The lionfish culling program in Sint Eustatius island, Dutch Caribbean
Effectiveness and knowledge contribution
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Special thanks to Jessica Berkel for allowing me to do this internship with STENAPA and discover this amazing place. Thanks for her great help and to teach me her knowledge. Thanks to Matthew Davis for his expertise about the lionfish and the field work. I thank also Nadio for all his wise words. I would like to thank all the interns and volunteers (Matt, Katie, Tom, Will, Mark, Jenny and Tim) for hunting and dissecting lionfish with me and for their supports (especially for your correction Will). Thanks to Scubaqua for their precious data about the lionfish. A special thanks to Adrien for everything, especially to be with me in this adventure. Thank you very much to the La Rochelle team: nico, zozo and niels for their help, advice, support and friendship (since 5 years now)! Thanks also to Anne Gassiat for her help with the maps and my report.
During my internship, I have participated in various projects. I did the monitoring of the Red-billed tropic birds. The goal of this study was to measure the breeding success of this species. For that, STENAPA has monitored a tropic bird colony in the north west of the island. For each chick and adult different metrics were measured, like the length of the beak or the weight. I learnt how to manipulate birds. I also took part in a project about iguana. Nobody had ever done a complete assessment of the Lesser Antillean Iguana, an endemic species of the Lesser Antilles. The goal of this study was to sample blood in the maximum individual founded, to have an idea of the genetic biodiversity of the population in Statia. Beach clean, beach mapping, animation of the junior rangers club, maintenance of the trails in the National Park and in the Botanical Garden were the other activities in which I was involved.
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INTRODUCTION

In 1990, di Castri defined an invasive species as an organism which “colonizes and spreads into new territories some distance from its home territory”. According to Rejmánek et al. (2002), this definition is incomplete and too general. Indeed, it seems very important to adapt it for each case and each species. This very complex phenomenon depends on a multitude of factors like establishment capacity or invasion resistance (Bax et al., 2003; Ruiz et al., 2000). Marine biological invasions were rare until the 1980’s (Ruiz et al., 2000; Cohen and Carlton, 1998) but by 2008, 84 % of the marine ecoregion (Appendix 1) was invaded by non-native species (Molnar et al., 2008). These introductions are principally due to international shipping and aquaculture (Molnar et al., 2008) and in general, invaders have strong impacts on a variety of marine communities. They can be beneficial for the ecosystems (Tassin and Kull, 2015) or they can replace native species, modify community structure or alter some physical and biological process (Molnar et al., 2008). Once established, it seems impossible to eradicate marine invaders (Bax et al., 2003). During the last century, more than 68 invasive species were identified in the Caribbean sea (Morris, 2009). Most of them occupied low trophic levels (Byrnes et al., 2007) including macroplanktivores, deposit feeders, and detritivores. Thus, the occurrence of lionfish within the Caribbean region is exceptional. This is because it is one of the rare invasive predators, the first one in the north west Atlantic ocean and around the Caribbean sea (Morris and Akins, 2009; Schofield, 2009).

Lionfish is the common name for two species of Scorpaenidae, *Pterois volitans* and *Pterois miles*. These allopatric species (Schultz, 1986) are anatomically and behaviorally very similar (Morris et al., 2011). It is, therefore, complicated to differentiate them without genetic analysis (Hamner et al., 2007; Kochzius et al., 2003). *P. volitans* is originally a Pacific species, while *P. miles* originates comes from the Indian Ocean (Schultz, 1986). The overlap between their two ranges is not well delimited. In their native range both species densities are roughly 26 fish per ha which is 400 times less than in the north west Atlantic invaded ecosystem (Kulbicki et al., 2011; Grubich et al., 2009). Owing to hundreds of years of co-evolution, the lionfish do not have a negative impact on their native reef populations. It could be due to a natural control of the population in the Indo-Pacific ecosystems (Cure et al., 2012; Kulbicki et al., 2011).

In the western North Atlantic Ocean, lionfish were introduced by humans and spread very quickly, a lot faster than many other marine invaders (Schofield, 2010; Fogg et al., 2013). *Pterois volitans* and *Pterois miles* were introduced in Florida around 1985 (Schofield,
The first introduction could be due to the lionfish being released from aquarists (Semmens et al., 2004; Whitfield et al., 2002). The second cause could be from Hurricane Andrew in 1992, which potentially damaged a public aquarium permitting lionfish to escape (Courtenay, 1995). The lionfish only started expanding their range since the 2000’s (Figure 1) (Freshwater et al., 2009; Schofield, 2010; Whitfield et al., 2007). The first sighting in the Caribbean sea was in The Bahamas in 2006 (Snyder and Burgess, 2007) and only 3 years later, lionfish were observed in Colombia, roughly 1500 km in the south (González et al., 2009). In 2012, the lionfish were present in most of the Caribbean islands and the Gulf of Mexico (Figure 1). But apparently P. volitans is better adapted to this new invaded range because it represents roughly 90% of the invaded lionfish population (Hamner et al., 2007; Hines et al., 2011).

