An Ecological Analysis of the Lionfish Invasion in Anguilla

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SUMMARY

The Indo-Pacific lionfish (*Pterois volitans*) is a venomous, voracious predator that is currently causing ecological and economical harm throughout the Caribbean. Their generalist diet and habitat preference coupled with their rapid growth rate and lack of natural predators has allowed their population to explode throughout the Caribbean and has deemed them as one of the worst marine invaders of all time. Anguilla confirmed its first lionfish in August 2010. However, since 2009 the authorities in Anguilla had taken a proactive approach and embarked on their lionfish awareness scheme and response strategy in a means to quell the lionfish invasion. However additional scientific research was required in order to further develop Anguilla’s Lionfish Response and Management Plan hence warranting this study. The purpose of this study is to conduct an ecological analysis of the lionfish invasion in Anguilla by performing habitat density surveys and stomach content analysis in order to make further recommendations for lionfish management within Anguilla. In Anguilla, a total of 214 transects (50m x 2m) were conducted (180 SCUBA; 34 snorkel) at depths ranging from 3 – 28m. Lionfish were observed in 60.71% of the sites surveyed (n = 28), but only occurred in 23.89% of the SCUBA transects (n = 180) and in 0% of the snorkel transects (n = 34). The majority of lionfish found within the surveyed area were solitary/single (n = 47). Of the sites where lionfish was observed, the density ranged from 0.04 – 0.65 lionfish per 100 m² with the satellite islands possessing the highest density of lionfish. Of the 163 lionfish analysed ranging in total length (TL) from 4.7 cm – 37.6 cm; the majority (83.33%) had prey in their stomachs, with 60.52% being found with ‘fish only’ in their stomach contents, 14.91% possessed a mixed diet, 7.89% possessing ‘invertebrates only’ and finally 16.67% had empty stomachs at the time of capture.

ACKNOWLEDGEMENTS

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LITERATURE REVIEW:

Introduction to lionfish

What are lionfish? The Red lionfish (*Pterois volitans*) is primarily an aquarium fish (Albins and Hixon 2013) but has been used as a food fish in particular areas of its native range which extends from Southern Japan, south to Lord Howe Island, throughout Indonesia, Micronesia and French Polynesia (Ruiz-Carus et al. 2006; Gonzales et al. 2009). Reports suggest that lionfish are established in the waters surrounding the South Eastern United States coast and all of the Caribbean islands with Trinidad and Tobago being the last island to have lionfish confirmed (Figure 1). Lionfish are expected to continue their invasion southward along the South American coast (Morris 2012). Lionfish signify the first marine fish invader from the Western Pacific to the Atlantic and are believed to have been introduced via intentional and/or unintentional aquaria releases (Whitfield et al. 2002; Morris et al. 2010). Two species (*P. volitans* and *P. miles*) have been confirmed in the invaded range (Kojis 2009; Morris et al. 2010). Molecular analyses revealed that *P. volitans* is more than one order of magnitude more common than *P. miles* (Hamner et al. 2007). Throughout this report, the focus will be on *P. volitans*, commonly referred to as lionfish.

Venom: Lionfish, as other Scorpaenids, are venomous and possess a highly developed venom apparatus comprised of 13 dorsal spines, 2 anal spines, and 2 pelvic spines (Figure 2). Venom glands are located along 2 anterior-lateral grooves of each spine and extend three quarters of the distance from the base of the spine towards the tip (Morris 2009; Morris 2012). The toxin in lionfish venom contains acetylcholine which affects neuromuscular transmission and causes cardiovascular and neuromuscular effects in animals and humans (Morris 2012).

Feeding ecology: Lionfish are principally piscivorous, but are known to feed on invertebrates (Morris 2009) and in their native range, they occupy the higher levels of the food chain (Hare and Whitfield 2003; Bervoets 2009). In the Bahamas, the occurrence of teleosts in lionfish diets is size-dependent with larger lionfish feeding on teleosts, and smaller ones feeding more heavily on crustaceans (Morris 2009; Morris and Akins 2009). Lionfish stomachs can expand to more than 30 times in volume (Figure 3) (Freshwater et al. 2009). Lionfish are adept in undergoing periods of starvation of over 12 weeks without

![Figure 1: Lionfish distribution in the Caribbean](image1)

![Figure 2: Location of venomous spines](image2)

![Figure 3: Lionfish stomach](image3)
mortality due to their capability of long-term fasting (Fishelson 1997; Morris 2009). Lionfish are nocturnal and most active during dawn and dusk, which coincides with the peak activity of reefs where diurnal crustaceans are retreating and smaller nocturnal fishes are becoming active (Syngajewski 2004; Green and Cote 2011). Lionfish are opportunistic predators consuming fish and invertebrates (Whitfield et al. 2007). They employ a diverse range of feeding strategies making them well suited for feeding on benthic and cryptic prey (Morris 2009; Albins 2013; REEF 2012). Prey species in the Atlantic region are naïve to lionfish’s novel predation strategies, resulting in lionfish having higher predation efficiencies in the invaded range compared to its native range (Albins and Hixon 2008).

