Quantifying the Pterois volitans Caribbean Invasion

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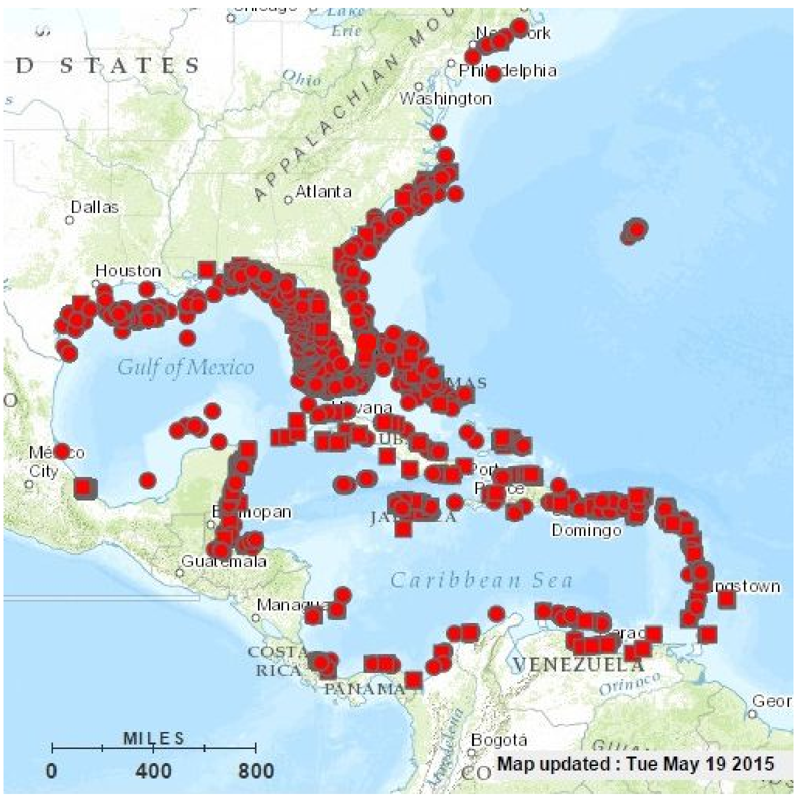
Abstract

The Caribbean Red Lionfish invasion is one of the worst threats to the marine ecosystem. However, the adverse effects of this species on the local fauna are still poorly quantified. During the course of two week-long expeditions in Belize, seventy lionfish were captured and dissected. They were analyzed for morphological parameters, stomach content and gonad stage. Deeper, structured reefs were observed providing a greater ecological niche for lionfish, housing larger fish with more fat reserves. Enough information was gathered to strongly suggest a model of how habitat characteristics can play a role in determining the effect of lionfish on biological communities.

Introduction

Over the course of the past few decades, the Caribbean waters have been overcome with a voracious predatory invasion. The indo-pacific predators Red Lionfish (*Pterois volitans*) (see figure I) and Devil Firefish (*P. miles*) have taken the waters by storm. While the Red Lionfish has spread throughout a majority of coastal Atlantic waters (see Map I below), the Devil Firefish has remained relatively secluded in its area of introduction, off the coast of Florida.[9]



Map I: An up-to-date map showing all Atlantic lionfish sightings as of May 19^{th} 2015, where circular points indicate an accurate population status and square points indicate an approximate known population status. This map was adapted from Hixon and USGS.[5, 9]

Figure I: A specimen of *P. volitans*.

The origin of the introduction is unknown, although a few theories keep resurfacing as plausible. The initial confirmed sighting was reported in 1985, off the coast of Dania Beach, Florida, indicating the release of a few specimen out of a home aquarium.[7] Another theory suggests that the most significant lionfish introduction was off the coast of Biscayne Bay, Florida, when several specimen were released from an aquarium during Hurricane Andrew in 1992, producing a strong founder effect.[1 8] Regardless of their method of introduction, the species have now established themselves as permanent members of the Caribbean ecosystem.[5] They now occupy a massive territory, spanning the northeast United States to Southern Venezuela, including the entirety of the Gulf of Mexico, occupying reef depths up to 300 metres deep.[8]

Lionfish have been described as “the perfect invader”.[5] This attribution is due many habits and characteristics of the species. First, they are voracious predators; they eat all the species that surround them with impunity. Some of our gathered data found a specimen whose stomach contained 16 identifiable fish, indicating they had all been eaten in rapid succession prior to capture by utilizing predation techniques that are foreign to the native fish. This foreign technique and the recency of their introduction make the native reef fish not recognize the lionfish as a predator.[5] Second, they are protected by venomous spines, which shield them from the native predators of the Caribbean, such as the shark or the endangered Nassau Grouper, deterring them after one taste.[3 5 8] The only observed predator of the lionfish is itself, as instances of cannibalism have been documented.[9] Third, lionfish are endowed with a cryptic coloration which, in their benthic habitat, allow them to blend in with the corals even in broad daylight.

However, one of the leading factors of this invasion is the reproductive success of the *Pterois*.[5] Every 3 - 4 days, in all seasons of the year, a female will lay two (2) fertilized egg sacks containing 10000 - 20000 eggs (the number varying in accordance to the size of the female).[6 8] All members of the *volitans* species are deemed morphologically identical upon hatching, but can later be identified through gonad observation.[8]

Given all these morphological characteristics and habits, the presence of this foreign predator has caused a cascading effect on the Caribbean coral reefs. *P. volitans*’ habit of eating any reef fish it finds has been driving important ecological species toward extinction. Albins and Hixon (2008) provided some of the first evidence of the predation impacts of the lionfish on reef communities: they observed a 79% reduction in recruitment rate on experimental patch reefs over a five-week observation period in the Bahamas.[1] These experimental reefs contained only one lionfish. With the steady disappearance of important species such as the Parrotfish (family *Scaridae*) due to predation, coral grooming is reaching an all time low, providing an ecological shift toward a floral dominated ecosystem, covering the corals with algae, therefore annihilating the current reef ecosystem.[5 7 8] A hypothetical model comparing the reef ecosystem in a natural state compared to the potential worst case scenario can be observed in figure II below.

