish removal certification badge and showing proof of their lionfish removal equipment. Furthermore, STINAPA chartered dive boats once or twice a year for removal in targeted areas whilst other dive operators give dedicated volunteers discounted prices on tank fills and boat diving. Providing lionfish removal tools and tank fills to dedicated volunteers can help to minimise costs to volunteers and also encourage a more long-term participation in lionfish removal and should be considered for future lionfish control strategies, especially when there is need to recruit or retain participants.

Besides the financial costs of lionfish hunting, there is also the potential cost of personal injury or in very extreme cases, death. Lionfish possess a highly developed venom apparatus (Church and Hodgson 2002; Forrester 2008; Morris 2009) which can affect neuromuscular transmission and causes cardiovascular and neuromuscular effects in animals and humans (Nair et al. 1985; Morris 2009). By being so closely involved in removal, volunteers increase their risk of envenomation. Although there have been no confirmed fatalities within North America and the Caribbean region as a result of envenomations, a lionfish sting often results in great pain and swelling which can indirectly cause great danger to divers, especially when at depth (Vetrano et al. 2002; Morris 2012).

In addition to increasing the probability of envenomation through lionfish hunting, divers also put themselves at greater risk of dive related injury and trauma. Lionfish removal is an evolutionary relationship which can be comparable to predator-prey interactions whereby 'evolutionary changes' by the prey to 'outsmart' the predator are met by subsequent responses in the predator (Lima 1998; Abrams 2000; Peckarsky et al. 2008). Over time lionfish learn from failed attempts at being captured, modify their behaviour and activity patterns and are generally more vigilant to volunteers's movements and sounds (Côté et al. 2013). Simultaneously, the volunteers improve their personal hunting skills and enhance their equipment; creating longer spears to remove lionfish hidden far under ledges, have larger containment devices, use larger scuba tanks or venture into decompression diving or technical diving allowing them to go deeper and stay underwater longer. Divers increasingly use re-breathers (closed circuit scuba) to minimise the sounds associated with breathing whilst diving, whilst also extending their depth and time underwater. As a result, volunteers increase their risk of suffering depth related issues such as decompression sickness and narcosis. Thus, another question emerges. why do lionfish volunteers put themselves at greater risk to remove lionfish?

<u>The benefits of removing lionfish</u>

Lionfish has been deemed as one of the worst marine invasive species of all time due to its high growth, feeding and reproductive rate along with its generalist diet, lack of natural enemies and its great, unabated reproductive output (Albins and Hixon 2011; Kulbicki et al. 2012; Diller et al. 2014). Of the 11,161 lionfish analysed over the four-year study period, a total of 10,495 prey items (7,383 fish and 3562 invertebrate) were documented. Thus removal of lionfish is viewed as being beneficial due to ecological benefits. Other literature has suggested that lionfish feed on species such as herbivores (maintain algal growth on reefs) and cleaner species (maintain health of fish by removing parasites), which mean that native ecosystems may be at risk from the removal of these ecologically important species (Cecarelli et al. 2005; Albins and Hixon 2008; Lesser and Slattery 2011; Côté and Green 2012). This desire to protect and conserve native species from invasives, rather than financial motivations seems to be the main incentive for involvement in lionfish removal amongst volunteers throughout the Caribbean (Fig. 5.3). This behaviour is similar amongst other programmes where volunteers participate for their own enjoyment, their interest in science or due to their love for conservation, rather than for any financial gain (Cohn 2008; Raddick et al. 2008; Parfitt 2013).

The majority of lionfish volunteers utilised lionfish as a food fish, via personal consumption, sharing with family or friends or selling to restaurants. Marketing lionfish as a food fish has excellent ecological impacts (Morris et al. 2011; Green et al. 2013). Not only is there a direct reduction on ecological stress from predation on native species, there is an indirect impact on native predators (Green et al. 2013; Côté et al. 2014; Pasko and Goldberg 2014). Species such as snappers, groupers or even lobsters are already greatly overexploited throughout the Caribbean (Mendoza and Larez 2004; Johnson 2010; Mumby et al. 2011; Mateos-Molina et al. 2014), as they are the preferred seafood choice amongst locals and also visiting tourists (Morris et al. 2011). Thus the introduction of lionfish as a food fish helps to reduce fishing pressure on these previously exploited species, thereby allowing for their replenishment which can benefit future generations (Aguilar-Perera 2012; Gallagher 2013; Pasko and Goldberg 2014).

In addition to utilising lionfish as a food fish, other respondents reported that they used lionfish to make jewellery, donated the specimens to research, or used them for education and awareness purposes (Fig. 5.8). Artists take advantage of the unique; ornate beautifully patterned spines, rays and tails of lionfish to make an assortment of jewellery (Smith 2014). Depending on the design, at least 2-4 creations can be made from a medium sized lionfish. The venomous spines are easily denatured and rendered inactive by simply applying heat through baking and roasting (Karp 2014). Subsequently, some artists dye the spines, rays and tails to enhance their colour or to also create more intricately coloured pieces (pers. comm. Karp 2014). Karp (2015) estimates that the sale of fins and spines can increase the landed value of lionfish from 16 – 61%. Seeing that jewellery and handicraft utilises materials that are typically discarded, there is great potential for profits to be made. However, considering that only one of the 112 respondents interviewed within this study utilised lionfish as jewellery and handicraft reveals that there is scope for the development of this market.

Figure 5.8. Sample lionfish jewellery designs being sold throughout the Caribbean from The Frapper (circle) and Kaj Expressions (diamond)

5.5.3 Lionfish volunteers. motivations, recruitment, reinforcement and retention

With regards to citizen science type activities, motivations of volunteers may range from the want to gain knowledge and discover; to contribute or assist; to become part of a community and meet others; for fun, enjoyment, novelty or competition; or simply to become a better individual (Raddick et al. 2008). Individuals may be motivated intrinsically (i.e. derived from the task itself) or extrinsically (i.e. the outcomes of the activity) (Everleigh et al. 2004). It has been established that high intrinsic motivation led to greater and more dedicated participation as compared to extrinsic motivation which led to more casual engagement in activities (Everleigh et al. 2004). Furthermore, although there may be some overlap, in general short-term and long-term participation are derived from different motivations (Rotman et al. 2014). There is need for some form of personal interest for participation to occur in the first place, but there needs to be a more far-reaching motivation that goes beyond the individual for long-term participation to occur (Rotman et al. 2014).