Reproductive ecology: Morris (2009) suggested that lionfish courtship begins shortly before dark, and extends well into night time whereby females release two buoyant egg masses which are fertilised by the male, and then ascend to the surface (Fishelson 1975; Morris et al. 2011). Based on captured specimens in the Caribbean, lionfish are reproducing throughout the year (REEF 2012). Their reproduction shows no apparent timing relative to moon and tidal regimes (Department of Marine Resources 2008; Morris 2009). They are prolific breeders, with one female being able to eject up to 15,000 eggs during a single mating event, of which she can have at least three per month (Bervoets 2009; Morris 2009). The eggs are bound in an adhesive mucus that disintegrates a few days later, allowing the embryo and/or larvae to become free-floating (Hare and Whitfield 2003; Morris et al. 2009).

The released free-floating egg masses develop into planktonic larvae, (Ruiz-Carus et al. 2006); thereby permitting dispersal by oceanic currents (Freshwater et al. 2009). Based on spawning information and the collection of larvae from the water column, lionfish have a pelagic larval stage similar to other marine fish (Hare and Whitfield 2003). The actual larval distribution of lionfish still remains unknown, but has been estimated to be between 25-40 days (Morris 2009). Settling from the water column to the benthic habitat is proposed to occur at about 12mm (Hare and Whitfield 2003). The juveniles develop rapidly and begin to actively hunt at approximately 7 cm length and have been observed to consume prey up to two thirds their body length (Bervoets 2009).

Habitat preference: Lionfish are benthically associated and in its native range, they occur over coral, sand and hard-bottom substrates from the surface to 50m (Whitfield et al. 2002; 2007; Vasquez- Yeomans et al. 2011). In their invaded range, they have occupied all major seafloor and substrate types and a range of depths- from the shoreline to more than 300m deep (Morris 2012). During the day, lionfish 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 are adaptable to many habitats and have colonised areas ranging from 1 to 140m on reef walls, patch reefs, rocky areas, hard bottoms, ledges, crevices, mangrove creeks, isolated coral heads, blue holes, ship wrecks, and man-made structures (NOAs Coris 2009). 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).

Thermal tolerance: Thermal tolerance limits are a crucial factor dictating the distribution of lionfish along the east coast of the U.S. (Kimball et al. 2004). Temperature affects the survival, reproduction and dispersal of P. volitans since lionfish temperature tolerance is affected by faster temperature decline rates experienced during autumn and winter (Kimball et al. 2004). The predicted winter water temperature on the north-east coast of the U.S. is possibly too cold to allow overwintering by lionfish (Whitfield et al. 2002). As a result, juveniles are likely to perish when water temperatures decline below their critical thermal minimum (Ruiz-Carus et al. 2006). Thermal tolerance studies revealed that lionfish possess a mean lethal temperature minimum of 10.0 °C and a mean temperature at feeding cessation of 16.1°C (Kimball et al. 2004). 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).
Management of lionfish: Preventing the introduction and the establishment of any non-native species is the most efficient and safest way to avoid the costs and impacts associated with biological invasions (Floerl et al. 2005). Thus with lionfish, like any other invasive species, the key to successful eradication is rapid response, and the commitment of adequate resources to these efforts (Simberloff 2000). There is little time to respond to marine invasions, and this is especially exacerbated due to the open nature of marine environments (Bax and Thresher 2009). Thus, 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, drastically decreases over time (Bax et al. 2003). Since their invasion of the North Atlantic/Caribbean region, various management measures have been instilled to quell lionfish (Morris et al. 2010). Natural control of lionfish is very unlikely; firstly due to the lack of large, native predators and also because of its exceptionally high density which greatly exceeds that of its native range (Fishelson 1975; Morris et al. 2012; Albins and Hixon 2013).

Lionfish management has been an evolutionary process in terms of the schemes established, the tools used and the means to increase removal efforts (de Leon et al. 2011). At the beginning of the lionfish invasion, scientists and government or state department officials are usually the primary persons involved in lionfish removal. Most lionfish management strategies involve targeted removal by SCUBA divers or snorkelers using spears. However, due to the invasion characteristics of lionfish, there is need for a larger, community effort to be more successful at removal (Morris et al. 2012). Thus, removal activities were subsequently introduced to dive operators and professionals and eventually extended to volunteer divers, no matter what their dive certification level (BNMP 2010). This involvement of volunteer divers has been instrumental in the successful control and management of lionfish in some islands in the Caribbean such as Cayman Islands, Bonaire and Curacao. Removal via trapping has also been proving increasingly successful, but the issue of by-catch remains the major obstacle to its use to effectively control lionfish populations.