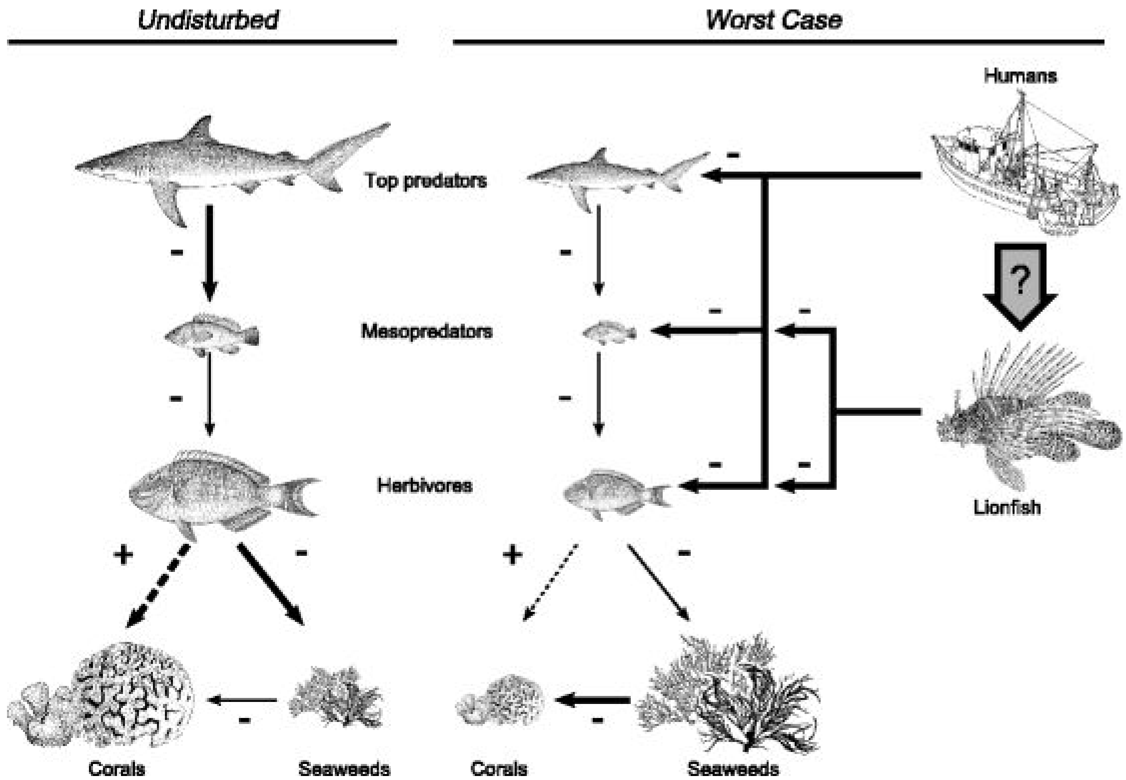


Figure II: A model of the worst case scenario of the lionfish invasion, as defined by Albins and Hixon.[2] Such a scenario would cause a cascading effect on the coral abundance and ecosystem, preventing the thriving of reefs and covering them with algal growth and deposits.[5] The size of each organism reflects its relative abundance within the ecosystem, and the thickness of each arrow is relative to the strength of the interaction between the two linked organisms. Solid arrows reflect effect of predation and/or competitive effects, while dashed arrows indicate indirect positive effects on the species at the tip of the arrow. The unknown effect of humans on lionfish presence is displayed as a question mark, as control efforts are currently underway.[2 3 6 8]

The objective of this research project was to observe the variation in lionfish prosperity and competition in various reefs and habitats by observing and measuring different morphological parameters. This was done in hopes of establishing relations between said parameters and the ecological niche of the invasive lionfish, and defining factors that affect lionfish prosperity and competition within their established habitats. Results could eventually concretize themselves into the monitoring and control process of the lionfish invasion, which is the central cycle attempting to control and contain the invasion. Refer to figure III below for the monitoring and regulation process.

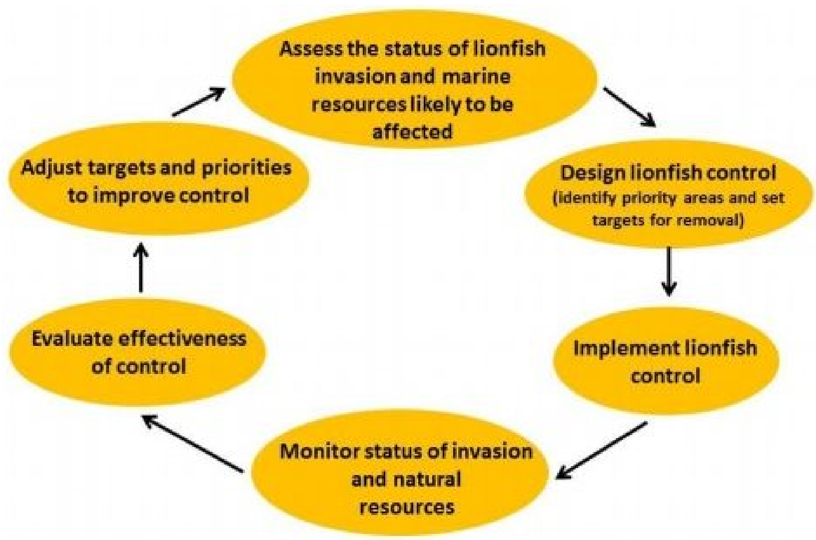
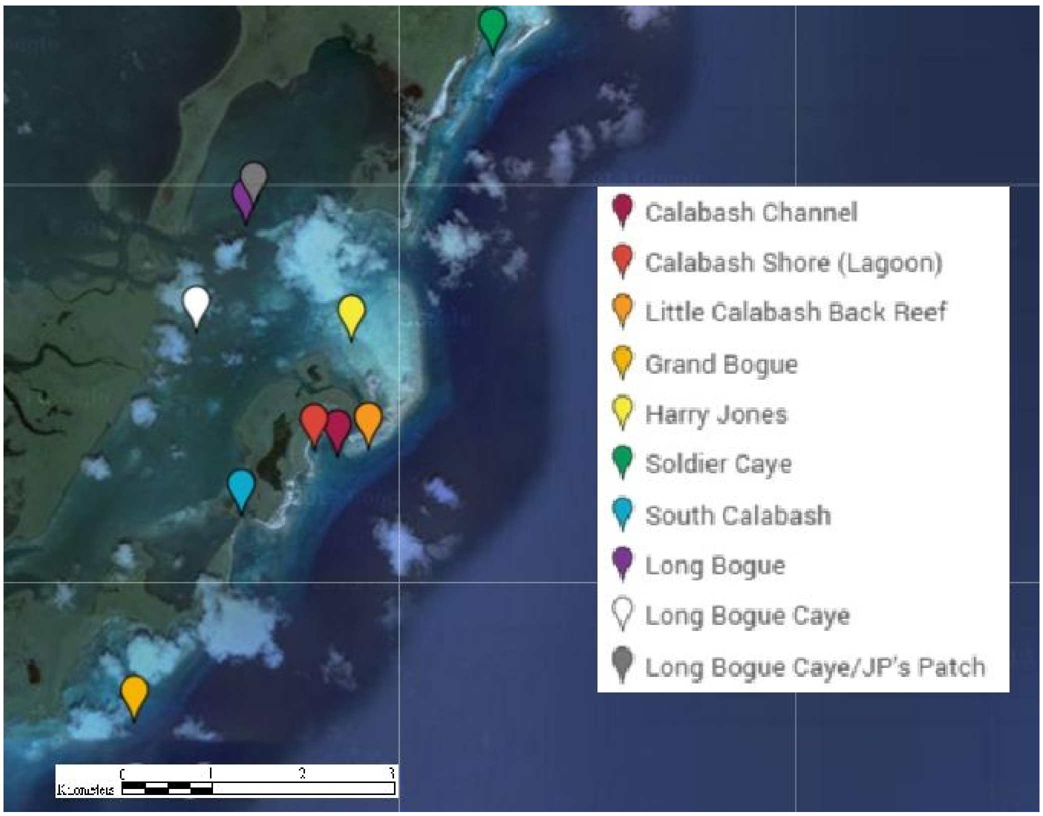


Figure III: The monitoring component of the Adaptive Management Cycle in regards to lionfish control. Adapted from S. J. Green.[3]