Within the invaded region, lionfish removal creates a sense of community and comradery amongst volunteers which can serve as motivation for more long-term participation. These individuals often share hunting tips based on their experiences and give advice on best areas and techniques for hunting lionfish. Additionally throughout the invaded region many team up to hunt lionfish recreationally or at annual tournaments, since the overall goal of lionfish eradication is shared amongst this group. Within Bonaire removal activities are co-ordinated by social media such as Facebook and these volunteers also share their knowledge with one another, giving tips on the best places or times to go hunting or also techniques that they have found to be most successful in removing lionfish. Furthermore, Facebook allows for positive reinforcement of volunteers by researchers as well as local management. One aspect that has proven successful in encouraging, motivating and retaining volunteers is reinforcement of their work. When volunteers can see that the time and effort they invested has reaped some benefit or is actually making a considerable contribution towards the overall project they are more likely to continue participating or even encourage others (Hong et al. 2008). Kollmuss and Agyeman (2002) have suggested that positive reinforcement helps to encourage certain environmental behaviours whether it be intrinsic or extrinsic. Efficacy along with other factors likes time requirement, supervisory assistance, volunteer training, group interaction and fulfilment from task completion have also been associated with volunteer retention (Farmer and Fecor 1999; Brown 1999; Galindo and Guzley 2001; Keith and Schafer 2002; Hong et al. 2008).

Financial motivation amongst volunteers did not feature highly within this study, however throughout the invasive region this factor may need to be considered. Throughout the invaded region, lionfish as a food fish has been developing as lucrative market, which may appease those financially motivated individuals. In other countries small quantities of money (referred to as bounties) have been offered for lionfish specimens to be submitted, however the longevity of this scheme is often questionable since it requires a large investment. Thus this scheme is likely to be successful only when there is private sector involvement or on-going and dedicated sponsorship. Nonetheless, offering tank fills or sponsored lionfish removal trips for free or at a reduced cost can be other simple ways to appeal to these individuals. As previously stated within this research, most respondents claimed to neither be gaining nor benefitting financially from lionfish removal, with some even suggesting that their benefits were higher than their costs (Table 2). This shows great promise for future management of in these areas since there is minimal financial loss from removal. The vast majority of lionfish volunteers were divers first, and hunters second. Thus hunting acts as a supplemental activity to their already established hobby. diving. Hunters have suggested through responses on the questionnaire that lionfish hunting was a new way to make diving more exciting. This can prove to be an important factor when sustaining lionfish hunting or the retention of volunteers are concerned. If volunteers are focused on personal enjoyment rather than financial benefit, a dive where few or no lionfish are caught will still be beneficial/enjoyable as they enjoy the dive and are not deterred by the lack of fish caught. Furthermore, education also is an important factor here. When encouraging lionfish hunting, the aim should be for removal, not as a sustained sport (Ali et al. 2013). Thus if people keep this as their mind-set, lionfish hunting will exist as long as the lionfish persists (de Leon et al. 2013). However, the opinions of conservation-minded divers might be different to that of fishermen who are dependent on fisheries as their main form of income.

Throughout the lionfish invaded region, fishers have been involved and affected by lionfish in varying ways. Within Bonaire, fishers are not involved in lionfish removal activities because of limitations on their fishing practices. Fisher folk in Bonaire typically use hook and line as their main method (a method which has proven unsuccessful to lionfish capture) and the majority do not even dive or swim, whereas in Jamaica and other islands, spearfishing is one of the biggest fishing industries and these fishers are therefore more directly affected by and involved with the lionfish invasion. Understanding the opinions of these fisher-folk and their perceptions on how they are being financially affected by the lionfish invasion is important for future research. This is reiterated by Aguilar-Perera (2012), who questioned how fishermen could be persuaded to invest their low income on this hopefully temporary fishery, especially since the aim is for this fishery to disappear in the long term. Furthermore, because of over-fishing and the current state of most Caribbean reef ecosystems, it seems that low-income fishermen dependent on reef fish assemblages stand to suffer the most losses from the lionfish invasion. Although dive operators are dependent on the local reef fish and ecosystem diversity, lionfish and their removal can be incorporated, for financial gain.

Whereas with fishermen, especially within the smaller Caribbean islands, there is already widespread over-exploitation, so lionfish seem to be the final nail in the coffin in the current state of their dismal fishing economy, unless they are able to capitalise on lionfish as a food fish.

5.6 Conclusion

Throughout the invaded range, various lionfish management measures have been initiated and have continuously evolved in terms of the schemes established, the tools used, and the means to increase and enhance removal efforts. Due to the invasion characteristics of lionfish, a need was identified for a larger removal effort and necessitated the involvement of divers. The success of lionfish removal at local levels within some countries has been underpinned by the involvement of volunteers. Thus, knowledge of how to reinforce and amplify volunteers' inputs and actions can be used to encourage further lionfish control and be invaluable towards tailoring future management schemes utilising volunteers by understanding people's motivations, and which groups to target. This study aimed to establish the profile of lionfish volunteers, determine why and how these individuals participate in lionfish removal and also investigate what needs to be done to enhance volunteer usage, retention and reinforcement. By establishing this profile and understanding how these individuals are motivated helps to inform the most appropriate means to reinforce and subsequently recruit new volunteers by considering these factors in combination (Fig. 5.9).

This research established the profile of the typical lionfish volunteer in the Caribbean to be relatively experienced, male divers within the 40-60 year age group. These lionfish volunteers have not only aided in the detection, removal and monitoring of lionfish from local coral reefs, but they have also helped to create and contribute to new markets. Lionfish has now been established throughout the Caribbean as a food fish and especially as a more environmentally friendly alternative to consuming other reef fish and invertebrates. This research also recognised that the majority of lionfish volunteers were not financially motivated to remove lionfish and reinforcement proved to be the most effective means of volunteer retention based on responses from questionnaires and discussions with volunteers. Evidence that their actions were having meaningful impacts on reducing lionfish populations and helping to protect the environment they love proved to be the main factors motivating volunteers. The lionfish volunteer circle especially appears to be dominated by altruistic, conservation-minded individuals, characteristics that can be of great value in other areas within the invaded region dealing with the lionfish invasion.