The incredible success of this invasion owes itself to a lot of different factors particularly features of the lionfish and the community it has invaded (Côté et al., 2013). Firstly, the reproductive dynamic of the lionfish is its main advantage, allowing it to become so successful (Morris Jr et al., 2011). The lionfish spawn roughly 2,000,000 eggs per year.
Eggs maturation is asynchronous, this means they release eggs continuously all year long. Every 2 or 3 days, eggs are released in a gelatinous matrix by the female (Fishelson, 1975; Gardner et al., 2015) after courtship. The male then fertilizes the eggs which then float to the surface (Freshwater et al., 2009; Hines et al., 2011). The fertilized eggs can therefore be transported by the wind or the current and colonize other sites relatively easily (Hare and Whitfield, 2003). The well protected eggs and the addition of a chemical deterrent in the egg matrix (Moyer and Zaiser, 1981) permits lionfish to have a high reproductive efficiency, despite an average larval duration (Ahrenholz and Morris Jr, 2010). These factors allow them to be dispersed over long distances and facilitate rapid establishment. Jud and Layman (2012) observed that lionfish have high site fidelity: this permits them to increase their population in the surrounding area. Furthermore, lionfish are habitat (Albins and Hixon, 2013; Barbour et al., 2011; Claydon et al., 2011; Kulbicki et al., 2011) and trophic generalists (Albins and Hixon, 2008; Côté et al., 2013; Layman et al., 2011; Morris Jr and Akins, 2009; Muñoz et al., 2011; Valdez-Moreno et al., 2012). This means they are able to reside in many different types of ecosystems, such as mangroves, sea grass meadows, coral reefs and artificial reefs. In the Atlantic, their only dispersal barriers are the temperature in the north, the salinity in the south and the depth of water towards the east (Kimball et al., 2004). But recently, Jud et al. (2014) demonstrated that a lionfish can survive in water with a salinity value of 7 for 28 days. Moreover, the Nemo submarine recorded an individual at 300m in The Bahamas, suggesting that lionfish are adapted to deep ecosystems. Lionfish might be able to extend their range for more than scientists previously thought. Their broad diet is also a huge advantage which facilitates their settlement. For example, in The Bahamas, Côté et al. (2013) reported that lionfish can eat 57 different native reef fish species, with teleosts fish representing roughly 80% of their prey volume (Morris Jr and Akins, 2009). The characteristics of the native community, which have allowed the invasion to occur more easily, are more difficult to identify. At first, lionfish do not have a lot of natural predators, this could be because many Caribbean predators have been overfished (Paddack et al., 2009; Jackson et al., 2001) or wary of eating the lionfish (Diller et al., 2014). Lionfish have large fins with many venomous spines, (Halstead et al., 1955) which provides very good protection against predation. But apparently the presence of native predators could not influence the lionfish densities (Hackerott et al., 2013). Loerch et al.(2015) also demonstrated that the lionfish is not susceptible to infection by ecto-parasites, however it could be infected by several other parasites as recorded by Ramos-Ascherl et al. (2014). Many publications suggest that the great success of the lionfish is primarily due to the naïveté of the prey (Albins, 2013;
Albins and Lyons, 2012; Cure et al., 2012; Côté et al., 2013; Diller et al., 2014; Jud and Layman, 2012; Jud et al., 2011). For example, Kindinger (2014) demonstrated that the three spot damselfish, *Stegastes planifrons*, actively respond toward native predators but not in presence of lionfish. This could indicate that the damselfish simply does not see the lionfish as a threat and is naïve as a result. Contrary to that, Black et al. (2014) has shown that the beaugregory damselfish, *Stegastes leucostictus*, can recognize this new predator and actively avoid them. In fact, the principal impact of the lionfish on this damselfish species is to decrease their reproductive success (Black et al., 2014). The habitat can also influence the abundance of lionfish. According to Valdivia et al. (2014), the density of this invader is largely driven by abiotic components of the environment. For example, fewer individuals have been observed living upon exposed-wave and windward coastlines (Hackerott et al., 2013; Anton et al., 2014). Bejarano et al. (2014) also demonstrated that lionfish densities are higher in rugose sections of the reef in Little Cayman. However, this is apparently not the case in The Bahamas (Anton et al., 2014).

Lionfish impacts are highly negative (directly or indirectly) on native populations and the entire Caribbean ecosystem (Albins and Hixon, 2008; Albins, 2013; Green et al., 2012; Lesser and Slattery, 2011; Rocha et al., 2015). Thanks to its life history traits, lionfish can colonize and proliferate all around the Caribbean. Invasive lionfish densities and their maximum size are higher in the Caribbean than in its native range (Green and Côté, 2009; Kulbicki et al., 2011; Darling et al., 2011). According to Albins (2013), lionfish have a greater growth rate than the native predators. Moreover, they catch larger prey than in the Indo-Pacific area (Cure et al., 2012) and have higher consumption rates (Côté and Maljkovic, 2010), even though there is no significant difference in the time they allocate to hunting (Cure et al., 2012). They have a very specific and effective hunting method (Albins and Lyons, 2012) producing a water jet to destabilize prey and swallow it easily. The same authors explain that lionfish use it less in their invaded range, and also eat parrotfish which they do not in their native range. Owing to these features, lionfish are a real threat to Caribbean’s ecosystem balance. Albins and Hixon (2008) were the first to study the impact of lionfish on fish assemblages. Their results show a significant decrease in the recruitment and abundance of native fish in the presence of lionfish. Furthermore, lionfish are more voracious than the native predators and can cause a significant decrease of 93.7% in small native reef fish communities in just 8 weeks (Albins, 2013). In The Bahamas, an increase in lionfish abundance inevitably leads to a decrease in the abundance of the majority of the fish species they predate upon (Green et al., 2012). In only two years, a decline of 65% in 42 lionfish prey
species was observed. Rocha et al. (2015) proved that the wrasse *Halichoeres socialis* is the most threatened species in the world because of the lionfish predation. Additionally, Albins (2015) showed a significant decrease of biomass, species richness and densities of lionfish prey, that are less than 10 cm in length during the 14 month experimental period. Apparently, the biggest decrease of native fish abundance occur in the presence of low lionfish densities (Benkwitt, 2014). Concerning the indirect effect, lionfish could contribute to the decline of other predators, by competing for food and shelter, which could lead to an imbalance in the ecosystem. The reduction of native prey fish could suggest a high competitive ability. Indeed, lionfish seem to monopolize the majority of food resources. Côté et al. (2013) highlighted that the competition between lionfish and native predators is not clearly defined. Layman and Allgeier (2011) showed an important overlap between lionfish diet and others native predators diet. Moreover, lionfish do not seem to have an effect on the growth rate of native predators (Albins, 2013). By contrast, a lionfish increase could contribute to a loss of shelter for the Nassau grouper *Epinephelus striatus* (Raymond et al., 2014). Even at deeper depths, lionfish predation can cause a decrease in the number of herbivorous, thus causing an increase of the macro algal cover (Lesser and Slattery, 2011). Morris Jr and Whitfield (2009) also emphasize that lionfish could also have a strong impact on the fisheries and tourism industries.