Methods

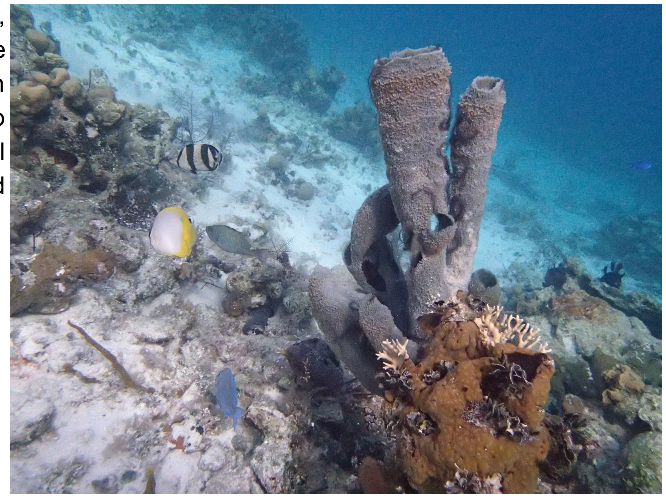
The data collection portion of this experiment was carried out at Calabash Caye Field Station (CCFS) in Belize, while the specimen collection portion was carried out in reefs surrounding the waters, in an approximate twenty (20) km² area around the field station. For a complete visual of the visited sites, see Map II below. Over the six (6) day period of January 6 - 11 2015 inclusively, fifty-two (52) lionfish were captured and dissected. Data from the previous year’s expedition was available and utilized, which was composed of nineteen (19) lionfish captured at the same time of year in similar locations.



Map II: The locations of sites where lionfish were hunted and captured. Note: a few sites where lionfish were captured are not recorded here. *Mangroves* housed a single caught lionfish and the exact GPS coordinates were not recorded, while *Long Reef Channel* is embedded within *Long Bogue*, it was recorded as a different location as the visited reef was not the same as the one visited during the *Long Bogue* visit

Each of these reefs provided different habitats for the native fish and invasive lionfish which can be characterized over two spectra: shallow to deep and structured to unstructured. Examples of the extremes of both of these categories can be seen in figures IV and V below.

Figure IV: An example of a deep and structured reef, this one specifically seen at the Great Blue Hole. These extreme ends of the spectra house larger native fish and a more thriving ecological community. This leads to higher competition between the resident fish. The coral heads stand tall and are plentiful, giving a third dimension of structure to the habitat.



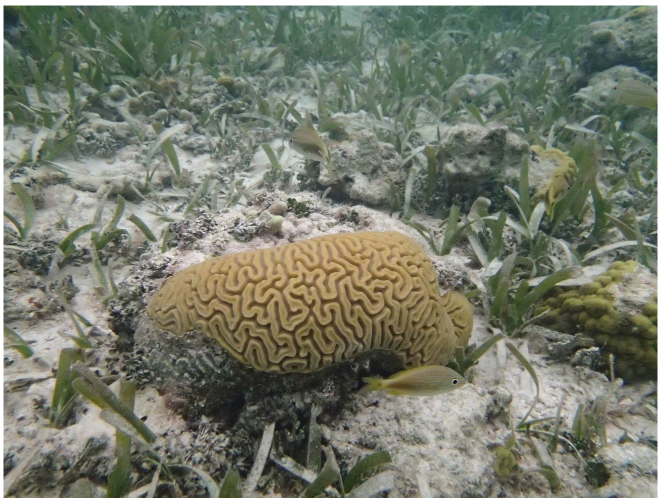


Figure V: An example of a shallow and unstructured reef, this coral head being found in the *JP's Patch* section of *Long Bogue Caye*. These two other extremes of the spectra in which we categorized the reefs house significantly smaller native fish and a near inactive ecological community. This leads to lower competition between resident fish. The surrounding area is typically flat with Sea Grass spread all around the spaced out and typically minimalistic coral heads. This environment is typically less thriving due to its general lack of a third habitable dimension.

As mentioned, lionfish were hunted and captured in reefs spanning both of these extremes, providing for a wide variety of differing dimensions and ecological trends. It was these varying trends which were the central study point of this research.

The fish were hunted using hawaiian slings and were transported back to the field station in order to dissect them. The employed dissection techniques were the standardized techniques and methodologies defined by Green et al. in order to avoid envenomation.[4] At the wet lab, the fish were examined for qualitative and quantitative morphological characteristics, the the list of specific measurements obtained and observations is as follows:

- The total length, which is the length of the fish from the tip of the caudal fin to the tip of the gape;
- the standard length, which is the total length minus the caudal fin;
- the gape (mouth) height and width;
- the total weight of the fish;
- the fish's intestinal fat volume;
- the sex of the fish and the development stage of its gonads, and
- a description of the stomach content.

Additionally, the capture date and location were recorded for future use, and every fish was given a name by its dissectors in order to refer to it with additional ease in the data compilation. For images of the dissections and brief explanations of certain events, refer to figures VI, VII and VIII below.

Figure VI: A lionfish is observed to have a fresh prey in its mouth. Dissectors promptly attempt to remove the partially digested fish for examination.

Figure VII: The prey is successfully removed and shown to be a Brown Chromis (*Chromis multilineata*). This picture gives an appropriate representation of the lionfish's length as opposed to its target prey's length, illustrating the potential adverse effects of the predator on the ecosystem.

Figure VIII: A large amount of intestinal fat is scraped off organs of a lionfish, to be measured once it is all gathered.

Once the data was obtained, statistical analyses of the data were undertaken to find significant ecological trends using the obtained population parameters. Regression analysis was used in order to draw parallels between several variables, while analysis of variance (ANOVA) was utilized in comparing the means of every location, thus observing variation for inter-site differences in length, fat, number and size of prey item, and other morphological parameters.

The complete data set and analysis can be seen below within the graphs produced from the data extraction. To view the tables containing the raw data, refer to Appendix I. For the exact GPS coordinates of all hunting locations, refer to Appendix II.