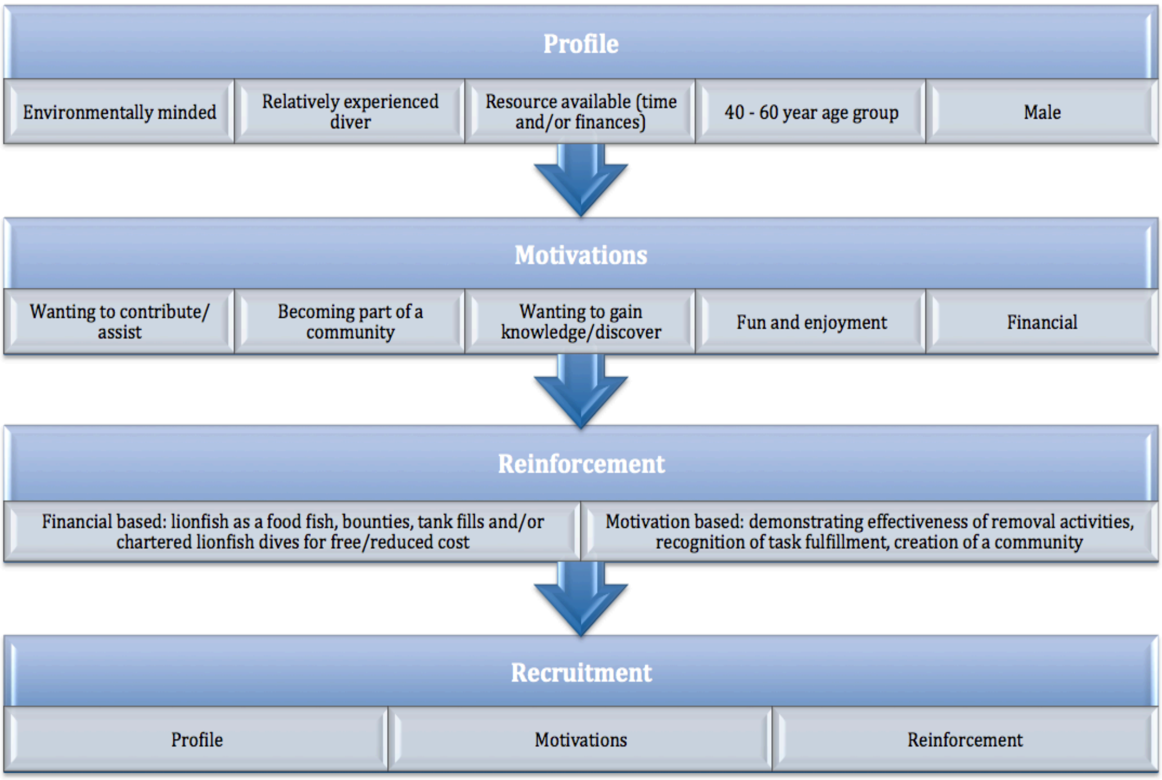


Figure 5.9. Summary of the profile and motivations of lionfish volunteers as well as the factors affecting reinforcement and recruitment

Chapter 6: CONCLUSION

Although often highly difficult, when managing any invasive species the desired end goal needs to be considered and the applied strategy tailored accordingly (Willis et al. 2007; Davis et al. 2011). Throughout the invaded range there have been demands for the creation of a unified lionfish removal strategy. However lionfish management should not be a universal strategy (Nunez and Pauchard 2010; Perrault and Muffet 2002) and should instead be more intricate, and consider the location, ease and accessibility of sites; availability and proficiency of volunteers along with local legal frameworks on fishing and gear restrictions (Morris 2012; Lozano 2013; Trotta 2014; Carballo-Cardenas 2015).

Lionfish are now established extensively throughout the Caribbean region, the Gulf of Mexico and the coasts of North, South and Central America (Schofield 2009; Morris et al. 2010; Barbour et al. 2011; Côté et al. 2013; Elise et al. 2014). Within their introduced range, lionfish have infiltrated a diverse array of habitats (Cure et al. 2014; Pusack 2014) including hard bottom, shallow and mesophotic reefs (Whitfield et al. 2007; Albins and Hixon 2011; Biggs and Olden 2011; Lesser and Slattery 2011; Côté 2013); mangroves (Barbour et al. 2010); seagrass (Claydon et al. 2012) and estuarine habitats (Jud et al. 2011, Jud and Layman 2012; 2014). In addition to their diverse habitat association, lionfish have been found at depths ranging from <1 to >300m (Côté et al. 2013) thereby confounding the reality of how difficult management truly is. Furthermore due to their extensive dispersal, lionfish are a regional problem, requiring a dedicated, co-operative but resource intensive effort. If left unmanaged, the magnitude of the threat they pose to Caribbean ecosystems remains uncertain, thereby warranting the need for effective and efficient management schemes. Therefore, knowledge of their ecology and whether any patterns exist regarding their size structuring, sexual dimorphism or depth/habitat association can help to tailor removal efforts and improve management.

This work contributes to new knowledge by identifying which lionfish should be removed, what was the most effective depth for removal along with which tools and education strategies were most effective as well as the value of a dedicated volunteer response effort as well as their motivations and means for recruitment and reinforcement. Furthermore, by conducting analyses where lionfish response was assessed between islands with varying responses to management, and also within a single island with different hierarchies of hunting pressure, this provided new insight into management dynamics. Finally, this work provided the first direct comparison of lionfish diets within distinctly different habitats aas well as stages of the invasion timeline.

6.1 What impact is lionfish feeding ecology having on local ecosystems?

Lionfish within Bonaire, Klein Bonaire and Curaçao like the rest of the introduced range possess very generalist diets, dominated by teleost fish. Within this study, when sex was considered within lionfish feeding ecology it was found that female and immature individuals possessed significantly more prey in their stomach contents than male and mature ones. A total of 10,945 prey items (7,383 fish and 3562 invertebrate) belonging to 29 families (11 invertebrate, 18 fish) were documented in the stomach contents of 11,161 the lionfish stomachs examined in this study. Just under 4% of the 8,901 lionfish with prey in their stomachs possessed >5 individual prey items at the time of capture. Generally as lionfish increased in size, there was a decrease in the number of prey items consumed (See Chapter 4) but a higher frequency of larger prey items in their diet (See Chapter 4). Current scientific literature persistently presents lionfish as voracious, gluttonous individuals but contrary to these reports, those within this study did not appear to have as an insatiable a diet as being suggested.

Lionfish also do not appear to be removing large quantities of ecologically or economically important species but this could simply be a limitation of stomach content analysis and its representation of the last meal before capture. Instead, they appear to be offering top-down control of 'over-abundant' species such as *S. partitus*, or species that have a somewhat negative impact (*Stegastes sp.* and *Sparisoma sp.*). Thus based on their feeding ecology, they appear to be acting as a typical predator rather than leading to the demise of native ecosystems. However, this scenario involved high resident biodiversity levels along with a persistent and thus quite successful management strategy. Thus it would be interesting to compare lionfish diets to areas with reduced or little management and/or reduced prey level.

Due to their very generalist diet and the lack any clear patterns in terms of dietary choices, the role of trait-based selection was introduced to determine whether any attributes could make prey species more vulnerable to predation. Based on stomach content analysis, this study suggested that lionfish possessed a preference for slender/elongated shaped fish within the orange, red and yellow colour spectrum. Thus, species such as *Apogon townsendi, Apogon binotatus, Apogon phenax, Apogon maculatus, Halichoeres garnoti, Lipoproma mowbrayi, Thalassoma bifasciatum* and *Serranus tabacarius* appear to be potentially vulnerable to lionfish predation and it would be wise to monitor these populations, but also consider these specific species attributes as bait for passive lionfish removal devices such as traps.