Total eradication of lionfish remains impossible due to the great depths they can inhabit and the densities they have achieved, but especially because of the continuous influx of larvae from other islands (Ahrenholz and Morris 2010; Vasquez-Yeomans et al. 2011). However targeted local control via individuals or organised groups of divers have proven most effective and are effective at reducing the number and size of lionfish (de Leon et al. 2013). Morris et al. (2010) suggested that for small-scale populations with low connectivity to larger populations, control via fishing mortality and targeted removal may be a viable management strategy. Green and Cote (2009) found that targeting all individuals more than 15 cm removed 89% of the population; more than 20 cm removed 87% and more than 25 cm removed 79% of the population. These results signify that size selectivity in removal efforts can significantly affect the success of lionfish population management efforts (Green and Cote 2009).

Introduction to the Study:

Anguilla confirmed its first lionfish in August 2010. However, since 2009 the authorities in Anguilla had taken a proactive approach and embarked on their lionfish awareness scheme and response strategy. This initiative was achieved through a partnership between the Department of Environment, the Department of Fisheries and Marine Resources and the Anguilla National Trust. As a result numerous education and awareness campaigns have been undertaken and workshops conducted with various stakeholders such as the diving, fishing and hotel/tourism sectors. This study was warranted since the Department of Environment, Ministry of Home Affairs and the Government of Anguilla required further scientific research to assist in the further development of their Lionfish Response and Management Plan. The purpose of this study is to conduct an ecological analysis of the lionfish invasion in Anguilla by performing habitat density surveys and stomach content analysis in order to make further recommendations for lionfish management within Anguilla.
Study Site

Anguilla one of the more northerly islands in the Lesser Antilles of the Caribbean is an elongated island, running in an east-northeast to west-southwest direction and measures about 25.5km (16 miles) by 5.5km (3.5 miles) (Clarke 1971; Sheppard et al. 1995, Parr 2002, Homer 2004). Several surrounding islets or satellite islands such as Dog Island, Scrub Island, Sombrero Island, Anguillita, Blowing Rock and Prickly Pear Cays also form part of Anguilla’s Archipelago (Homer 2004). Positioned approximately 240km east of Puerto Rico and 7km north of St Maarten, Anguilla is primarily coral-limestone ‘karst’ with the highest point reaching an elevation of 65m above sea level (Parr 2002, Carder et al. 2007). The coastline is generally comprised of coral sand beaches and limestone cliffs with some large sand dunes and salt ponds existing behind some beaches (Carder et al. 2007). Anguilla is also exposed to North-East trade winds off the Atlantic Ocean with its ‘wet season’ (June – November) coinciding with the North Atlantic hurricane season (Hodge et al. 2011). A comprehensive reef system off the north coast along with fringing reefs along the south coast shelters the island whilst simultaneously providing excellent resources and conditions for scuba diving, snorkeling and sailing (Homer 2004).

MATERIALS AND METHODS

Fieldwork was conducted between 11th January and 21st January 2014 using a combination of SCUBA (Self Contained Underwater Breathing Apparatus) and snorkeling. All SCUBA dives were conducted on the leeward coast of Anguilla, since diving rarely occurs on the windward coast due to unfavourable conditions. Since the research was conducted during the peak of the groundswell season, in the interest of safety, dives were conducted on the more sheltered, leeward coast. SCUBA surveys were conducted on various habitats/sites ranging from shallow-water patch reefs, to fringing reefs, trenches and fallen boulder sites and sunken wrecks (some fully intact) either on sandy bottom, surrounded by reef or seagrass. Sites were chosen based on consultation with local divers and staff from the Department of Fisheries and Marine Resources who regularly dive and encounter lionfish in Anguilla’s waters. Following consultation, the study sites were decided upon and consisted of a mixture of lionfish hotspot sites, sites with habitat importance, and unknown/previously unsurveyed sites. All satellite islands and wrecks were also surveyed with the full site list being presented in Table 1 and displayed in Figure 6.

A total of 214 transects were conducted during the duration of the research, 180 via SCUBA and 34 via snorkeling. All SCUBA surveys were conducted between 09:15 and 12:45 whilst the snorkel surveys were conducted between 11:00 to 17:00. Using SCUBA equipment, the divers descended to the maximum depth the site allowed. Then, using a 50m measuring tape, the divers swam at a slow pace, maintaining the same depth and as straight a line as possible whilst searching and extensively surveying all holes, ledges and crevices for lionfish within 2m on either side of their center body line (Figure 5). Whenever a lionfish was encountered within the transect; the information listed in Table 2 was recorded on the diver’s wrist slate.
All transects were covered in both directions, i.e. first whilst laying out the tape, and then secondly when recovering the tape. Fish outside the transect area were also recorded but not included in the analytical portions.