Data

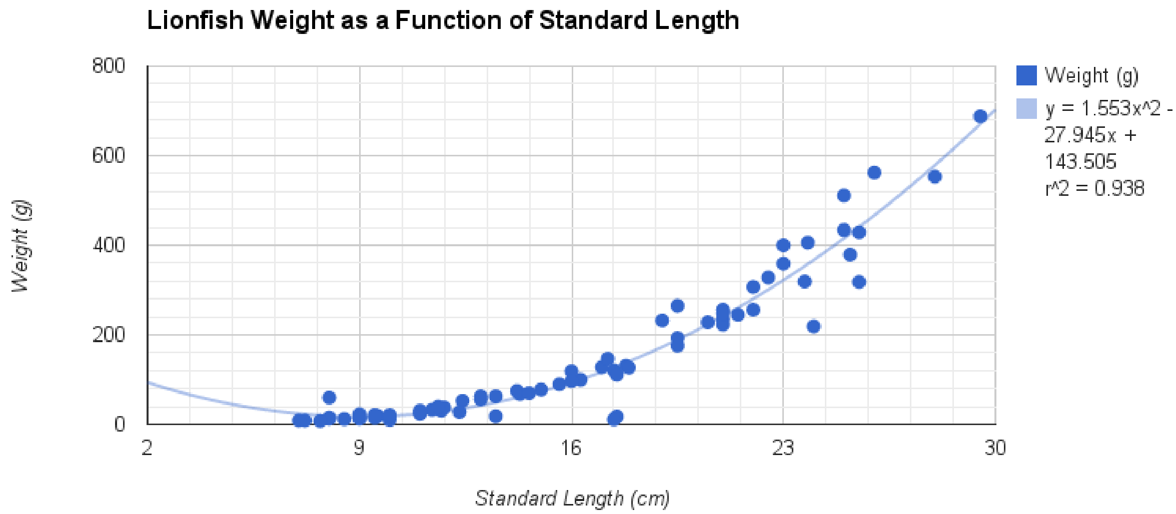


Figure IX: Lionfish Weight Compared to Standard Length

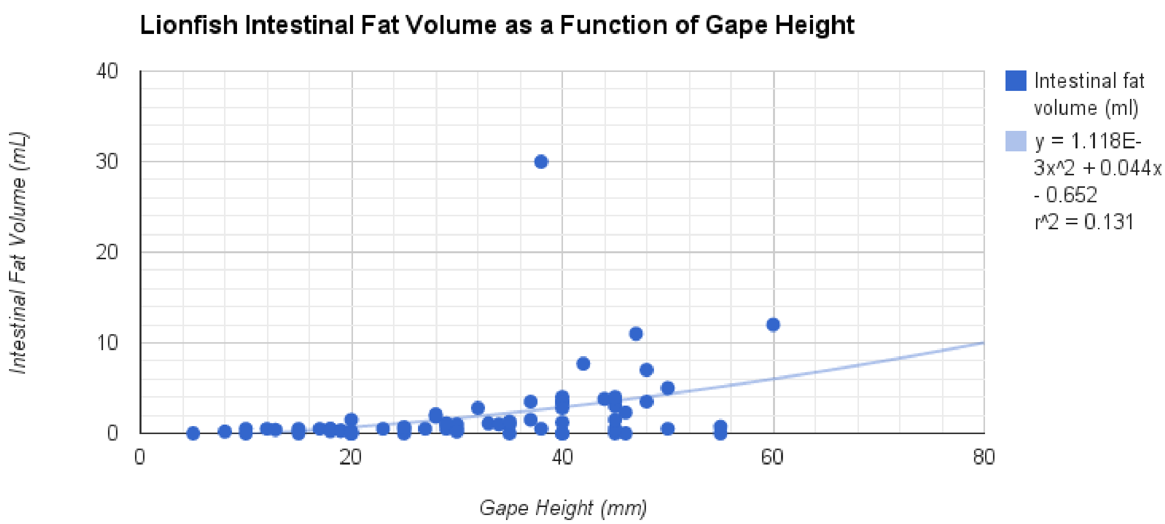


Figure X: Lionfish Fat Volume Compared to Gape Height

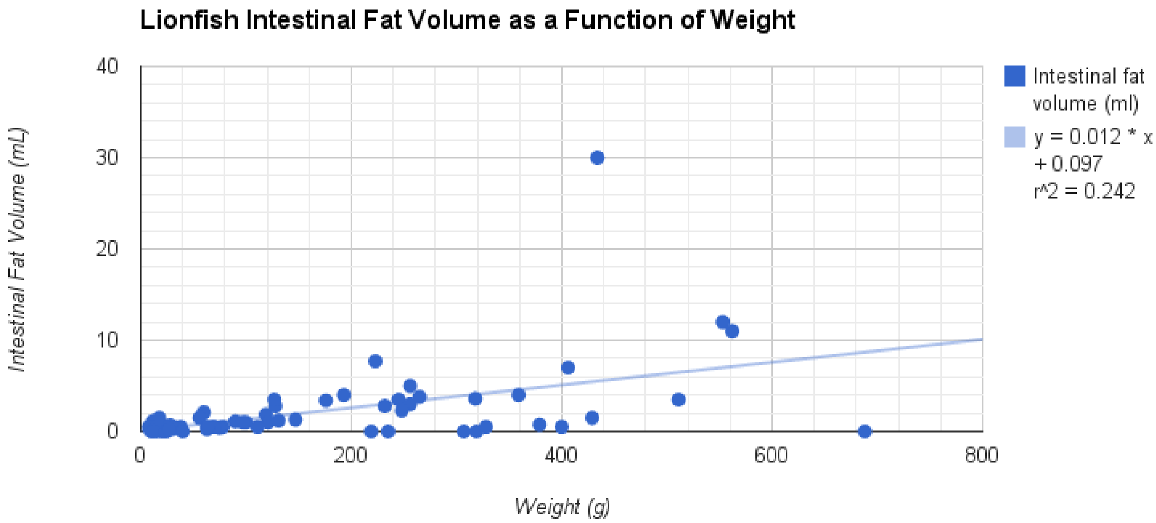


Figure XI: Lionfish Intestinal Fat Volume Compared to Weight

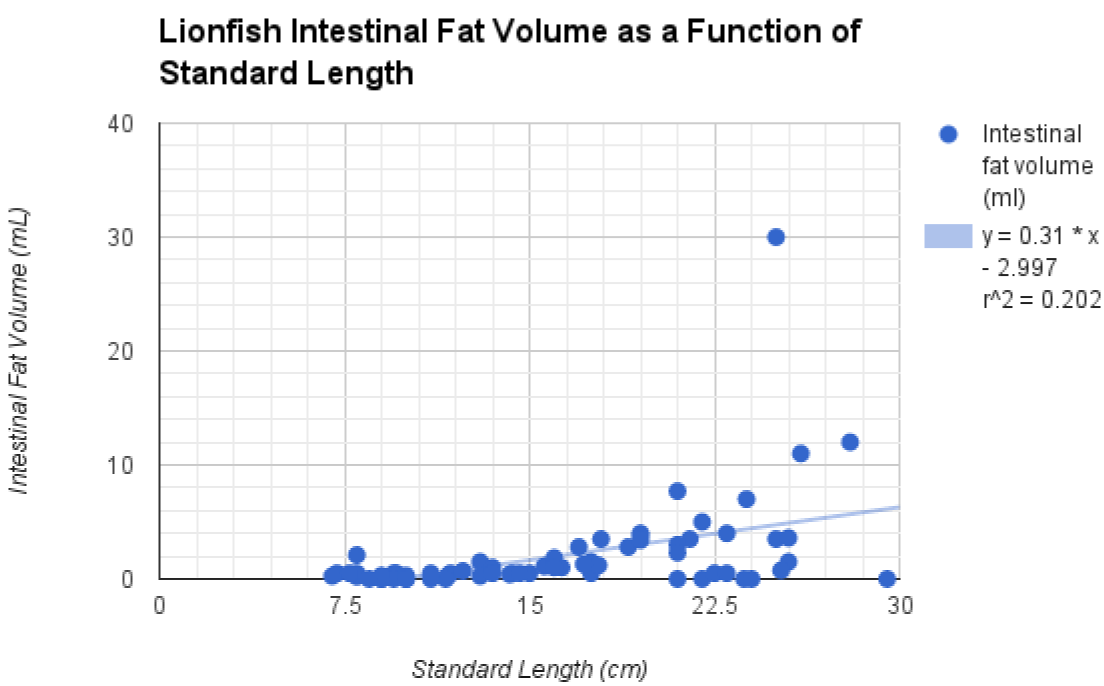


Figure XII: Lionfish Intestinal Fat Volume Compared to Standard Length

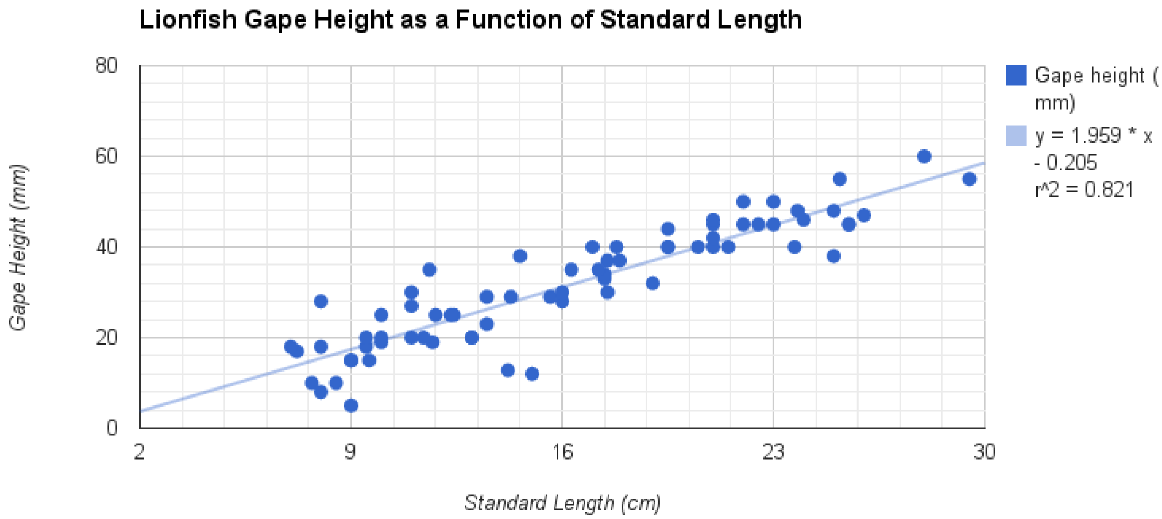


Figure XIII: Lionfish Gape Height Compared to Standard Length

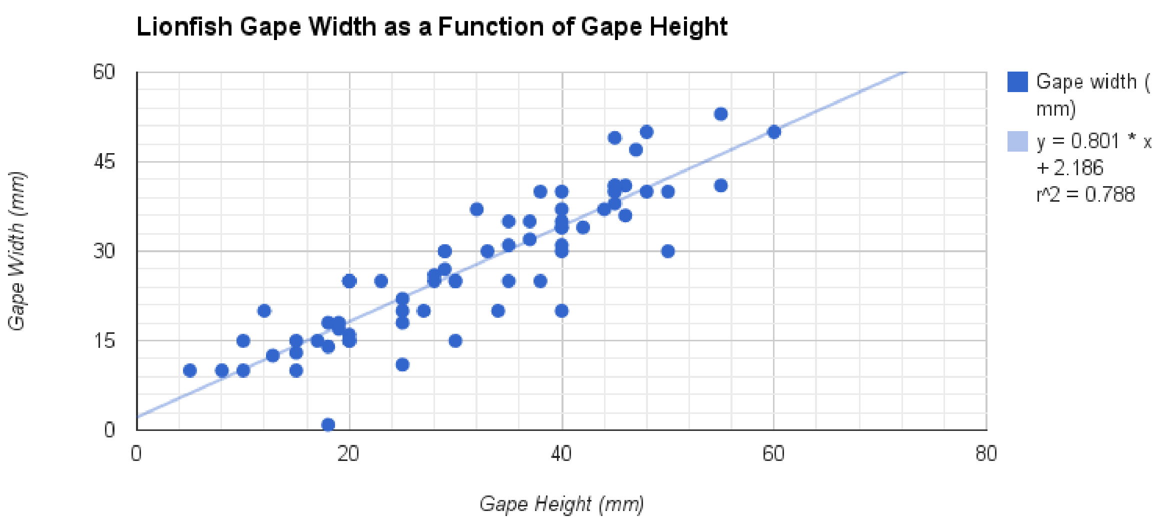


Figure XIV: Lionfish Gape Width Compared to Gape Height

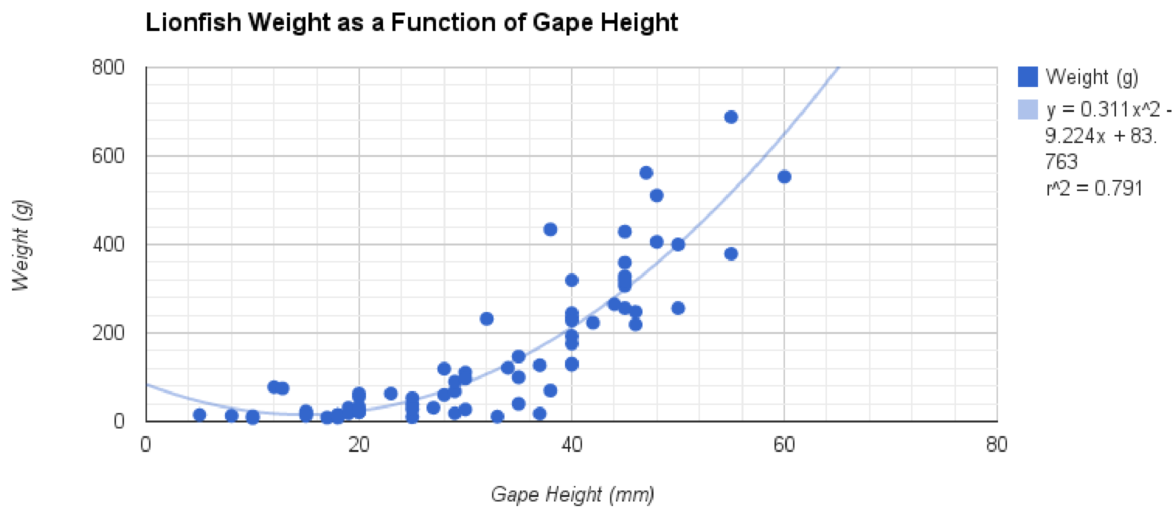


Figure XV: Weight Compared to Gape Height

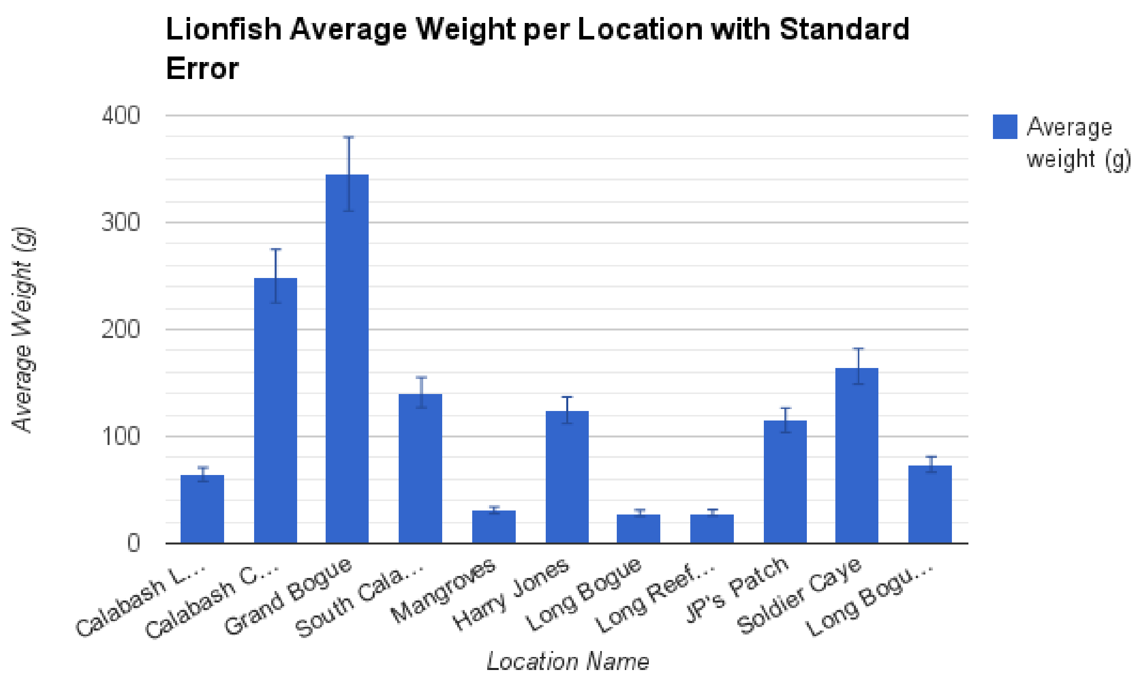


Figure XVI: Average Weight per Location

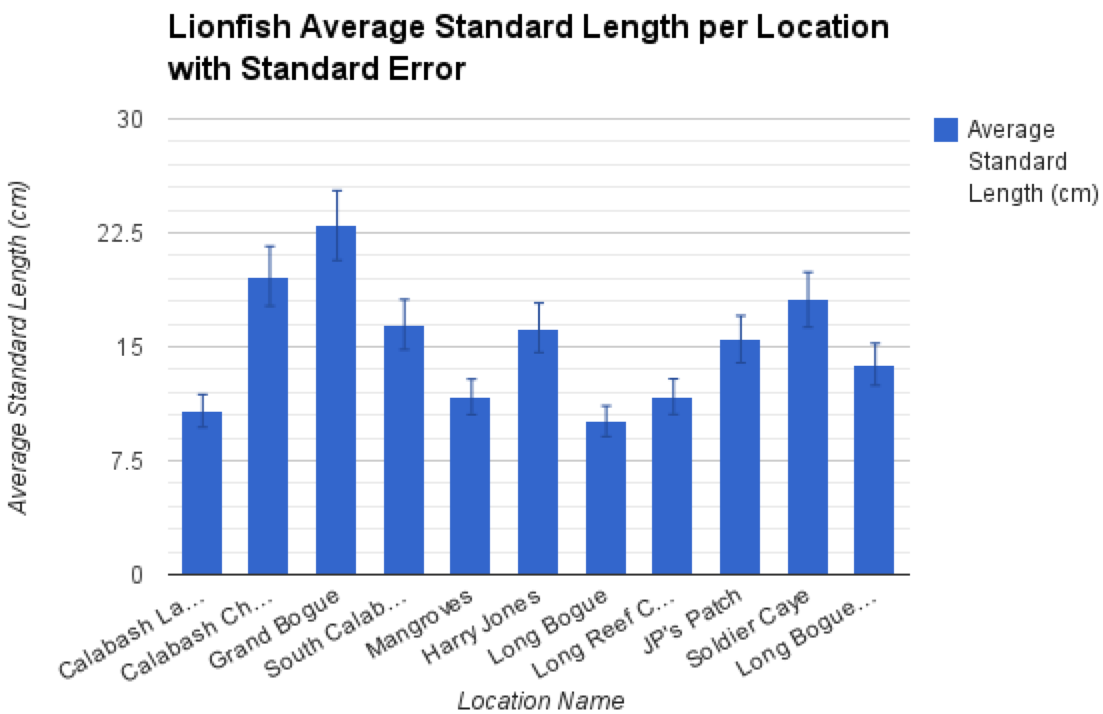


Figure XVII: Average Standard Length per Location