6.2 Which lionfish should be removed?

Since their introduction to the Caribbean region, lionfish have continually grown in size, exceeding reported maximum sizes from the native range (Morris 2009). Although considerable achievements have been made with limiting their growth (Barbour et al. 2011; Frazer et al. 2012; de Leon et al. 2013), with existing tools and technology, it is highly unlikely that lionfish can be completely eradicated from the Atlantic Ocean (Muñoz et al. 2011; Cure et al. 2012; Côté et al. 2014). Total eradication is also inefficient, costly and ineffective (Zavaleta et al. 2001; Reagan et al. 2006; Thresher and Kuris 2004; de Leon et al. 2013) since the resources required to remove the last 1% of a population often demands as much resources needed to manage the first 99% (Simberloff 2003). Partial removal however requires much less time and effort but has been effective in limiting lionfish numbers (Barbour et al. 2011; Morris et al. 2011; de Leon et al. 2013; Côté et al. 2014). Thus, knowing which individuals cause more damaging impacts can help to tailor management schemes.

Sexual dimorphism regarding size was observed throughout this research whereby females attained maximum size at 400mm but males exceeded 470mm. Since this size disparity helps to visually differentiate adult lionfish to an extent, gender specific removal is possible. A female adult can be more damaging to ecosystems due to their reproductive potential, releasing millions of eggs in their lifetime (Morris 2009; Albins and Hixon 2011; Biggs and Olden 2011) whereas males pose minimal risk in comparison. Furthermore those in the earlier life stages (i.e. smaller size classes) appear to have a greater negative impact since during this stage they consume more prey in order to fuel their rather rapid growth rate whereas larger lionfish tended to have minimal prey/empty stomachs (See Chapter 3) possibly because they are no longer exhibiting exponential growth and don't require as much resource intake. Thus focussing on smaller individuals rather than the elusive >400mm giants would be a more successful strategy, especially since these larger fish are more likely to be male and have developed excellent elusion and survival techniques and are more difficult to capture compared to smaller size classes which are relatively naïve to current harvesting strategies. Côté et al. (2014) suggested that lionfish possess very plastic behaviour and quickly learn from failed removal efforts leading to the occurrence of higher flight rates in areas with more intensive culling, but this was a size dependent occurrence, with larger fish showing quicker flight response.

6.3 Where should lionfish be removed?

After determining which size class and/or sex of lionfish to target, knowledge of where to focus efforts remains the greatest priority. Lionfish have been confirmed in diverse conditions from <1 to >300 m depth (Côté et al. 2013) in varied habitats (Whitfield et al. 2007 Albins and Hixon 2011; Barbour et al. 2010; Claydon et al. 2009; 2012; Jud and Layman 2014) making removal challenging. Within this study, individuals were found in a rather broad depth range (<1 – 92m), but there was an observed size-depth relationship whereby larger lionfish inhabited greater depths (See Chapter 3). Although this research was conducted mostly on coral reef habitat, there have also been other reports of variation in habitat association according to size. In areas where there is connectivity amongst mangrove, seagrass and coral reef habitats, smaller individuals inhabited mangroves and seagrass whilst larger ones were more dominant on coral reefs (Barbour et al. 2010; Claydon et al. 2012) with migration amongst habitats occurring (Claydon et al. 2010).

Popular areas or those with better access tend to be more heavily hunted, thus from a management perspective, there is need to encourage efforts on those areas with less hunting pressure. Estuarine, mangrove and seagrass habitat receive considerably less hunting effort compared to coral reefs, but these areas are important nursery habitats, and if lionfish are left unabated, serious negative implications could arise (Claydon et al. 2012). Similarly amongst coral reef habitats, generally sites with rougher conditions or those requiring more advanced dive experience, boat access and long travel times receive less hunting pressure. Within Bonaire, STINAPA recognised this disparity in hunting and in addition to removing lionfish themselves, they also chartered removal trips encouraged dive operators to undertake control efforts in these areas and organised regular removal events at the No-Diving reserve (de Leon pers. comm.). When managing lionfish it is important to understand the area being managed as well as the people conducting removal activities.

Interestingly this study found that focusing removal efforts within the 15 – 25m depth range would allow for removal of a higher proportion of fish within the 101 – 200 mm size class. This is especially beneficial for management purposes since this depth range allows for volunteers to have relatively long dives within no decompression limits, allowing for more efficient removal per effort extended. It has been proposed that lionfish are learning from failed culling attempts and in areas with higher culling frequencies, there was a greater flight response as compared to areas where culling was not as dominant (Côté et al. 2014). Thus, lionfish within this size class are expected to be easier to catch as they are likely to be more naïve to these removal efforts (Côté et al. 2014), but their size makes them more visible and more easily detected and caught, allowing for a higher probability of successful capture.

6.4 When should lionfish be removed?

Despite their reported cryptic behaviour in their native range (Fishelson 1997), lionfish were observed and also captured at all times of the day ranging from 5.00-23.00. This study along with others (Fishelson 1975; Green and Côté 2011) suggested that their peak activity coincides with crepuscular periods of dawn and dusk. This knowledge can enlighten volunteers as to the best time to go hunting, however, for practicality purposes, more divers tend to hunt at dusk rather than dawn. Moreover, based on findings from this study, dusk is an effective time to focus removal efforts. Not only can more lionfish be seen and captured; but also they are removed before they have a chance to make their impact, i.e. start feeding. This feat was revealed when 60% of the individuals caught at dusk possessed empty stomachs, as compared to 20% at night.

6.5 How often should lionfish be removed?

Although it has been accepted that lionfish eradication is nearly impossible (Muñoz et al. 2011; Cure et al. 2012; Côté et al. 2014), management has proven highly effective (Barbour et al. 2011; Frazer et al. 2012; de Leon et al. 2013). The frequency of removal efforts is key, and the more often removal occurs the better. Through modelling, Barbour et al. (2011) estimated that an annual removal effort of 35-65% was required to have an effect whilst Green et al. (2014) recommended a removal rate of 75-95% to allow for a 50-70% increase in local fish biomass (Tilley et al. 2015). However, there is need to monitor not only lionfish removal rates, but also their recovery.

Large-scale events such as derbies/tournaments are highly effective at removing large amounts of lionfish in a very short space of time, but are often very infrequent, usually occurring annually or biannually (Johnston and Purkis 2015). However, these sporadic culls can leave remnant populations behind and instead regular monthly removal efforts have proven to be more effective than yearly culling efforts (Johnston and Purkis 2015). Furthermore, due to lionfish characteristics and source and sink dynamics within the invaded Caribbean, Gulf of Mexico and North Atlantic region, there is need for dedicated region-wide management, however this feat has yet to be realised (Morris and Akins 2009, Barbour et al. 2010, Albins and Hixon 2011, Jud and Layman 2012, Johnston and Purkis 2015). However if such an effort is envisaged, based on extensive modelling scenarios within the Carolinas, Johnston and Purkis (2015) proposed a 20% basin-wide removal rate to be a critical level for successful regional lionfish control.