![Figure 5: Researcher conducting transect underwater](image)

Table 1: Survey site list

<table>
<thead>
<tr>
<th>Site No.</th>
<th>Site</th>
<th>Type</th>
<th>Site No.</th>
<th>Site</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sarah Wreck</td>
<td>Wreck</td>
<td>18</td>
<td>Dog Island 1</td>
<td>Satellite Island</td>
</tr>
<tr>
<td>2</td>
<td>Ida Marie Wreck</td>
<td>Wreck</td>
<td>19</td>
<td>Dog Island 2</td>
<td>Satellite Island</td>
</tr>
<tr>
<td>3</td>
<td>Sandy Deep Satellite Island</td>
<td>Patch Reef (B)</td>
<td>20</td>
<td>Deep South</td>
<td>Patch Reef (A)</td>
</tr>
<tr>
<td>4</td>
<td>Crystal Reef</td>
<td>Patch Reef (B)</td>
<td>21</td>
<td>Viceroy</td>
<td>Patch Reef (A)</td>
</tr>
<tr>
<td>5</td>
<td>Shoal Bay</td>
<td>Patch Reef (B)</td>
<td>22</td>
<td>No Name</td>
<td>Satellite Island</td>
</tr>
<tr>
<td>6</td>
<td>Little Bay</td>
<td>Patch Reef (A)</td>
<td>23</td>
<td>Lobster Reef</td>
<td>Patch Reef (B)</td>
</tr>
<tr>
<td>7</td>
<td>Oosterdiep Wreck</td>
<td>Wreck</td>
<td>24</td>
<td>Sea Fan</td>
<td>Patch Reef (B)</td>
</tr>
<tr>
<td>8</td>
<td>Anguillita Satellite Island</td>
<td>Patch Reef (B)</td>
<td>25</td>
<td>Limestone Bay</td>
<td>Patch Reef (A)</td>
</tr>
<tr>
<td>9</td>
<td>Blowing Rock</td>
<td>Satellite Island</td>
<td>26</td>
<td>Island Harbour</td>
<td>Patch Reef (B)</td>
</tr>
<tr>
<td>10</td>
<td>MV Meppel Wreck</td>
<td>Wreck</td>
<td>27</td>
<td>Captain Turtle</td>
<td>Patch Reef (B)</td>
</tr>
<tr>
<td>11</td>
<td>Seal Island</td>
<td>Satellite Island</td>
<td>28</td>
<td>Katouche</td>
<td>Patch Reef (A)</td>
</tr>
<tr>
<td>12</td>
<td>Prickly Pear</td>
<td>Satellite Island</td>
<td>A</td>
<td>Rendezvous Bay</td>
<td>Snorkel</td>
</tr>
<tr>
<td>13</td>
<td>Commerce Wreck</td>
<td>Wreck</td>
<td>B</td>
<td>Cove Bay</td>
<td>Snorkel</td>
</tr>
<tr>
<td>14</td>
<td>Catheley H Wreck</td>
<td>Wreck</td>
<td>C</td>
<td>Lockrum Bay</td>
<td>Snorkel</td>
</tr>
<tr>
<td>15</td>
<td>Crocus Bay Pipeline</td>
<td>Patch Reef (A)</td>
<td>D</td>
<td>Forest Bay</td>
<td>Snorkel</td>
</tr>
<tr>
<td>16</td>
<td>Scrub Island 1</td>
<td>Satellite Island</td>
<td>E</td>
<td>Seafeathers Bay</td>
<td>Snorkel</td>
</tr>
<tr>
<td>17</td>
<td>Scrub Island 2</td>
<td>Satellite Island</td>
<td>F</td>
<td>Junk’s Hole Bay</td>
<td>Snorkel</td>
</tr>
</tbody>
</table>
Figure 6: Location of study sites
Table 2: Description of data recorded during lionfish survey

<table>
<thead>
<tr>
<th>Data Recorded</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>Depth the lionfish was observed at</td>
</tr>
<tr>
<td>Cluster/Aggregation</td>
<td>Whether the lionfish was found single, in a pair or in a group</td>
</tr>
<tr>
<td>Size</td>
<td>Estimation of the total length (TL) of the lionfish in cm</td>
</tr>
<tr>
<td>Distance from transect line</td>
<td>Location of the lionfish in relation to the transect line and whether it was observed up or down of the transect line</td>
</tr>
<tr>
<td>Habitat Association</td>
<td>Whether the lionfish was found associated with a particular substrate such as coral, sand, rubble, sponge, gorgonians, rock, wreck or some other substrate type</td>
</tr>
<tr>
<td>Reaction to diver</td>
<td>Whether the lionfish moved away, towards or had no reaction to the diver</td>
</tr>
<tr>
<td>Behaviour</td>
<td>Whether the lionfish was observed out on the site or hidden under a ledge or in a crevice or a hole or cave.</td>
</tr>
</tbody>
</table>

At constant depth/flat sites multiple transects were conducted at a single depth, whilst at gradient depth/sloping sites, paired transects were conducted at 2 – 3 varying depths with a minimum of 6 non-overlapping transects being conducted at each site. Where possible, lionfish were captured using an Eliminating LionFish Tool (ELF) and removed from the site for further analysis.