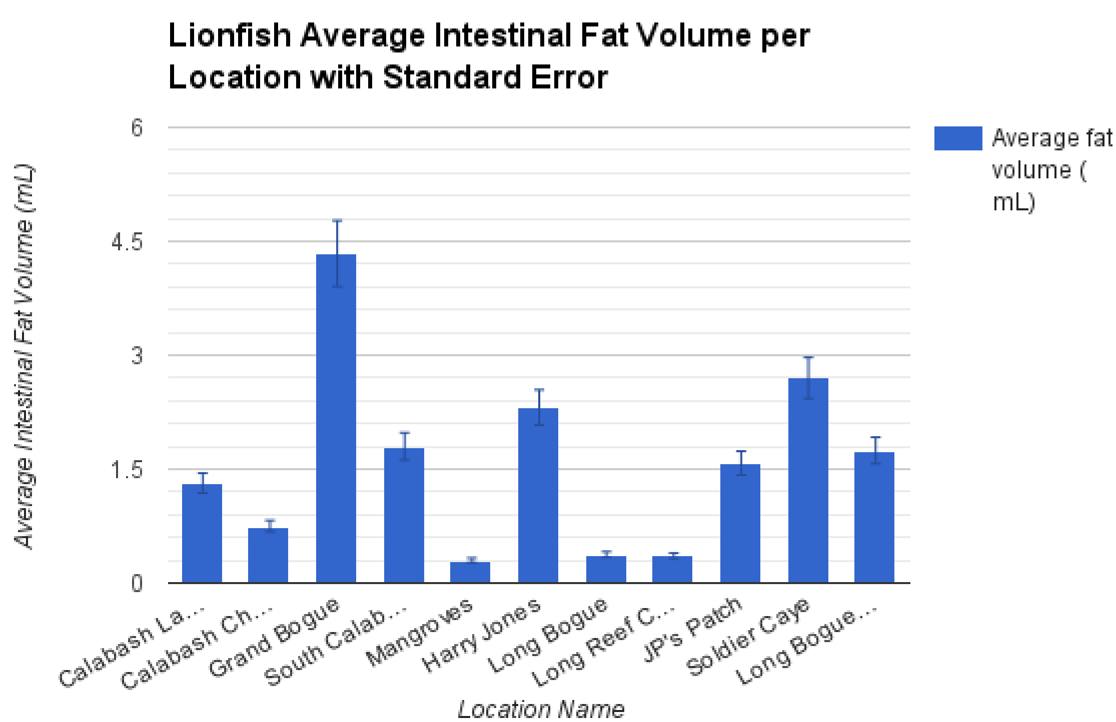


Figure XVIII: Average Intestinal Fat Volume per Location

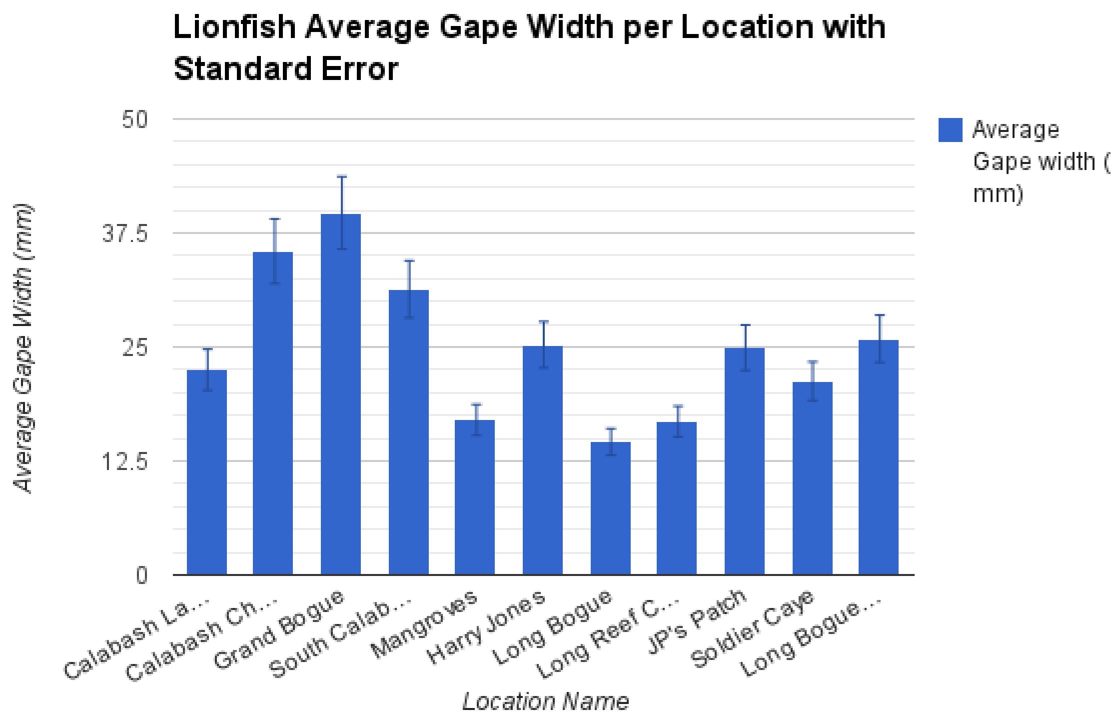


Figure XIX: Average Gape Width per Location

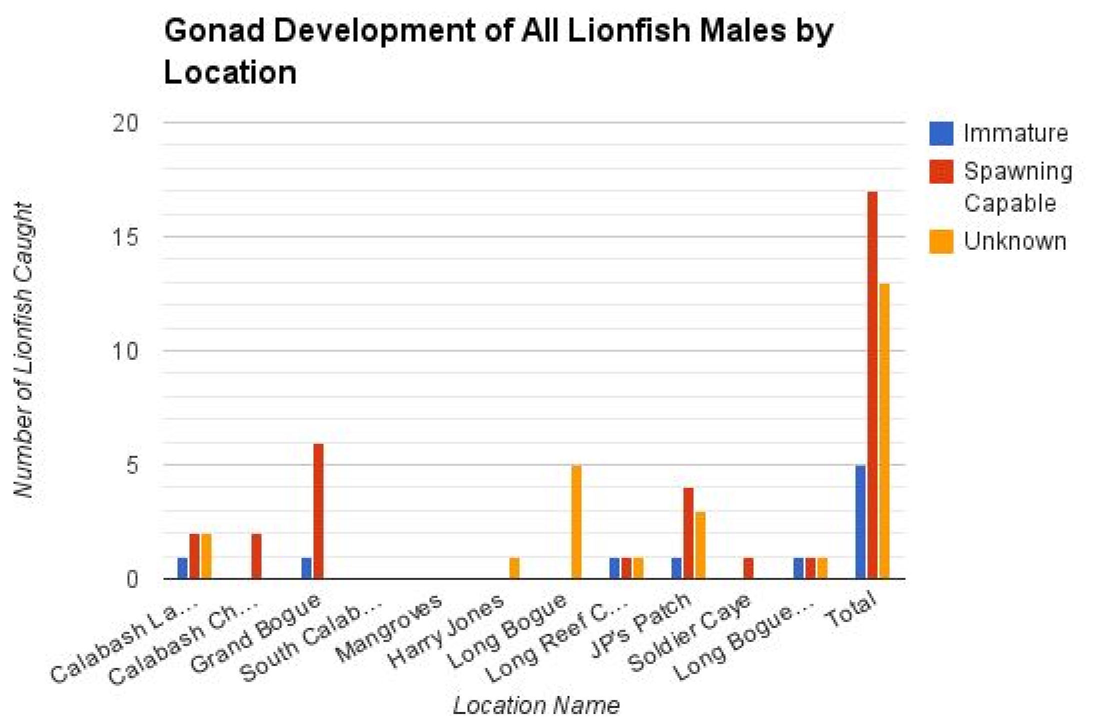


Figure XX: Gonad Development of all Caught Males by Location

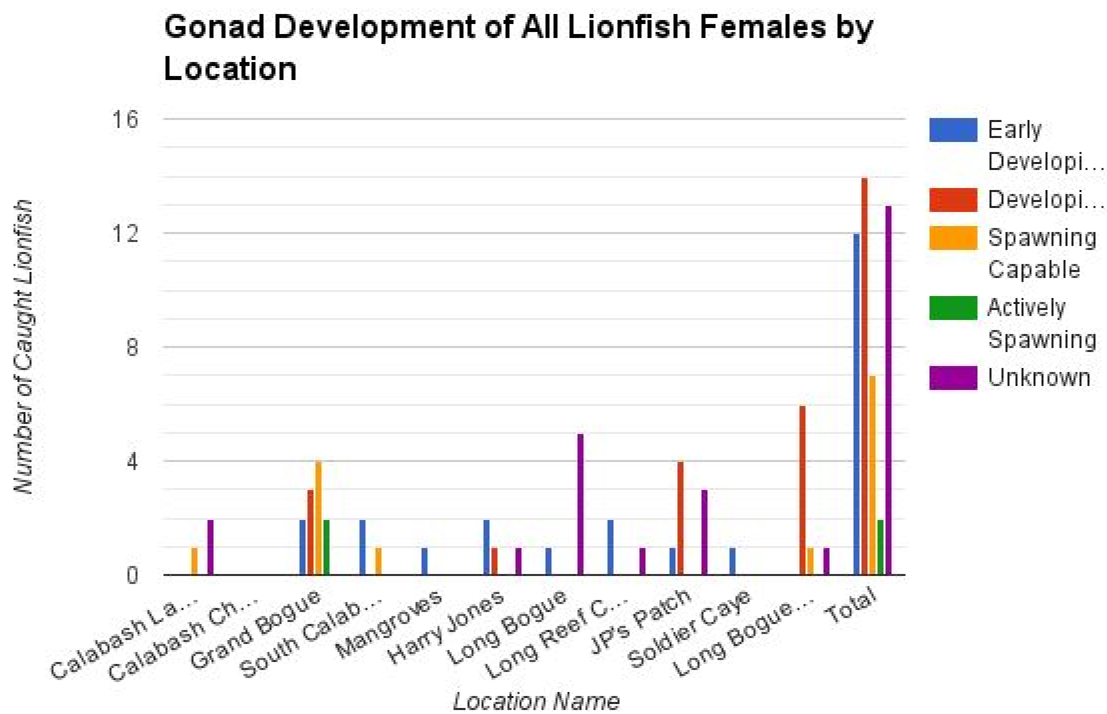


Figure XXI: Gonad Development of all Caught Females by Location

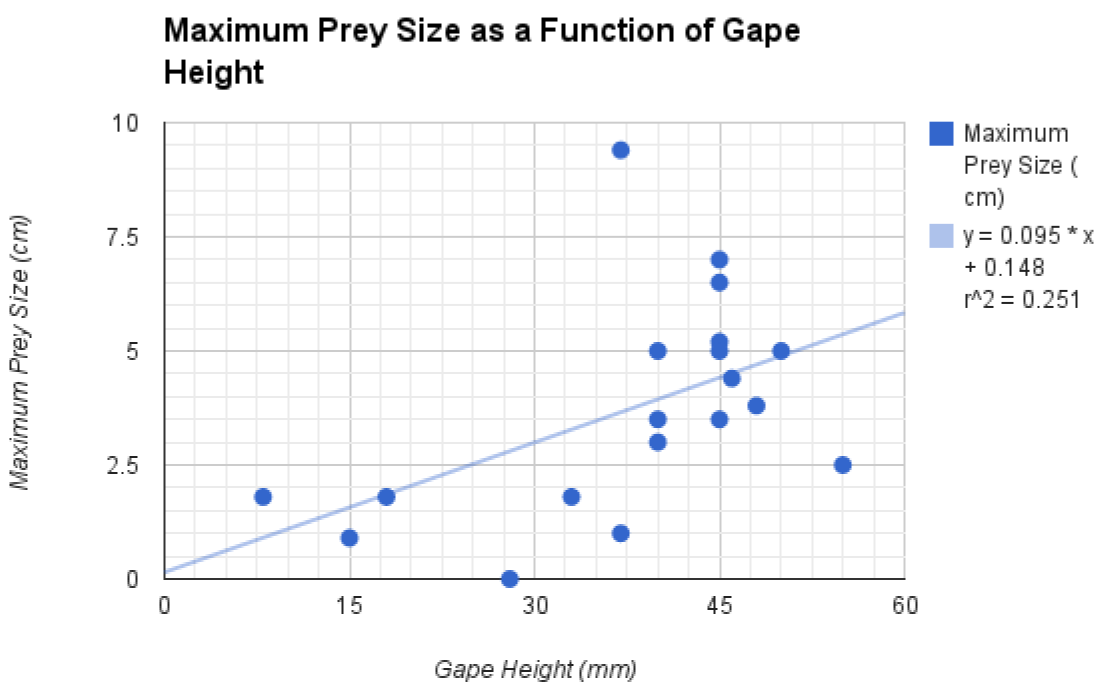


Figure XXII: Maximum Prey Length Compared to Predator Gape Height

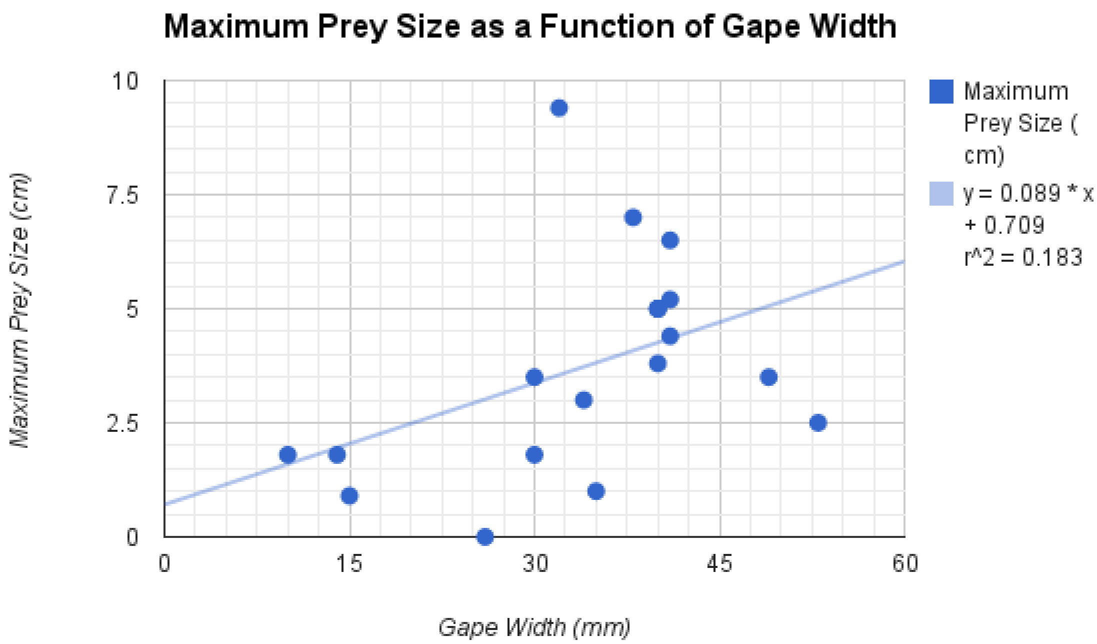


Figure XXIII: Maximum Prey Length Compared to Predator Gape Width

Discussion

Figures IX - XV display evidence of allometric growth in *P. volitans*. Some figures display a strong correlation, as observed in figure IX, relating weight and standard length in a strong fashion, similar to most species. More importantly, figures XIII and XIV display a strong