6.6 Which methods and tools should be used?

Within their invasive range, lionfish have been confirmed in diverse habitats (Cure et al. 2014; Pusack 2014) ranging from 1 – 300m (Côté et al. 2013) on hard bottom, shallow and mesophotic reefs (Whitfield et al. 2007; Albins and Hixon 2011; Biggs and Olden 2011; Lesser and Slattery 2011; Côté et al. 2013); mangroves (Barbour et al. 2010); seagrass (Claydon et al. 2012) and estuarine habitats (Jud et al. 2011, Jud and Layman 2012; 2014). Lionfish have mostly been collected via targeted removals by divers (snorkel, recreational scuba and technical divers) but also through fish traps and occasionally via hook and line. However, scuba diving within recreational dive limits remains the safest and most cost-efficient and effective means of lionfish removal. Free divers although effective at removing lionfish without by-catch, are very inefficient due to the limitations of breath-hold ability and depth.

A variety of tools are available for lionfish removal and containment, but each has its own advantages and shortcomings. Lionfish have successfully been captured in traps and by hook and line, but the majority have been caught by hand netting and spearing via scuba and free-diving (Morris 2012). Spearing using tools such as spear guns, pole spears, Hawaiian slings or the ELF Tool have proven most effective since it involves very targeted removal and avoids by-catch. Hand nets, although effective against by-catch is inefficient in areas of high lionfish density, high coral rugosity and when capturing large lionfish and is thus best suited for hunting smaller individuals, often in shallower habitats (de Leon pers. comm.). Nonetheless, the best tool for removal is ultimately dependent on the legislation in individual countries where restrictions on removal of marine life, or the ownership and use of spears may exist. Furthermore, tool choice is not set in stone and just like invasive species management; it should be a continuously evolving process taking into account the experiences of those involved in removal. As increasing numbers of lionfish are being found at depths exceeding recreational dive limits, the use of a passive device such as a lionfish specific trap is needed. Using knowledge of their prey preferences (See Chapter 4), using items of a taeniform shape or in the orange, yellow or red colour range could be experimented with as preferred bait for lionfish.

Initially in Bonaire, due to legal restrictions on spearing, hand-nets were the only tool allowed for lionfish removal. However, with growing densities and size of lionfish, this soon became inefficient leading to the introduction of the original ELF tool via an amendment in the 2010 Marine Ordinance (STINAPA 2015). The ELF tool was successfully utilised in Bonaire, but as lionfish continued increasing in size, the efficiency of this tool in its original form decreased thus requiring enhancements like thicker, longer shafts and the addition of a trigger to increase effectiveness. Nonetheless, in countries with no restrictions on tool use, pole spears (especially fold-spears) with a minimum 1m-shaft length is reported as being most ideal as it provides the distance and power needed to efficiently capture lionfish. However, these tools can equally be very damaging to local habitats such as coral reefs and be used to hunt native, overexploited species. Thus great consideration needs to be taken by those governing lionfish management as to what tools will be allowed and which persons or groups should be involved in lionfish removal.

Available lionfish containment devices range from mesh bags and dry bags to homemade paint cans and buckets, to more elaborate structures such as the Zookeeper. The Zookeeper which is a plastic PVC tube with a funnel that allows for safe storage of lionfish after collection is the most effective lionfish containment device as it provides a smooth and safe system whereby volunteers can efficiently capture and contain their lionfish without having to handle the lionfish. The number of reported envenomations has significantly decreased since the introduction of the Zookeeper (pers. comm. Allie El-Hage). All other devices require divers to remove lionfish off the spear to place into the containment device, a process that is both inefficient and dangerous. Mesh bags are ineffective due to the potential for envenomation whilst dry bags and other homemade devices, although not completely puncture proof, tend to be bulky.

6.7 What are the potential end-uses of lionfish?

Lionfish as a food fish. Throughout the Caribbean and the Americas, lionfish have been utilised as a food fish in a means to control the population (Morris et al. 2011b; Aguilar-Perera 2012; Landers 2012; de Leon et al. 2013; Hoo Fung et al. 2013). The use of invasive species as culinary treats, also known as the invasivore movement (Tuminello 2014) has been ongoing for decades, e.g. the use of nutria (*Myocastor coypus)*, Asian carp (*Hypophthalmichthys molitrix, H. nobilis, Mylopharyngodon piceus* and *Ctenopharyngodon idella*) or Snakehead *(Channa argus)* etc. (Aguilar-Perera 2012; Landers 2012; Gallagher 2013; Galperin and Kuebbing 2013; Kuebbing et al. 2013). The general unwillingness to eat lionfish varies across territories and stems from misconceptions and misinformation especially related to its venomous spines and the issue of ciguatera (Côté et al. 2013; Robertson et al. 2014). Adequate public education and awareness will always remain the major challenge to the effective management of invasive species especially when it comes to marketing them for culinary purposes (Landers 2012; Kuebbing et al. 2013; Simberloff et al. 2013; Pasko and Goldberg 2014).

When enlightening people about the potential of lionfish as a financial benefit (Morris 2009; Barbour et al. 2011; Morris et al. 2011b; Aguilar-Perera 2012), it needs to be done in such a way that the overall aim is to eradicate rather than sustain (Aguilar-Perera 2012). When advocating the culinary use of lionfish or any other invasive species, education is necessary

(Ali et al. 2013). This aspect is especially important so as to avoid the species becoming incorporated into local culture which makes eradication even harder as in the case of the wild boar in Hawaii and Patagonia (Landers 2012; Nunez et al. 2012; Varble and Secchi 2013). Furthermore, there is the fear that invasive species develop into lucrative new products and become so desirable that there is the possibility that people will want them to persist and persons may begin cultivating them for profit (Aguilar-Perera 2012, Varble and Secchi 2013; Carballo-Cardenas 2015).

Furthermore people are becoming more environmentally conscious and the marketing of lionfish as a 'green' or environmentally friendly fish can encourage its consumption (Landers 2012). Throughout the Caribbean, campaigns such as 'Save the Reef – Eat a Lionfish' or 'Eat them to Beat them' have taken off and REEF has also created the Lionfish Cookbook all in a means to encourage lionfish consumption (Gallagher 2013; Hoo Fung et al. 2013). Lionfish campaigns promoting consumption also present great potential for education (Green et al. 2013; Pasko and Goldberg 2014). Tournaments not only remove large numbers of lionfish (Barbour et al. 2011; Albins and Hixon 2013), but also provide specimens for research which are then ultimately prepared for consumption (Claydon et al. 2011; Ali et al. 2013).