Many publications conclude that it is impossible to eradicate invasive lionfish, as the population is now too large and reach depths beyond recreational SCUBA diving (Côté et al., 2013). The best solution to controlling this species seems to setting up culling programs. According to Mumby et al. (2013), groupers could potentially reduce the lionfish abundance however their population is too small to have any major impact. As a result, the best solution is the active removal of lionfish. Many publications have proved the efficiency of this method. In 2011, Barbour et al. (2011) estimated that the lionfish population would be overfished if 35 to 65 % of the total individuals are culled. Frazer et al. (2012) used the CPUE (Catch Per Unit Effort) to demonstrate that there is a decrease in the number of lionfish caught per diver and per hour on a site after a repeated removal effort during roughly 200 days. In Curaçao and Bonaire, De León et al. (2013) proved the importance of setting up an efficient removal program early on. Indeed, the culling effort started in 2009 in Bonaire whereas it was started in 2011 in Curaçao. The lionfish abundance was significantly higher in Curaçao. Green et al. (2014) showed an increase in the native fish biomass after 18 months, during which lionfish were under threshold densities (when the consumption of the lionfish is inferior to the production of the native ecosystem). Finally, in addition to being delicious, the lionfish flesh is health, with their fillet representing 30.5% of their total weight body, which is
as much as some grouper species (Morris Jr et al., 2011). Some associations, like Reef Environmental Education Foundation (REEF), encourage the hunting of lionfish. Lionfish derbies are organized across the Caribbean, aiming to capture as many lionfish as possible. This kind of event provides an opportunity to educate people about the issues lionfish propose, while involving them in the culling program. Martinique, for example, adopted another strategy. Marine biologists and scuba divers promote lionfish as a refined dish. Now, fishermen and restaurants sell lionfish at a higher price than others reef fish species.

For all of the above reasons, it is very important to set up strong management plans and strategies. Most of the countries and islands legalized spear fishing while scuba diving, but only to kill lionfish. In 2009, Sint Eustatius National Park (STENAPA) set up a response plan (Bervoets, 2009) to provide advice for before and after the lionfish settlement. Concerning the pre-arrival action, it was necessary to inform the public and all the stakeholders (i.e Fishermen, divers, STENAPA staff) about lionfish. The post-arrival plan was to conduct a control effort on the population, to continue the education and public awareness and to start research and development about this invasive species. Currently, STENAPA continues to follow these recommendations. Since December 2010, when the first lionfish was sighted, marine park staffs are actively culling lionfish at different dive sites in and out of both marine reserves (Figure 2). Since 2010, a large set of data has been created. Previous park rangers have analyzed this data, but some questions remain unanswered, with results needing further analysis:

→ **Does the culling program significantly reduce the lionfish population in St Eustatius?** The aims of this question are: (i) to prove the efficiency of the removal effort, while describing any evolution of the lionfish population, (ii) to bring out the site where it is necessary to focus the culling program, (iii) to make recommendations to improve the efficiency of the current culling program.

→ **What can we learn with the culling program data about the lionfish and its behavior?** This second part aims to learn more about the lionfish on Statia and to compare the results with other data due to (i) the identification of the diet composition and feeding behavior of the lionfish by analyzing their stomach content and (ii) the determination of the size distribution of the lionfish on Statia.
MATERIALS AND METHODS

Background

Sint Eustatius is a part of the Dutch Carribean. It is situated in the north of the Antillean arc, in the Lesser Antilles (Figure 2). This small island is 22 km² in area and is locally called Statia. The east coast is exposed to the wind and waves from the Atlantic Ocean. The Caribbean side, on the west coast, is generally more protected. The dormant volcano on Statia is known as the Quill, and has created an exceptional underwater landscape due to past eruptions. As a result, divers dive in the middle of lava fingers, which are colonized by corals and sponges. To protect the marine wildlife, the St Eustatius National Parks Foundation (STENAPA), a non-governmental association founded in 1988, established

Figure 2 : Localization of St Eustatius and invaded site by the lionfish in 2010 (bottom left) and in 2014 (bottom right) (maps created by Manon Sanguinet)
a Marine Protected Area. The Marine Park has existed for 18 years and extends all around the island. St Eustatius’ displays a wealth of marine life and is well preserved and some endangered species can be observed there. That’s why the island is attractive to recreational divers. To avoid damaging the ecosystems, STENAPA created two marine reserves (Figure 2) where it is forbidden to fish and to anchor. It exists one exception for local fishermen who can fish in the reserve with a line and only one hook. Each diver has to pay a fee to be allowed to dive in the St Eustatius National Marine Park. This founding helps for the management of the Marine Park including the lionfish culling program. The first lionfish sighted in Statia was in December 2010 at The Cliffs, in the Southern Marine Reserve. This lionfish was observed by Scubaqua divers, a local dive shop. The day after, STENAPA started the culling program. In only one month, lionfish were recorded in 3 others sites (Figure 2).

**Experimental methods**

The removal program started in December 2010, when the first lionfish was observed. Since then, sightings are still recorded by marine park rangers, tourists, professional divers and fishermen. The observation data is compiled in a dataset including the amount of lionfish that have been culled. Lionfish are hunted by scuba diving with pole spears using the Roving Diver Technique (RDT)\(^1\). Divers swim freely at a dive site and record and catch all lionfish present. Divers look under ledges and in crevasses to find as many lionfish as possible. Only Marine Park staffs are allowed to spear fish within the Marine Reserves. Lionfish culling dives are planned every week in at least one of the 56 different dive sites in which staffs control them. The time lapse between each sampling is irregular and depends on the site. Very few dives took place on the Atlantic side, this part is then not considered in this study.

Once lionfish have been captured, they are dissected. At first, the total length, which represents the distance between the beginning of the head and the end of the caudal fin (Figure 3A), is measured for each individual. Lionfish have highly venomous spines on all of their fins except the pectoral fins (Figure 3A 1,2,3). These spines can cause a lot of pain, thus it is necessary to remove all of them before each dissection (Figure 3B). The lionfish is filleted to identify its gender (Figure 3C) and its stomach contents analyzed. For individuals smaller than 18 cm, the differentiation between sex can be misidentified (Green et al., 2012) as immature ovaries and testes can be confused. In their native range, females mature at 18 cm, with the ovaries becoming easily recognisable after this stage. Concerning the stomach analysis, all the content is extracted and identified to the lowest taxonomic rank possible.

\(^{1}\) For more informations about this techniques : https://www.youtube.com/watch?v=Cuj7PqMQoHc (from 2min)
The data is recorded on a paper sheet (Appendix 1) and then inputted into the STENAPA’s network.