RESULTS

Density: In Anguilla, a total of 214 transects were conducted at depths ranging from 3 – 28m. Lionfish were observed in 60.71% of the sites surveyed (n = 28), but only occurred in 23.89% of the SCUBA transects (n = 180) and in 0% of the snorkel transects (n = 34). In the surveys conducted in Anguilla, a total of 80 lionfish were observed within the 180 transects (density: 0.22/100m²). Of the 28 sites surveyed, 0 lionfish were observed at 11 sites. Of the sites where lionfish was observed, the density ranged from 0.08 – 0.29 lionfish per 100 m² (Figure 7) with the satellite islands such as Dog Island and Scrub Island possessing the highest density of lionfish (Figure 8).

![Comparison of lionfish density amongst survey sites](image)

Figure 7: Comparison of lionfish density amongst survey sites (WR: Wrecks; SI: Satellite Islands; PR B: Patch Reefs towards the North/Eastern part of the island; PR A: Patch Reefs towards the South/Western part of the island)
Feeding ecology: Within Anguilla, since August 2010, 186 lionfish have been removed and submitted to the Department of Fisheries and Marine Resources but only 163 have undergone scientific analysis. The lionfish were removed using various methods including SCUBA diving, free diving/snorkeling and also via fish pots/traps and were caught at depths ranging between 1 – 62m. Of the 163 Anguillian lionfish analysed ranging in size (TL) from 4.7 cm – 37.6 cm; the majority (83.33%) had prey in their stomachs, with 60.52% being found with ‘fish only’ in their stomach contents, 14.91% possessed a mixed diet (i.e. fish and invertebrates), and 7.89% possessing ‘invertebrates only’. Only 16.67% had empty stomachs at the time of capture. It is important to note that stomach content analysis is only a representation of the lionfish’s last meal (Hyslop 1980) and are not necessarily a representation of what lionfish eat, since lionfish will not choose to have an empty stomach.

With regard to lionfish prey preference in Anguilla, of the identifiable prey items, the preferred fish families were Scaridae (parrotfish), Acanthuridae (doctor and surgeonfish), Labridae (wrasses), Carangidae (jacks), Haemulidae (grunts), Gobiidae (gobies), Apogonidae (cardinalfish), Pomacentridae (damselfish and chromis), Grammatidae (Basslets), Serranidae (groupers, hinds and basses), Holocentridae (squirrelfish) and Monocanthidae (filefish). Based on these findings, lionfish in Anguilla are feeding on both ecologically and economically important species. Within Anguilla, Acanthuridae and Serranidae are the main commercial species consumed, especially by the locals. Furthermore parrotfish, one of the more preferred families in lionfish diets in Anguilla is not only a commercially important species within Anguilla’s local fishing industry but it is also an ecologically important species along with wrasses which possess a vital role within the ecosystem as cleaners; and damselfish that are imperative due to their algal grazing on coral reefs.
DISCUSSION

**Density:** In the surveys conducted in Anguilla, a total of 80 lionfish were observed within the 180 transects (density: 0.22/100m²). This number is quite low compared to similar studies conducted in Bonaire and Curacao. In Bonaire, a total of 358 fish were observed in 416 transects (density: 0.43/100m²) in 2011 and 187 from 243 transects (density: 0.38/100m²) in 2012. Whereas in Curacao, 416 fish were recorded in 167 transects (density: 1.25/100m²) in 2011 and 289 from 144 transects (density: 1.00/100m²) in 2012 (de Leon et al. 2013) (Figure 9).

![Graph showing lionfish density in Anguilla, Bonaire, and Curacao.](image)

**Figure 9:** Comparison of lionfish density in Anguilla, Bonaire and Curacao (ANG 14: Anguilla 2014; BON 11: Bonaire 2011, BON 12: Bonaire 2012; CUR 11: Curacao 2011; CUR 12: Curacao 2012)