<u>Lionfish Jewellery and Handicraft</u>. In Belize the local men hunt the lionfish primarily as a food fish, but after the fillets are taken, the local women manipulate the carcasses into striking pieces of artwork (Karp 2014). The lionfish jewellery market is quickly expanding throughout the Caribbean and has taken off in Belize, Mexico and St Vincent and the Grenadines and most recently in Bahamas (CEI 2014). Throughout the Caribbean, a pair of lionfish earrings is sold at prices ranging from \$25 - \$40USD whilst necklaces are sold in excess of \$40USD (The Frapper 2016; Kaj Expressions 2016). Household incomes have reportedly doubled through the sale of lionfish as a food fish as well as a craft item (pers. comm. Karp 2014). Considering that jewellery and handicraft utilises materials that are typically discarded, there is great potential for profits to be made.

<u>Lionfish and Diving</u>. The diving industry has also capitalised on the presence of this new invasive inhabitant. Many countries within the Caribbean and Central America especially are dependent on tourism (Hawkins et al. 1999, Williams and Polunin 2000; Barker and Roberts 2004), and in some cases, dive tourism (Dixon et al. 1995; Doiron and Weissenberger 2014; Hilmer-Pegram, 2014). The lionfish invasion is now a household topic and most divers within the Caribbean and the Americas are especially aware of the potential danger of lionfish to native ecosystems (Ali, 2011). As a result, divers are a group of individuals that are not only the most educated about lionfish, but are also willing to remove lionfish. Dive tourism can benefit since tourist divers are willing to pay to either learn to remove lionfish, or actively participate themselves as spotters or shooters on organised lionfish trips. Throughout the

Caribbean dive shops are earning on average $100USD per diver on a lionfish specific dive. Lionfish derbies also stand to contribute greatly to local economies as participants travel to locations such as Bahamas and Florida Keys to participate in these events and each participant spends an average of $820USD locally during a typical weekend derby (Trotta et al. 2014).

Lionfish and the Aquarium Trade. Within the US, approximately 60,000 lionfish are imported annually for aquaria, with the majority coming from the Indo-Pacific Region (Semmens et al. 2004; Ruiz-Carus et al. 2006). As a result, there have been calls and petitions from conservationists and scientists for a complete ban on lionfish import or sale (Hamner et al. 2007, Claydon and Calosso 2008) within the United States. However, this action seems highly unlikely since passing of legislation at the country level needs to be taken up at Congress (pers. comm. Morris 2013). Nonetheless, individual states within the United States have taken the initiative and Florida was the first state to enact a ban on the import of live lionfish along with prohibiting the breeding of lionfish (Alvarez 2014). Anyone found guilty of these offences are subjected to a fine of $1000USD and up to a year in prison (Fagensen 2014). Throughout the Caribbean, other countries such as Trinidad and Tobago, Bermuda and Puerto Rico, were successful in initiating a ban on the import and sale of lionfish (Hare and Whitfield 2003; Ralof 2006). Nonetheless, there is still need to fuel the demand for lionfish within the US aquarium trade and locally caught lionfish have been suggested as an alternative to their imported counterparts. Not only does the supply of the aquarium trade with locally caught species reduce the introduction of new genes to the pool, it offers an incentive for the removal of juvenile fish, before they begin to reproduce. Furthermore, in areas where ciguatera is an issue, the aquarium trade still offers an incentive for lionfish removal when consumption of the fish is not an option.

6.8 Who should be involved in lionfish removal?

Lionfish removal by volunteers is mostly male-dominated, but there was also a high frequency of couples hunting together. Their involvement in removal activities was not financially motivated but instead a result of environmental consciousness and wanting to protect the reefs. These volunteers were typically quite experienced divers which is especially beneficial since this improves an individual's buoyancy control, and is key to successful hunting. Furthermore, willing individuals who are more aware of the lionfish invasion and can dedicate time and potentially even financial resources towards diving and hunting are valuable assets to any removal team. Lionfish volunteers have proven to be an important resource to managing the lionfish invasion and retention of these individuals for removal activities is a key factor governing the success of any management scheme.

Inclusive vs selective strategy

When managing invasive species, decisions need to be made on which individuals are allowed to participate in removal activities as well as the tools permitted for removal. The introduction and vast expansion of lionfish has been deemed as one of the worst marine invasions in the Caribbean of all time (Sutherland et al. 2010; Hoo-Fung et al. 2013; Anton et al. 2014; Cure et al. 2014; Pusack 2014; Johnston and Purkis 2014; Layman et al. 2014; Raymond et al. 2014; Sloan and Turingan 2014). It may seem obvious that such a vast problem would require an inclusive strategy in order to achieve maximum removal by equipping willing divers and letting them hunt as they please. However, throughout the Caribbean inclusive strategies as well as more selective strategies that have restrictions on the tools, individuals and areas allowed for lionfish removal, have been enacted, all with varying success. The concept of quantity vs quality needs to be applied in the assessment of whether to adopt an inclusive or a selective strategy.

One of the main benefits of an inclusive strategy is that not only are a larger number of individuals involved, but also that hopefully there will be the removal of the mid phase between sighting, reporting and removal, since that when a lionfish is sighted it is immediately removed via this inclusive strategy. For example, Bonaire is home to ~16,000 residents but receive 200,000 tourists via cruise ship and about 70,000 per year via airplane annually (Schep et al. 2012) of which 60% are estimated to be divers (Schep et al. 2012). In 2014, it was estimated that >275,000 tourists visited Bonaire (Statistics Netherlands 2016), of which ~36,000 were scuba divers (Lyons et al. 2015); doubling the reported 17,000 visiting in 1991 (Dixon et al. 1993). This magnitude of visiting divers represents a vast resource that can be utilised for lionfish detection and management. Lionfish hunting requires good buoyancy skills to minimise harm to the reef and also to increase the probability of successfully capturing the lionfish. Furthermore, since lionfish learn from failed attempts, an abundance of inexperienced volunteers may actually make lionfish removal more difficult, thereby worsening the problem (Côté et al. 2014).

Bonaire, unlike most other Caribbean islands has adopted a rather selective strategy in terms of hunter and gear restrictions. These restrictions stem from Bonaire's designation as a marine park since 1979 and their existing ban on the possession and use of any spearing device as well as laws against the removal of any wildlife from its waters. Amendments were achieved via a Marine Ordinance in 2010 which allowed the removal of only lionfish through a signed contract with the Marine Park Manager whereby they receive an eradicating lionfish tool (ELF Tool) with a unique number inscribed, after completing a lionfish removal course with an approved local dive operator. Most divers coming to Bonaire are short-stay tourists (typically for 7 -10 days), thus by the time the contract is requested, processed and created the recipient's vacation may be almost complete. Furthermore, due to the limited number of ELF Tools on island, it is more efficient for these contracts to be created with residents or longer-stay tourists. This strategy undoubtedly limits the quantity of hunters allowed to remove lionfish, but improves the quality. This more selective strategy allowing only more experienced volunteers can be more efficient and effective, especially in areas where lionfish removal does not occur very frequently or where lionfish have become wary and have a faster flight response. This strategy should especially be applied to marine protected areas whereby only elite/experienced volunteers are allowed to remove lionfish thereby enhancing the efficiency of management whilst minimising impact on the local ecosystems.