Data analysis

All the statistical analysis was carried out upon the statistical software R. Most of the graphs provided were made using the package ggplot2. The maps were created on ArcGIS.

Effectiveness -- In order to evaluate the effectiveness of the culling program, three different analyses were used. At first, the total number of lionfish observed (including culled) per dive was compared in 6 different areas: Global, Marine Park, Marine Reserve, southern Marine Reserve, northern Marine Reserve, Marine Park Caribbean side. The data was collected between December 2010 and June 2015. Normality and homoscedasticity was tested for using respectively a Shapiro-Wilk and Bartlett test with $\alpha=0.05$. When the assumptions were not met, Kruskal-Wallis and Wilcoxon test were applied to test for differences between these areas. The locally weighted scatterplot smoothing (LOESS) was used to describe the evolution of lionfish numbers. This non parametric method permits to generalize the linear regression. To test for an eventual significant trend, Kendall rank correlation (Tho coefficient) test was calculated and its significance was tested thanks to cor.test. This type of correlation was used because it is more relevant when a lot of ex-aequos exist in the data, which is the

Figure 3: Steps of the lionfish dissection. The numbers on the figure A show all the venomous spines (A1: Dorsal fin, A2: pelvic fin, A3: Anal fin). The figure D represent 3 different prey of 3 lionfish (D1: parrotfish, D2: syngnatidae, D3: Blue tang).
case here. Secondly, the previous data was used to create maps to show abundances and trends for each site. Then, average abundance of lionfish observed per dive (including culled) was calculated for each site over four and a half years. In addition, the presence of a trend for each site was detected using the Kendall correlation. Finally, the Catch Per Unit of Effort (CPUE) was used to show the evolution of the lionfish abundance. This analysis occurred between May 2014 and May 2015 i.e. over 13 month period. This is because, since May 2014, STENAPA ranger’s recorded new data regarding the number of divers and the dive length for each dive. The CPUE was calculated as the number of lionfish caught per diver and per hour (Frazer et al. 2012; Pimiento et al. 2015).

Diet -- Concerning the general diet, 457 lionfish stomach contents were examined. Empty stomachs, or those containing digested matter, were excluded from the analysis. A pie chart was created to display their diet composition. The proportion of each fish family in the diet of the lionfish was calculated. The majority of the time, it was difficult, or impossible, to indentify the prey because they were too digested. Identifiable prey was found in only 107 individuals. When possible, the length of the identified prey was recorded. This data was also used to test whether there was a possible relationship between the length of the lionfish and the size of its prey, therefore a linear regression was carried out. Each individual came from an independent sample, as raw data was used rather than averages. The normality and the homogeneity of the variances were checked using Q-Q plots and the Residuals vs fitted values plot. The data was transformed using log10+1, when it was necessary.

Size distribution -- Finally, the size frequency of the lionfish around Statia was studied across all years. A comparison between evolution of male and female frequency could be made. According to Morris Jr and Whitfield (2009), the monitoring of the lionfish size can provide data about the impact of the culling program on their population structure. Immature individuals were not considered for this study because data was not accurate and mixed with different lengths of non identified genders. Thus, only identifiable genders were studied. The length distribution in function of the depth was studied also thanks to the kendall correlation. The ratio of male to female was calculated and compare to the ratio 1:1 with the Chi-square test to detect a significant difference.

Influence of depth – To detect an eventual correlation between the number of lionfish and the depth, the depth was divided into two groups as defined by scuba divers: sites less than 18m were considered as being shallow, while those deeper than 18m were considered as deep. A two mean comparison was made, to find out whether the lionfish had any preference towards a certain depth. For the both depth groups, roughly 300 dives were carried out.
RESULTS

Effectiveness of the culling program

Annual culling effort

Since 2010, the annual culling effort (Table 1) shows the percentage of culled lionfish per year. The percentage of culled lionfish was stable until 2013 and then increase in 2014 and 2015. In only five months, more than 80% of the lionfish observed were culled in 2015. In 2011, 105 lionfish were culled all around Statia whereas 860 in only 5 months in 2015. In 2013, 141 lionfish were caught and 268 sighted which is much less than in 2012 and 2014.

Table 1: Annual removal rate

<table>
<thead>
<tr>
<th>Year</th>
<th>Culled</th>
<th>Total observed (including culled)</th>
<th>Percentage of culled lionfish (%) = Removal rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>2</td>
<td>5</td>
<td>40</td>
</tr>
<tr>
<td>2011</td>
<td>105</td>
<td>235</td>
<td>45</td>
</tr>
<tr>
<td>2012</td>
<td>456</td>
<td>821</td>
<td>56</td>
</tr>
<tr>
<td>2013</td>
<td>141</td>
<td>268</td>
<td>53</td>
</tr>
<tr>
<td>2014</td>
<td>628</td>
<td>921</td>
<td>68</td>
</tr>
<tr>
<td>2015 (Jan-May)</td>
<td>860</td>
<td>1061</td>
<td>81</td>
</tr>
</tbody>
</table>

Evolution of lionfish number

The number of lionfish observed and culled per dive was estimated to show the progression of the lionfish abundance during the length of the entire culling program. The data concerning the number of lionfish observed and culled per dive did not meet the assumptions to apply a parametric test.

Figure 4 shows the locally weighted scatterplot smoothing (LOESS) results for different part of the Marine Park. No significant difference was found between Marine Park and Marine Reserve (p-value=0.21; Wilcoxon test). All the correlation of Kendall are significant. Thus, a trend exists for the 3 areas considered in Figure 4. The global number of lionfish seems to increase slowly between 2010 and 2015. In the Marine Park, the growth of the lionfish number seems to be stronger. Indeed, since 2014, the number of lionfish appears to increase more than before. The Kendall coefficient Tho ($\Theta$) is also higher for the Marine Park than in the others areas ($\Theta$=0.28; p-value=1.68e-09). The “tho” explain that 28% of the
variation in the lionfish numbers is a function of time, however trend is different for the Marine Reserve. Lionfish numbers appear stable until the beginning of 2015 then the curve tends to drop off.