Although it appears that Anguilla has a rather low lionfish density when compared to Bonaire and Curacao, this can be misleading. The low abundance of lionfish at many sites throughout Anguilla may be related to the general lack of food resources observed during the survey period. In addition to a low prey density, most sites were characterized by a lack of large predators such as sharks, or large groupers, snappers or barracudas. The highest abundance of large predators as well as suitable prey were observed at the satellite islands such as Dog Island and Scrub Island where the highest lionfish densities were also recorded (Figure 8). This can account for the higher lionfish density at Bonaire and Curacao, where lionfish are spoiled with an exceptional abundance of prey to choose from. Thus, prey density surveys need to be conducted in Anguilla to verify this theory of whether such an occurrence is limiting lionfish density, and if this hypothesis proves true, then it will help to inform management to predict which areas are the most effective to target removal efforts to. However, fishermen in Anguilla are reporting lionfish catches in great numbers (hundreds per day) from great depth (greater than 200 feet), which may make verification of this hypothesis difficult since these depths are beyond recreational diving limits and would require the use of technical diving. Furthermore, targeted lionfish removal is not a viable option when managing lionfish at great depths and will instead require the use of traps.
**Aggregation & Behaviour:** The majority of lionfish found within the surveyed area were solitary/single (n = 47). There were a dozen occurrences of lionfish in pairs and the largest group observed was a group of 5. When compared to surveys conducted in Bonaire, the largest group recorded was one of 5-7 individuals, whereas in Curacao, a group of 16 was observed (de Leon et al. 2013). Lionfish are renowned for being solitary, but tend to be limited by resources, thus when more resources are available, it is expected to find more lionfish (Morris 2009). This can account for the observations in Anguilla whereby lionfish were generally solitary, but were found in larger groups at the satellite islands where higher prey densities were recorded. All surveys were conducted between 9:30 – 12:30, a time period where lionfish are not renowned for being active. (Fishelson (1975) has suggested that lionfish in their native range actively foraged at dawn and dusk, but were generally inactive and sheltered in crevices and under ledges during the day (Green and Cote 2011). Of the 80 lionfish observed, 89% were observed to be out on the habitat they were observed at whilst 11% were found hidden under some sort of ledge or in a crevice or hole. Furthermore, the majority of the lionfish were naïve to being hunted as many had no reaction to the diver attempting to shoot it, which would account for why they were hidden. These lionfish have not recognized any form of danger, which would typically limit their behavior and restrict them to being reclusive during the day and only becoming active in periods of reduced visibility, i.e. crepuscular periods (dawn and dusk) (Green and Cote 2011).

**Feeding ecology:** Regarding the relationship between size and diet in Anguilla, as lionfish increased in size, there was an associated increase in the proportion of fish eaten, and a subsequent decrease in the proportion of invertebrates consumed. However, it is important to note that the sample size in Anguilla is too small for any explicit conclusions to be made. However, these findings are consistent with standard competition theory and Morris and Akins (2009) confirmed this in their study in Bahamas where they found that the proportion of fish in the diet increased with lionfish size. When competition exists in a community, the stronger competitor (i.e. the larger lionfish) will out-compete the inferior competitor (i.e. the smaller lionfish) for the profitable prey. The implications for this in Anguilla are simple but potentially damaging since the longer lionfish remain in Anguilla, the larger they will become and consequently remove larger quantities of native prey. Thus it is essential for all lionfish, even the smaller ones to be removed. When lionfish becomes popular as a food fish, there may be the temptation to concentrate on larger, 'plate-sized' fish and ignore the smaller ones. However through proper education, and safe handling and preparation workshops, demand can be created also for smaller lionfish as a food fish.
IMPLICATIONS

These factors compounded together confirm that lionfish have the potential to cause great ecological harm to Caribbean ecosystems. The impacts of lionfish have been grouped by Whitfield et al. (2007) into 5 categories: habitat alteration, introduction of parasites/diseases, trophic alterations, hybridization and spatial alterations. An effective larval dispersal mechanism coupled with a generalist diet is likely to have favoured the successful invasion of lionfish (Whitfield et al. 2007). Evidence suggests that lionfish are capable of removing significant proportions (78%) of prey communities on isolated patch reefs and it is also possible that lionfish's 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 lionfish may compete with native piscivores by monopolizing the food resource (Albins and Hixon 2008). However, continuous mortality of native predators through overfishing may open niche space, and subsequently increase available resources for lionfish (Whitfield et al. 2007). Unlike other native species, lionfish experience little or no fishing mortality. These factors combined bequeath lionfish with a competitive advantage over native species (Whitfield et al. 2007).

Lionfish are especially effective predators of small post-settlement reef fish and this can have a consequent effect on population densities and also the structure of fish communities (Carr and Hixon 1995; Almany and Webster 2006; Albins and Hixon 2013). Albins and Hixon (2008) demonstrated that lionfish presence on experimental reefs led to a 79% decline in overall reef fish recruitment (including herbivorous parrotfish Scaridae spp.). This consumption of herbivorous species can amplify macroalgal production on coral reefs, and consequently contribute to pervasive phase shifts on Caribbean coral reefs (Williams and Polunin 2001; Bellwood et al. 2004; Mumby et al 2006; Barbour et al. 2010). Territorial herbivorous damselfish and grazers influence important coral reef processes including: controlling the rate of reef erosion (Sammarco et al. 1986); nutrient fluxes and the faunal community structure and abundance (Klumpp et al. 1988; Hoey and Bellwood 2010). The effects of damselfish have been so remarkable that their role has been recognized as a keystone in the maintenance of the structure of coral and algal assemblages (Ceccarelli et al. 2005). The territories which damselfish maintain play key roles in trophic processes as they are sites of amplified primary productivity; high algal standing crops and intense grazing activity (Polunin and Klumpp 1989).