6.9 Final thoughts

Knowledge of how the lionfish invasion proceeds is invaluable to tailoring management strategies in other countries still in the early invasion stages. The overall aim of this research was to conduct an analysis of the ecological and socio-economic impacts of the lionfish invasion in Bonaire, Klein Bonaire and Curaçao. This aim was addressed via the following objectives (1) Determine whether lionfish size distribution changes as the invasion progresses; (2) Examine and compare the dietary preferences and habits of lionfish around Bonaire, Klein Bonaire and Curaçao; (3) Assess the efficiency and effectiveness of lionfish control and management; (4) Establish the profile of the typical lionfish volunteers in the Caribbean; and (5) Investigate the effectiveness and longevity of utilising volunteers for lionfish removal and control. Lionfish management is not a 'one size fits all' strategy and is instead rather intricate, where there is need to consider both biotic and abiotic factors (such as wind, wave action, currents, site accessibility). Thus an understanding of the species to be managed as well as the location; ease and accessibility of sites; availability and proficiency of volunteers along with local legal frameworks on fishing and gear restrictions should be factored into all lionfish management decisions.

APPENDIX

Appendix A

Appendix A. Tools used for lionfish capture and containment. Clockwise from top left. Eradicating Lionfish Tool (ELF Tool); lionfish travel polespear, lionfish carbon fibre polespear, add-on tip for polespears or ELF tool, Zookeeper lionfish containment device, clear dry/collection bag, Hex-Armor puncture resistance gloves, clear vinyl lionfish collection net. All images obtained from www.reef.org/catalog

Appendix B

Appendix B: Summary of traits possessed by prey items found in lionfish stomach contents (G/S represents Group/Scooling and S/P represents Single/Pair. NA represents data being not available

Family	Scientific name	Common Name	Freq Reef	Dens Reef	Freq Diet	Main Colour	Other Colour	Body Shape	Behaviour	Ecological Role	Aggregation
Acanthuridae	*Acanthurus chirurgus*	Doctorfish	0.667	2.1	0.0052	Brown	NA	Compress-iform	Swimmer	Herbivore	G/S
	Acanthurus bahianus	Ocean Surgeonfish	0.935	2.7	0.0052	Brown	NA	Compress-iform	Swimmer	Herbivore	G/S
Apogonidae	*Apogon phenax*	Mimic Cardinal	0.057	1.5	0.0007	Orange	NA	Taeniform	Cryptic	Planktivore	S/P
	Apogon townsendi	Belted Cardinal	0.452	2.1	0.0019	Orange	NA	Taeniform	Cryptic	Planktivore	S/P
	Apogon binotatus	Barred Cardinal	0.374	2.1	0.0078	Orange	NA	Taeniform	Cryptic	Planktivore	S/P
	Apogon maculatus	Flamefish	0.424	2.1	0.0093	Orange	NA	Taeniform	Cryptic	Planktivore	S/P
	Phaeoptyx pigmentaria	Dusky Cardinalfish	0.051	1.8	0.0104	Orange	NA	Taeniform	Cryptic	Planktivore	S/P
Aulostomidae	*Aulostomus maculatus*	Trumpetfish	0.951	2.4	0.0019	White	NA	Filiform	Swimmer	Predator	S/P
Blennidae	*Malacoctenus triangulatus*	Saddled Blenny	0.342	1.8	0.0171	Brown	White	Taeniform	Bottom	Prey	G/S
	Ophioblennius atlanticus	Redlipped Blenny	NA	NA	NA	Black	Red	Taeniform	Bottom	Prey	G/S
Cirrhitidae	*Amblycirrhitus pinos*	Red spotted Hawkfish	0.553	1.8	0.0048	Brown	Red	Fusiform	Cryptic	Prey	S/P
Gobiidae	*Gnatholepis thompsoni*	Goldspot Goby	0.552	2.7	0.0004	White	Brown	Taeniform	Bottom	Prey	G/S
	Ctenogobius saepepallens	Dash Goby	0.026	2	0.0007	White	Brown	Taeniform	Bottom	Prey	G/S
	Tigrigobius macrodon	Tiger Goby	0.002	1.4	0.0007	White	Brown	Taeniform	Bottom	Prey	G/S
	Coryphopterus glaucofraenum	Bridled Goby	0.715	3.1	0.0011	White	Yellow	Taeniform	Bottom	Prey	G/S
	Coryphopterus dicrus	Colon Goby	0.277	1.9	0.0019	White	Brown	Taeniform	Bottom	Prey	G/S
	Coryphopterus eidolon	Pallid Goby	0.366	2.1	0.0026	White	Yellow	Taeniform	Bottom	Prey	G/S
	Coryphopterus punctipectophorus	Spotted Goby	0.001	1.9	0.0034	White	Yellow	Taeniform	Bottom	Prey	G/S
	Coryphopterus personatus	Masked Goby	0.72	3.9	0.2238	Orange	White	Taeniform	Bottom	Prey	G/S
Grammatidae	*Gramma loreto*	Fairy Basslet	0.897	3	0.0723	Indigo	Yellow	Taeniform	Cryptic	Prey	S/P
Haemulonidae	*Haemulon striatum*	Striped Grunt	0.013	2.5	0.0007	White	Black	Fusiform	Swimmer	Predator	G/S
	Haemulon aurolineatum	Tomtate	0.013	2.4	0.0022	White	Yellow	Fusiform	Cryptic	Predator	G/S
Holocentridae	*Neoniphon marianus*	Longjaw Squirrelfish	0.672	1.8	0.0004	Orange	NA	Fusiform	Cryptic	Planktivore	S/P
	Sargocentron vexillarium	Dusky Squirrelfish	0.672	1.8	0.0004	Orange	NA	Fusiform	Cryptic	Planktivore	S/P
	Myripristis jacobus	Blackbar Soldierfish	0.888	2.8	0.0019	Orange	Black	Fusiform	Cryptic	Planktivore	S/P