![Graph showing lionfish number variation over time](image)

Figure 4: Evolution of the lionfish number (Number of lionfish observed per dive) and their smoothed conditional mean for 3 different sites: Global ($\hat{T}=0.23$; p-value=6.66e-16), Marine Park($\hat{T}=0.28$; p-value=1.68e-09) and Marine Reserve ($\hat{T}=0.18$; p-value=1.94e-07)

To provide more clarification on the evolution of lionfish numbers, figure 5 represents the local regression at a smaller geographic scale. Post hoc tests reveal significant differences between the Southern Marine Reserve and Northern Marine Reserve (p-value=0.0014; Wilcoxon test) and between the Northern Marine Reserve and the Marine Park within the Caribbean side (p-value = 0.0063; Wilcoxon test). The kendall Tho for the Northern Marine Reserve data is not significant which means there is no trend concerning the number of lionfish within this area. With relatively high correlation coefficient ($\hat{T}=0.29$), the results indicate that lionfish numbers have increased significantly in the Southern Marine Reserve. This increase can be clearly observed between December 2010 and January 2015. However, the lionfish numbers have tended to decrease from the beginning of 2015. In the Marine Park Caribbean side, the trend is significant and increase more rapidly throughout years than in the others areas. In May 2015, the local regression mean reaches 7 lionfish per dive in the Marine Park Caribbean side whereas it reaches less than 5 in the Southern Marine Reserve.
The following maps (Figures 6, 7 and 8) provide the mean number of lionfish observed and culled and the trend that follows over the four and half years of the culling program for each site. The lionfish number is represented by the size of the circles and the color of these circles shows the trends. Most of the time, a trend was revealed when STENAPA divers visited controlled sites regularly. Thanks to these three maps (Figure 6,7,8), it was possible to know where the removal program has to occur in the future. The red circles reveal an increasing trend. Even if a trend was not highlighted on certain sites, a big circle indicates a large number of lionfish, thus highlighting a site where divers have to focus their effort. The number of lionfish increased in five sites within the Southern Marine Reserve, one site in the Northern Marine Reserve and one in the Marine Park on the Caribbean Side. The lionfish number is superior to 17,4 observed per dive in 4 different dive site. On these four sites, only one has a significant decreasing trend (in green) : Mushroom gardens.
Figure 7: North part of the island including the Northern Marine Reserve. The Kendall coefficient was used to describe the trends.

Figure 6: Marine Park Caribbean side. The Kendall coefficient was used to describe the trends.
For more information, table 2 helps to identify the site where the lionfish number per dive is growing. For example, the kendall coefficient is 0.54 for Crook’s castle which means that the variation of the lionfish number is highly positively correlated with the time. Lionfish numbers tends to then increase.

<table>
<thead>
<tr>
<th>Location</th>
<th>Kendall coefficient (Tho)</th>
<th>p-value</th>
<th>Trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blair’s Reef</td>
<td>0.43</td>
<td>0.03</td>
<td>Increase</td>
</tr>
<tr>
<td>Coral Garden</td>
<td>-0.44</td>
<td>0.03</td>
<td>Decrease</td>
</tr>
<tr>
<td>Crook’s Castle</td>
<td>0.54</td>
<td>0.02</td>
<td>Increase</td>
</tr>
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<td>Gibraltar</td>
<td>0.22</td>
<td>0.04</td>
<td>Increase</td>
</tr>
<tr>
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<td>0.29</td>
<td>0.02</td>
<td>Increase</td>
</tr>
<tr>
<td>Hangover</td>
<td>0.40</td>
<td>0.01</td>
<td>Increase</td>
</tr>
<tr>
<td>Nursing Station</td>
<td>0.72</td>
<td>&lt;0.001</td>
<td>Increase</td>
</tr>
<tr>
<td>Stenapa Reef</td>
<td>0.45</td>
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<td>Increase</td>
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</table>

Figure 8 : South of the island Southern Marine Reserve. The Kendall coefficient was used to describe the trends.
Evolution of the Catch Per Unit of Effort between May 2014 and May 2015

As seen on the Figure 4, lots of data exists between May 2014 and May 2015. Thanks to the new recorded data (dive length and number of diver), the following study of the CPUE (Figure 9 and 10) helps to explore more accurately the different trends occurring in this period. As a reminder, the CPUE was calculated as the number of lionfish caught per hour per diver.

![Figure 9](image)

**Figure 9**: mean and standard deviation of the CPUE (number of lionfish caught per hour and per diver) for each month

The figure 9 shows the evolution of the CPUE during the period of May 2014 and May 2015. All the highest values were removed using a boxplot graph to detect the outliers. By month comparison shows that a significant difference between June and December 2014 (p-value=0.05; Wilcoxon test), between June 2014 and February 2015 (p-value=0.02; Wilcoxon test), between December 2014 and Mars 2015 (p-value = 0.005; Wilcoxon test) and between February 2015 and Mars 2015 (p-value= 0.002; Wilcoxon test). There is an apparent increase of the number of lionfish caught per hour per diver between May 2014 and December 2014. Then, the CPUE tend to decrease until May 2015.
The results of the two linear regressions between time and CPUE are shown in Figure 10. To meet the assumptions i.e. normality and homoscedasticity, the data were transformed using log10 +1. The increase between May and December 2014 and the decrease between January to May 2015 seems to be proved. Indeed, both regressions are significant and the time can explain roughly 10 % of the CPUE variation for both regressions. The correlation is positive for the first period and negative for the second one.

Figure 10: CPUE (Number of culled lionfish per diver and per hour) between May 2014 and May 2015. Linear regression: In red, $r^2=0.1158$ and p value = 0.0001032. In blue, $r^2=-0.1042$ and p value = 0.000696
Knowledge contribution

Diet

The diet is mostly composed of fish (Figure 11). Indeed, they represent 75% of the lionfish’s prey. Shrimp represents 23% of the total diet. Crabs, copepods and others crustaceans were also found in their stomach.

Concerning the composition of the fish prey (Figure 12), a wide variety of prey fish families could be observed. The most abundant prey can be found in the family Labridae, with the two most common species being the bluehead wrasse Thalassoma bifasciatum and the yellowhead wrasse Halichoeres garnoti. The Caranguidae are also well represented (22%). The third most abundant family is the Pomacentridae (11%) including damselfish (e.g. Blue chromis). 16 others families are represented in the diet of the lionfish.