Lionfish have the potential to generate powerful trophic cascades via their prey consumption (Sililman and Bertness 2002; Barbour et al. 2010). Trophic cascades involve reciprocal predator-prey effects that modify the abundance, biomass or productivity of populations, communities or trophic levels across more than one link in the food web (Pace et al. 1999; Beschta and Ripple 2009). Lionfish may decrease herbivorous reef fish populations that are crucial for regulating macroalgal growth. Devoid of these controls, macroalgal proliferation may impede further coral reef recruitment, growth and recovery following the initial physical disturbance (Barbour et al. 2010). An increase in algal growth on coral reefs can exacerbate already stressed coral, resulting in coral mortality, negative economic effects and a potential decrease in dive tourism (Bervoets 2009; Frazer et. al 2012).
RECOMMENDATIONS

ENCOURAGE RESTAURANTS TO SERVE LIONFISH

MARKETING CAMPAIGN TO EAT LIONFISH

TASTING EVENTS

MORE PEOPLE WANT TO TRY LIONFISH

GREATER DEMAND FOR THE RESTAURANTS

BETTER PRICE

PROFIT TO FISHERMEN (FISHING)

PROFIT TO DIVERS (FISHING)

PROFIT TO DIVERS (LIONFISH COURSES)

DEEP WATER

SHALLOW WATER

OVERFISHING OF LIONFISH

LOW DENSITY

Figure 10: Summary of recommended actions
Monitoring

- Repeat lionfish density surveys to assess how the lionfish population may be changing.
  - If possible, studies should be repeated outside of groundswell season so that sites on the windward coast can be surveyed to assess the density.
  - Local fishermen suggested that they were not seeing many lionfish this time of the year (January) and suggested that a similar pattern was noticed the previous year, which might be related to the local ‘groundswell’ season. However, in late February/early March 2013 the fishermen noticed an increase in lionfish numbers and were finding lionfish in their traps in high numbers. Thus conducting surveys in late February/early March will be useful in proving whether this observation by the fishermen actually represents a pattern, which means that removal efforts can be concentrated at this time to allow for more efficient removals.

- Conduct prey density surveys regularly firstly to establish a baseline and then to monitor how lionfish may be affecting the ecosystem

- Get pot fishermen to supply simple catch data: location, depth of fish-pot and number of lionfish caught. Additional data such as time the pot was set at, length of time the pot was left for, the bait type, and the average length of the lionfish caught are desirable, but due to time and effort constraints it may deter fishermen from providing data.

Lionfish removal

- Focus/get more removal effort on the satellite islands.
  - The lack of lionfish on the wrecks and other popular dive sites are due to the fact that local dive operators are continuously removing lionfish once they see them. However the satellite islands are not visited as frequently by the dive operators possibly due to the distance and also the more advanced diving conditions there. A lot of the divers coming to Anguilla are either uncertified or newly certified, thus more advanced sites such as Scrub Island and Dog Island are not often visited. Thus by subsidizing diving trips to the satellite islands or hosting lionfish derbies focused in these areas, a greater removal effort on the satellite islands can be achieved. A perfect time to pioneer these removal efforts would be during Festival del Mar, a time of year where fishermen suggest that there are the largest numbers of lionfish. It is also recommended that the said event be used as an avenue to promote awareness of the lionfish.

- Provide divers with more effective lionfish removal tools
  - Pole spears and fold spears are more effective than the ELF tool, both in terms of cost and lionfish removal. Currently some dive operators do not remove lionfish due to fear of being injured whilst handling lionfish underwater. Lionfish containment devices such as the Zookeeper or lionfish collection bags should also be purchased in order to encourage more lionfish removal whilst making it safer and more efficient for removing lionfish from
Anguilla’s waters. Such an initiative will also have added benefits, as it will provide a larger amount of lionfish to be supplied for further analysis or to restaurants and residents for consumption. Based on effectiveness and efficiency, it is highly recommended that zookeepers and fold spears/travel pole spears should be provided to the dive operators. It is also recommended that these spears be used only for lionfish removal and there should be a movement towards reducing spearfishing of other species within Anguilla.

- Educate and equip fishermen to increase their efficiency and effectiveness at lionfish removal
  
  o Encouraging fishermen to have separate containment devices (e.g. used 5 gallon buckets) for storing their fish (i.e. one for lionfish and another for all other fish) can reduce the frequency of envenomations. Furthermore, supplying the fishermen with heavy duty/puncture proof gloves will make it safer and easier for them to handle lionfish, and will thus encourage them to remove lionfish from their traps.
  
  o To encourage fishermen to provide data some sort of incentive needs to be created. For example for every 100 fish they provide data on they receive an appropriate fuel subsidy.

**Developing the lionfish market**

- Repeat the safe handling and preparation of lionfish workshop periodically to encourage local restaurants to place lionfish on their menus. Use local chefs who have already attended past workshops and have them integrate lionfish to their menus to assist and/or prepare samples for others to taste.