Labridae	*Halichoeres bivittatus*	Slippery Dick	0.876	3.2	0.0011	White	Black	Taeniform	Bottom	Cleaner	G/S
	Halichoeres maculipinna	Clown Wrasse	0.559	2.4	0.0019	Multi	NA	Taeniform	Cryptic	Cleaner	G/S
	Clepticus parrae	Creole Wrasse	0.914	3.6	0.0145	Indigo	NA	Taeniform	Swimmer	Cleaner	G/S
	Halichoeres garnoti	Yellowhead Wrasse	0.939	3	0.0309	Yellow	Blue	Taeniform	Bottom	Cleaner	G/S
	Thalassoma bifasciatum	Bluehead Wrasse	0.969	3.5	0.0313	Yellow	Black	Taeniform	Bottom	Cleaner	G/S
Lutjanidae	*Lutjanus analis*	Mutton Snapper	0.066	1.5	0.0004	Brown	Yellow	Fusiform	Swimmer	Predator	S/P
	Ocyurus chrysurus	Yellowtail Snapper	0.861	2.6	0.0022	White	Yellow	Fusiform	Swimmer	Predator	G/S
Monocanthidae	*Monacanthus tuckeri*	Filefish	0.157	1.4	0.0019	Orange	Brown	Compress-iform	Cryptic	Herbivore	S/P
Pomacentridae	*Stegastes diencaeus*	Longfin Damselfish	0.894	2.7	0.0007	Black	NA	Fusiform	Swimmer	Cultivator	G/S
	Stegastes planifrons	Threespot Damsel	0.932	3.1	0.0037	Yellow	Black	Fusiform	Swimmer	Cultivator	G/S
	Chromis cyanea	Blue Chromis	0.924	3.3	0.0175	Blue	NA	Fusiform	Swimmer	Planktivore	G/S
	Chromis multilineata	Brown Chromis	0.979	3.9	0.0998	Brown	NA	Fusiform	Swimmer	Planktivore	G/S
	Stegastes partitus	Bicolor Damselfish	0.976	3.9	0.1907	Black	White	Fusiform	Swimmer	Planktivore	G/S
Scaridae	*Scarus taeniopterus*	Princess Parrotfish	0.956	2.8	0.0004	Black	White	Fusiform	Swimmer	Herbivore	G/S
	Sparisoma viride	Stoplight Parrotfish	0.98	2.9	0.0048	Brown	White	Fusiform	Swimmer	Corralivore	G/S
	Sparisoma aurofrenatum	Redband Parrotfish	0.961	2.6	0.0104	Brown	Red	Fusiform	Swimmer	Corralivore	G/S
	Scarus iseri	Striped Parrotfish	NA	NA	0.0186	NA	NA	Fusiform	Swimmer	Herbivore	G/S
Scorpaenidae	*Scorpaenodes caribbaeus*	Reef Scorpionfish	0.036	1.2	0	Orange	Brown	Globiform	Cryptic	Predator	S/P
Serranidae	*Centropristis ocyrus*	Bank Sea Bass	0	1.3	0.0004	Brown	NA	Taeniform	Bottom	Predator	S/P
	Liopropoma mowbrayi	Cave Basslet	0.007	1.3	0.0004	Orange	Black	Taeniform	Cryptic	Prey	S/P
	Hypoplectrus randallorum	Tan Hamlet	0.011	1.3	0.0007	Brown	NA	Fusiform	Cryptic	Predator	S/P
	Cephalopholis fulva	Coney	0.709	2.1	0.0015	Multi	NA	Fusiform	Cryptic	Predator	S/P
	Diplectrum formosum	Sandperch	0	2	0.0022	Brown	White	Taeniform	Bottom	Predator	S/P
	Liopropoma carmabi	Candy Basslet	0.008	1.1	0.0041	Orange	Indigo	Taeniform	Cryptic	Prey	S/P
	Cephalopholis cruentata	Graysby	NA	NA	0.0056	Brown	Red	Fusiform	Cryptic	Predator	S/P
	Serranus tigrinus	Harlequin Bass	0.903	2.3	0.0067	Black	Yellow	Taeniform	Bottom	Prey	S/P
	Liopropoma rubre	Peppermint Basslet	0.169	1.4	0.0164	Indigo	Yellow	Taeniform	Cryptic	Prey	S/P
Synodontidae	*Synodus synodus*	Red Lizardfish	0.004	1.1	0.0045	Red	White	Filiform	Bottom	Prey	S/P

Appendix C

Appendix C. Lionfish hunter questionnaire

Question	Possible responses				
Have you ever heard of lionfish?	Yes	No	Not Sure		
Have you ever caught a lionfish?	Yes	No	Not Sure		
How did you first hear about lionfish?	Television	Newspaper	Radio	Internet	Other people
	Other (please specify)				
If yes, approximately how many have you caught in your lifetime?	<10	10-25	25-50	50-100	100-250
	250-500	500-1000	1000-3000	3000-5000	>5000
How often do you go out to catch lionfish?	Every day	3-5 days a week	Once a week	Once a fortnight	Once a month
	3-5 times a year	Once a year	Never	Other (please specify)	
What do you do with the lionfish when you catch them?	Leave on the reef	Feed to other fish	Use for personal consumption	Give to family and friends	Sell to hotels/restaurants
	Other (please specify)				
What made you decide to go out to actively remove lionfish?					
Has catching lionfish (or the presence of lionfish in this country) been responsible for incurring any financial costs or benefits to you thus far? *Consider costs of making/purchasing lionfish equipment, transport and diving costs as well as selling fish to restaurants/hotels*	Yes	No	Not sure		
Can you suggest approximately how much money per month lionfish may be COSTING you in USD?	$0	$1-25	$25-50	$50-100	
	$100-250	$250-500	>$500		
Can you suggest approximately how much money per month lionfish may be BENEFITTIING you in USD	$0	$1-25	$25-50	$50-100	
	$100-250	$250-500	>$500		
Do you think lionfish are currently having an impact in this country?	Yes	No	Not sure		
If yes, please state some of these impacts					

If no, do you think lionfish are likely to have an impact in the future?	Yes	No	Not sure		
How much would you be willing to pay (one-time fee) for there to be total removal of lionfish from this country in USD? *This is a hypothetical question and you will not be expected to pay any money*	$0	$1-25	$25-50	$50-100	$100-250
	$250-500	$500-1000	$1000-5000	$5000-10,000	>$10,000
	Other (please specify)				
Have you ever eaten lionfish before?	Yes	No	Not sure		
If no, do you think you may eat lionfish in the future?	Yes	No	Not sure		
Are you in favour of there being a market/industry to promote the consumption of lionfish?	Yes	No	Not sure		
What country do you conduct the majority of your lionfish hunting?					
How long have you been visiting/living in this country?	<6 months	6-12 months	1-3 years	3-5 years	5-10 years
	>10 years	Other (please specify)			
Where is the region of your origin located?	North America	South America	Caribbean Islands	European Union	Other (please specify)
Do you currently work in the dive industry/Have you previously worked in the dive industry?	Yes	No			
Approximately how many dives have you done in your lifetime?	0	1-15	15-50	50-100	100-250
	250-500	500-1000	1000-2500	2500-5000	>5000
What is your age?	<18	18-25	25-40	40-60	>60
What is your gender	Male	Female	Other		

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