Figure 11: Diet composition of 457 lionfish caught between December 2010 and February 2015

Figure 12: Fish composition (families) of lionfish diet for 107 individuals caught between 2010 and 2015
**Lionfish length-prey size relationship**

To meet the assumptions for a linear regression, data concerning the size of the lionfish prey were firstly transformed using log10+1 (Appendix 3). Table 3 permits to study the mean size of prey fish as a function of the length of the lionfish. The results of the linear regression (Graphs in appendix 3) show that 8% of the size of the lionfish can explain the length of the fish prey eaten (Table 3). This correlation is highly significant (p-value=0.00117). And concerning the crustaceans prey, the correlation coefficient is higher. The length of the lionfish can explain 17% of the crustaceans prey size variability but is less significant (Table 3).

<table>
<thead>
<tr>
<th>Prey size</th>
<th>R²</th>
<th>p-value</th>
<th>Homoscedasticity &amp; Normality after transformation (log10+1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>0.08</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Crustaceans</td>
<td>0.17</td>
<td>0.0274</td>
<td></td>
</tr>
</tbody>
</table>

**Size frequency and distribution**

Due to the Figure 13, it was possible to study the size frequency of the male and female over the four different years. Concerning the mean size of the lionfish culled, it increased between 2011 and 2014. In 2011, the mean length of the lionfish was roughly 20 cm but in 2014 it was almost 30 cm. In only one year (between 2012 and 2013), mean lionfish length increased by roughly 4 cm. The mean of the total population was roughly the same between 2013 and 2014. In 2011, small females were apparently more frequent than small males around Statia. Females of 18 cm were more numerous than others female length. Bigger males seemed to be more frequent than female. In 2012, all the class length was represented and the mean length of the lionfish was 24 cm. In 2013, very few individuals were examined. In 2014, males in size from 29 to 42 cm appeared more frequent. The frequency of females tended to decrease. Females measuring more than 32 cm were underrepresented in 2014. The length range for males and females also changed over the years. It was from 10 to 27 cm for the female in 2011 and from 14 to 38 cm for male. In 2014, female lionfish length was from 14 to 39 cm whereas for the male is from 17 to 42 cm. This same year most of the male lionfish that were caught and measured were larger than 28 cm. The ratio of male to female is significantly different from 1:1 only in 2012 and 2014. The sex ratio is 1.4:1 ($X^2=7.074$, p-value=0.008) in 2012 and 1.8:1 ($X^2=33.824$, p-value=6.034e-09) in
2014. During these two years, the number of males is significantly higher than the number of females.

Figure 13: Evolution of length distribution of the lionfish all around the island. Pink color represents female (=F) and blue represents male (=M). The n represents the number of individuals analyzed. The red bars represent the average length of the total population.
The total length data of the lionfish has enabled us to study the depth preference of the biggest lionfish. Appendix 4 illustrates the relationship between lionfish size and depth. The assumptions were not met to draw a linear regression. Then, LOESS was used to describe the relationship between depth and lionfish length. Kendall coefficient was used to highlight the presence of a trend. The tho coefficient is equal to 0.11 and it is significant (p-value=2.6e-10). Thus, there is a slight increase of the lionfish in function of the depth. These results show that most of the biggest individuals do not live in deeper area.

**Relationship between number and depth**

Due to the data of the depth, it was possible to determine at what depth the lionfish is more abundant. Graphically, the difference between shallow water and deep water in term of lionfish number was not so obvious. That’s why only statistical results are presented in this part. The data did not meet the assumptions (i.e. normality and homoscedasticity), a non parametric test was thus used. A significant difference between shallow water and deep water (p-value=5.4e-09; Wilcoxon test) was found. It seems that more lionfish live in water deeper than 18m. This last result will permit to determine in which sites divers have to focus in the future.
DISCUSSION

EFFECTIVENESS OF THE CULLING PROGRAM

During the four and half years of the culling program in Statia, the global lionfish population has increased slowly and even decreased during the last few months in the Southern Marine Reserve. The Marine Park staff, which are becoming more and more efficient, killed more than 50% of the lionfish observed annually since 2012. Moreover De León et al. (2013) have demonstrated a significant decrease of lionfish with an immediate start and a constant removal effort. A significant decrease of the lionfish numbers was therefore expected around Statia. Nevertheless, this is not the case on a global scale. But a significant decrease was observed at the beginning of 2015 in the Southern Marine Reserve. The lionfish removal is mainly focused in this reserve because most of the dive activity is concentrated here. The Marine Park staff need to cull more lionfish in the Northern Marine Reserve and the Marine Park Caribbean side to make the lionfish population in Statia decrease. Despite all the efforts, the lionfish cannot be eradicated, but only controlled. Moreover, a permanent colonization by the other surrounding islands (Ahrenholz and Morris, Jr 2010; Johnston and Purkis, 2011) could cancel the removal effort. According to the model developed by Modglin and Lagerloef (2002), a southeast current is established in the Caribbean. Thus, lionfish eggs in the neighboring islands (e.g. Guadeloupe, Antigua and Barbuda, St Kitts and Montserrat) could be transported toward Statia. Moreover, there is a perpetual compensation also by the deepest lionfish and lionfish in uncontrolled area.

The decrease of the lionfish numbers in the Southern Marine Reserve at the beginning of 2015 occurred thanks to different processes. At first, a non constant culling effort between May 2013 and May 2014 (only 58 dives) may have caused an increase and expansion of the lionfish (De León et al., 2013). After May 2014, a high effort has occurred again to remove this large population of lionfish. This can explain the increase of the Catch Per Unit of Effort (CPUE) before December 2014. This high removal effort has led to a significant decrease in the lionfish numbers until May 2015. Since the unit of the dive length and number of divers has been recorded, it is possible to have a more accurate unit (i.e CPUE) to analyze trends. The slight increase during the last few months in the Marine Park within the Caribbean side is due to the exploration of a new site: Maximus. This site is part of a large reef where STENAPA went for the first time in April 2015. Roughly 34 lionfish are observed per dive on average in Maximus. This is a good site to analyze empirically the efficiency of the culling program set up by STENAPA. Considering all controlled sites, less than 10 lionfish are
observed per dive on average which is much less than at Maximus. The culling program seems therefore efficient on regularly controlled sites. The non significant trends in the Northern Marine Reserve and in the Marine Park Atlantic side could be due to a lack of data. In the Northern Marine Reserve, Marine Park divers did not cull enough lionfish but on the Atlantic side, only few individuals live there. The lionfish seems to be always less abundant on wave exposed coastlines (Anton et al., 2014; Hackerott et al., 2013; Valdivia et al., 2014) because waves could be a physical stress for the lionfish and disturb its hunting behavior (Anton et al., 2014). All these results show that it is important to maintain the culling effort in the Southern Marine Reserve, to cull more lionfish in the Northern Marine Reserve and to focus on certain sites in the Marine Park Caribbean side. The maps highlighted the sites where it is important to remove lionfish. These maps have to be interpreted carefully. Maps just show the most likely site to be invaded by lionfish at one given time. In my opinion, the kendall coefficients reveal the place where the lionfish number tends to increase if a removal effort is not done regularly. It is important also to focus on the sites where there is the highest number of lionfish for example Lost anchor, Maximus or Coral Gardens. Maximus and Lost Anchor are large reefs and need to be explored in greater. The trend is just an indication and permits to estimate the evolution of the lionfish in four and half years. According to all these results, table 4 shows where the future removal effort needs to be focused.