- Organise tasting events where locals have the opportunity to sample lionfish and then be encouraged to eat lionfish at an event such as Festival del Mar, Anguilla Day or during Carnival.

- Considering that the national dish of Anguilla is Peas, Rice and Fish; this can be a way of trying to integrate lionfish into local culture.

- Encouraging chefs such as those on the Culinary Team to integrate lionfish into their repertoire. Lionfish can be served as a special and help to raise the profiles of the restaurants to create a ‘greener’ image. Perhaps the Anguilla Hotel and Tourism Association can have a stamp of approval for ‘green restaurants’ within Anguilla.

- Have an ‘eat lionfish’ campaign with infomercials being circulated on TV, radio and newspapers.

- A lionfish specialty course can be conducted at dive shops whereby divers firstly learn all about the lionfish invasion, but then also what they can do to help. Divers can simply be lionfish spotters on dives, but more experienced divers can be instructed on how to handle the lionfish removal equipment and learn to shoot lionfish. Most divers are very environmentally conscious and wish to do their part to help the reef, and assisting with lionfish removal (even by simply acting as a lionfish spotter) is one such way. This course can also be complemented by an ‘eat what you catch’ add-on where the fish they catch can then be cooked up and served to them for lunch / dinner. This can be a benefit for the dive operators as they too can raise their profile, but also increase their revenue.
Table 3: Analysis of lionfish removal and containment devices being used in the Caribbean and North America

<table>
<thead>
<tr>
<th>DEVICE</th>
<th>ADVANTAGES</th>
<th>DISADVANTAGES</th>
<th>AVERAGE COST (USD$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eradicating LionFish Tool (ELF Tool)¹</td>
<td>Safe for the coral and does not have the power to kill larger fish</td>
<td>Not as effective with larger lionfish</td>
<td>70 - 160</td>
</tr>
<tr>
<td>Pole Spear²</td>
<td>Cost effective and also effective at removing lionfish</td>
<td>Does not fold up, so can affect a dive operation (e.g. if teaching). Has the power to cause damage to coral and larger fish</td>
<td>25</td>
</tr>
<tr>
<td>Travel Pole Spear³</td>
<td>Folds up and can be attached to the diver, so does not interfere with dive operation. Cost effective and also effective for lionfish removal</td>
<td>Has the power to cause damage to coral and larger fish</td>
<td>50</td>
</tr>
<tr>
<td>Fold Spear⁴</td>
<td>Folds up and can be attached to the diver, so does not interfere with dive operation. Effective for lionfish removal</td>
<td>Has the power to cause damage to coral and larger fish</td>
<td>150</td>
</tr>
<tr>
<td>Frapper⁵</td>
<td>Safe for the coral and does not have the power to kill other larger fish</td>
<td>Not as effective with larger lionfish. Spear is not attached making it hard to recover when dislodged. Not as effective for removing lionfish in deep crevices and holes</td>
<td>65</td>
</tr>
<tr>
<td>Zookeeper⁶</td>
<td>Safest way to remove and contain lionfish, especially in infested areas. No need to kill the lionfish completely before putting in the zookeeper, thus making it more time efficient. Motto applied with the zookeeper is 'shoot and stuff'</td>
<td>Can be a bit bulky for the diver and can affect a dive operation (e.g. if teaching)</td>
<td>85 - 100</td>
</tr>
<tr>
<td>Collection Bag⁷</td>
<td>Cost effective and can be rolled up and clipped to the diver, thus reducing drag</td>
<td>Not as effective for lionfish removal as it is not puncture proof</td>
<td>25 - 35</td>
</tr>
<tr>
<td>Hex Armour Gloves⁸</td>
<td>Protects diver from lionfish spines</td>
<td>Still exists some potential for the diver to be hurt by the spines</td>
<td>50</td>
</tr>
</tbody>
</table>

LIMITATIONS OF STUDY

- The results of this study only represent a snapshot appraisal of lionfish density within Anguilla.
- The study was conducted in the peak of 'groundswell season'; a time of the year where seas are rougher and less favourable. Interviews conducted with fishermen during the study period revealed that in the past years they have noticed a reduction in lionfish numbers at this time of the year, and a subsequent increase from late February/early March.
- Surveys were only conducted on the leeward coast of the island, which left the windward coast highly under-represented. The survey period unfortunately coincided with the peak groundswell season which is characterized by rough seas and inclement weather. Thus in the interest of safety, surveys using SCUBA were only conducted on the leeward coast and snorkeling surveys were conducted on the windward coast.
- The sample size for the ecological data (i.e. stomach content analysis) was small [n=163] and the stomach contents of quite a few specimens were too digested for identification down to species or family level. Stomach content analysis in itself is also a snapshot representation and only depicts the last meal of the lionfish before capture.

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