Table 4: Sites recommended for future lionfish culling dive

<table>
<thead>
<tr>
<th>Type</th>
<th>Characteristics</th>
<th>Culling frequency</th>
<th>Example of site</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep (&gt;18m)</td>
<td>High lionfish number</td>
<td>Regularly at least once a month</td>
<td>Drop off Coral Gardens</td>
<td>Figure 8 Lee et al., 2011 White, 2011</td>
</tr>
<tr>
<td>Complex reefs</td>
<td></td>
<td>Often At least twice a month until a decrease is observed</td>
<td>Maximus Lost Anchor Grand Canyon</td>
<td>Figure 7 Bejarano et al., 2014</td>
</tr>
<tr>
<td>Artificial</td>
<td>Attract lionfish in marginal habitat</td>
<td>Regularly at least once a month</td>
<td>STENAPA Reef</td>
<td>Figure 7 Table 2 Smith 2010</td>
</tr>
<tr>
<td>Other</td>
<td>Low number but upward trend</td>
<td>Sometimes Every 2 months (more if necessary)</td>
<td>Crook’s Castle Nursing station Hangover</td>
<td>Figure 8 Table 2</td>
</tr>
</tbody>
</table>
DIET

All the data proved definitively that lionfish are opportunistic in terms of the species and size of its prey. 75% of fish is found in the diet of the lionfish, which coincides with others studies of their diet. The percent of fish prey in the lionfish stomach is always higher than 70% (Morris Jr and Akins, 2009; Muñoz et al., 2011; Sandel et al., 2015). In Statia, the lionfish diet is composed of 20 different families of fish. The different publications describe from 9 to 21 different families of fish prey (Côté and Maljkovic, 2010; Morris Jr and Akins, 2009; Muñoz et al., 2011; Valdez-Moreno et al., 2012). The diet of the lionfish in Statia seems to be similar to other areas where it has invaded. The most represented fish families in the lionfish diet in Statia are Labridae, Carangididae, Pomacentridae, Serranidae and Apogonidae. All these families have a key role in the coral reef ecosystem (Bellwood et al., 2004; Hughes et al., 2007; Cole et al., 2008) and their possible decline due to the lionfish predation could cause imbalance in the coral reef communities (Barbour et al., 2011). These results could be biased by the few number of lionfish prey identifiable. As highlighted by Côté et al. (2013), the prey data could not be really accurate because it represents a small percent of the total prey stomach content. In two different studies (Morris Jr and Akins, 2009; Sandel et al., 2015), Labridae are present in the top 5 of the lionfish prey. The Carangididae family was the most abundant prey in the lionfish stomach in 2006 in the southeast coast of USA (Muñoz et al., 2011) which could match with the lionfish diet in Statia. However, this family is rarely found in the lionfish stomach (Matthew Davis, pers.comm). The 22% of Carangididae in the lionfish diet can be easily explained. In August 2014, Marine Park staf found two lionfish with 39 jacks (family of Carangididae) in their stomachs. Considering the few prey identifiable, this is clearly an outlier which has skewed the results.

Concerning the relationship between prey size and lionfish length, the correlation is positive but quite low. Apparently, the prey crustacean size is more correlated to the lionfish length rather than the fish prey size. This could be explained by a lack of data concerning crustacean prey size. Morris Jr and Akins (2009) used means to show a positive correlation between the prey size and the lionfish length. The results from Statia are a total contradiction to their results. If mean prey size was used for each lionfish length in Statia, the value of the $R^2$ was 0.837. However, the individuals are independent and do not come from the same sample. Thus, it would not be correct to use mean to determine a correlation here. Here, the results confirm that the lionfish eat a wide variety of prey, regardless of its length. Moreover, Scharf at al. (2000) studied the relationship between marine fish predators and their prey size. Roughly 18 piscivorous fish species of the US east coast were considered. According to their
results, the prey size eaten increased always with the predator size. The lionfish could be therefore an exception among the marine predators and confirm the exceptional characters of its diet.

**SIZE DISTRIBUTION**

There is a clear increase in the maximum length and the mean length of the lionfish adult population throughout the years. Larger males seem to become predominant in Statia in 2014. Between 2013 and 2014, the stabilization of mean length could reflect an establishment of lionfish population around Statia. The non increase of the length means between 2013 and 2014 show also that the lionfish have attained at their maximum length. The decrease of females should lead to an intense competition between male. This imbalance in the population could be due to the effectiveness of the culling program which may reverse the ratio male female. This could be also owed to the different behavior of the male and female. It is possible that females are less active during the day than males. Few observations show that individuals can spend some time reversed on their back under a rock. It is thus more difficult to find them. Unfortunately, no studies have been published about the evolution of the size frequency to date. The results of the present study are not comparable with a publication.

Some females were identified before the theoretical size maturity in 2011. In 2014, all the females identified were larger than 18cm. An invasion can lead to a decrease in the maturity size (Hutchings, 2002). An increase of this size could prove that the lionfish population is no longer undergoing its expansion (Morris Jr, 2009). It could mean that the lionfish population has stabilized around Statia. It is just a hypothesis given that this type of statement might be not valid on a small scale. Moreover, most of the time the males and females are difficult to identify under 18cm. This could be a big bias in the study of the size frequency.

No correlation was found between depth and size in Statia. Several studies have demonstrated that the smallest lionfish live preferentially in shallow water, whereas the biggest ones in the deepest water (Barbour et al., 2010; Biggs et al., 2011; Claydon et al., 2011). According to de León et al. (2013), this behavior can limit the effectiveness of a culling program. But in Statia, even if lionfish seems to be more numerous in the deepest sites, the mature individuals could be accessed at any depth. This could make the culling program in Statia more efficient than in the other islands. The fact that the lionfish are more numerous at deeper site are confirmed by several witnesses of professional and recreational divers (Kelly, 2013) all around the Caribbean.
CONCLUSIONS & PERSPECTIVES

The Lionfish culling program is relatively efficient around Statia. The slow increase of the lionfish numbers indicates that the culling program has maintained the population under a certain threshold. The culling program has being mostly focused on the Southern Marine Reserve, as a result there is a decrease of lionfish in this area. This definitely proves the effectiveness of the removal program when applied regularly. For the future, Marine Park staff must continue their efforts in the Southern Marine Reserve and cull lionfish more often in the Northern Marine Reserve and Marine Park within Caribbean side. The lionfish are more numerous at deeper sites but the depth does not influence the size distribution. The increase of the length throughout years shows that lionfish are now well established around Statia. The impact of the lionfish predation is not well known in Statia. It seems absolutely necessary to evaluate the impact of lionfish in St Eustatius. For that, an assessment of the native fishes in reefs with lionfish and without lionfish should be done. The biomass of the native reef fish can be evaluated counting the individuals and estimating their size through a visual survey (Green et al., 2012). The opportunistic behavior of the lionfish, confirmed in this study, could have a great impact on the fish assemblages.

Until now, all the studies that have studied the invasive lionfish have highlighted it as one of the biggest threat for the North West Atlantic ecosystem. The lionfish a priori greatly upset the ecosystem. Can these changes be reversible? Is it possible that an ecosystem, where the lionfish is established, come back to an initial state? A very recent study started to give some answers. According to Elise et al. (2015), the lionfish do not have any negative impact on the native fish assemblages in a Venezuelan marine protected area. The lionfish lead to a higher level of prey and do not change significantly the fish assemblages in this ecosystem. The lionfish impact could be therefore moderate in healthy reefs. The lionfish population in Statia seems to be stable since few months, is it still necessary to continue the culling program? Could the lionfish be integrated in the Caribbean ecosystem in few years? These two questions remain without answer and will be the principal challenges in the next few years.
BIBLIOGRAPHY


APPENDIX

Appendix 1: Definition of an eco region

Appendix 2: Lionfish culled form

Appendix 3: Graphs of the linear regression concerning the relationship between prey size and lionfish length

Appendix 4: Relationship between depth and lionfish length
APPENDIX 1:
Ecoregions defined by Spalding et al. 2007

**Definition of an eco region**: “Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features. The dominant bio geographic forcing agents defining the eco-regions vary from location to location but may include isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments, currents, and bathymetric or coastal complexity.”
APPENDIX 2

**Lionfish Culled Form** (for STENAPA)

Date when Lionfish was culled: (dd/mm/yy) ___/___/___              Time: _________

Location of culled Lionfish:
_____________________________     Depth: ______

Caught by: _____________________ Length of dive: __________

Number of specimens still alive: ______

Number of specimens caught: ______

Number of specimens brought in to office: ______

<table>
<thead>
<tr>
<th>Fish ID</th>
<th>Gender</th>
<th>Stage</th>
<th>Length (TL)</th>
<th>Stomach Content</th>
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<tr>
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APPENDIX 3

Result of the linear regression

**Fish prey:**

Mean fish prey size eaten by lionfish in function of the total lionfish body length. $R^2 = 0.07848$, p-value = 0.000117 (*****). From 189 lionfish stomach contents
Crustacean prey

Mean size of lionfish crustaceans prey in function of the total length of lionfish + Linear regression (R²=0.1676 and p-value = 0.02742) from 30 lionfish stomach contents

Residuals vs Fitted

Normal Q-Q

Fitted values

Theoretical Quantiles
Appendix 4:

Relationship between depth and lionfish length using a smooth curve
RESUMÉ

Le poisson lion, regroupant deux espèces de rascasses, est considéré comme invasif dans une grande partie des écosystèmes de l’Atlantique nord ouest. Observé pour la première fois dans les années 1980 en Floride, il a ensuite colonisé l’ensemble de la côte est des Etats Unis, les Caraïbes et le golfe du Mexique. Son incroyable expansion est due à ses caractéristiques physiologiques, notamment une reproduction efficace, mais aussi aux caractéristiques de sa nouvelle aire de répartition, qui facilite son installation. Espèce vorace et opportuniste, le poisson lion entraîne une diminution significative des poissons récifaux natifs. Le moyen le plus efficace de contrôler les populations de poisson lion semble être la mise en place de campagnes d’abattage, un maximum de poissons lion devant être prélevé pour un contrôle efficace. Un programme d’abattage a commencé fin 2010 à Saint Eustache (Antilles Néerlandaises). Depuis ce jour, les poissons lions tués sont mesurés et disséqués, mais ces observations bien que stockées dans une base données, n’ont pas fait l’objet d’analyses très approfondies. Cette étude a pour but d’analyser cette base de données afin de mieux connaître cet envahisseur qui s’est développé autour de Saint Eustache. Cette analyse permet dans un premier temps d’évaluer l’efficacité du programme d’abattage. Les résultats montrent que le programme aide à contrôler le nombre de poisson lion et même à le diminuer dans la Réserve Marine sud. Les sites sur lesquels il faut se concentrer ont été mis en évidence et des recommandations ont pu être faites. Dans un second temps, cette analyse révèle des connaissances plus générales sur le poisson lion lui-même. Le poisson lion est un opportuniste tant au niveau de la taille que de l’espèce de ses proies. Il semble toutefois se nourrir majoritairement de poissons. Sa population est bien installée autour de Saint Eustache et le nombre de mâle augmente au fur et à mesure des années. Le nombre d’individus est plus important à des profondeurs supérieures à 18m, en revanche les individus les plus gros ne sont pas nécessairement dans les zones les plus profondes.