correlation in the allometric growth between the standard length of a specimen and the size of the gape, indication that as a specimen increases in size, its potential prey size and variability are to increase along with it. Coupling the previous findings with figure XV, which displays a semi-consistent quadratic relationship between a fish's weight and the size of the gape shows a general increase in predator prosperity as their size and the size of the prey increases.

Despite these strong positive results in the strict comparison of morphology, namely figures X, XI and XII, which generally show a strong correlation barring one significant outlier. The one outlier that is shared among all three of those graphs is Darwin, which was captured at Grand Bogue on January 16th 2014. Grand bogue was one of the deepest and most structured reefs that was visited during the expedition. Darwin served as appropriate evidence for driving factors that could alter lionfish prosperity and intra-species competition, specifically reef depth and structure.

Figures XVI - XIX display the average morphological measurements of all specimen captured at every location. In comparing the variation between all of these measurements at every location (see figures XXIV and XXV below). These graphs display evidence of a factor driving lionfish growth and prosperity other than allometric growth, as intestinal fat volume is a factor whose growth is driven primarily by diet. Figure XXIV suggests that large and fat lionfish tend to be found together, with the exception of Calabash Channel, where large fish with little fat were found. Additionally, Calabash Channel is a reef characterized as a deep reef with structure. It's not overly structured, like Grand Bogue, but, subjectively, lies midway between structured and unstructured on one of the evaluation spectra of reefs (sadly, it is a subjective scale, as there is no unit of measurement for structure like there is the metre unit to measure depth). Referring back to figure XI, the relationship between the fat volume and weight of every fish, it can be observed that the two generally go hand-in-hand, exhibiting a strong correlation with few exceptions. Through these observations, a few hypotheses can be generated regarding the success of a lionfish's life. Since larger fish were found within deeper reefs, where ecological communities tend to be more diverse, the deeper reefs may be hotspots of increased prosperity. On the other hand, fatter lionfish had a tendency of being found within structured reefs, hiding in reef crevices where prosperous prey dwelled. The availability of these larger prey may lead to decreased competition among the invasive predators.

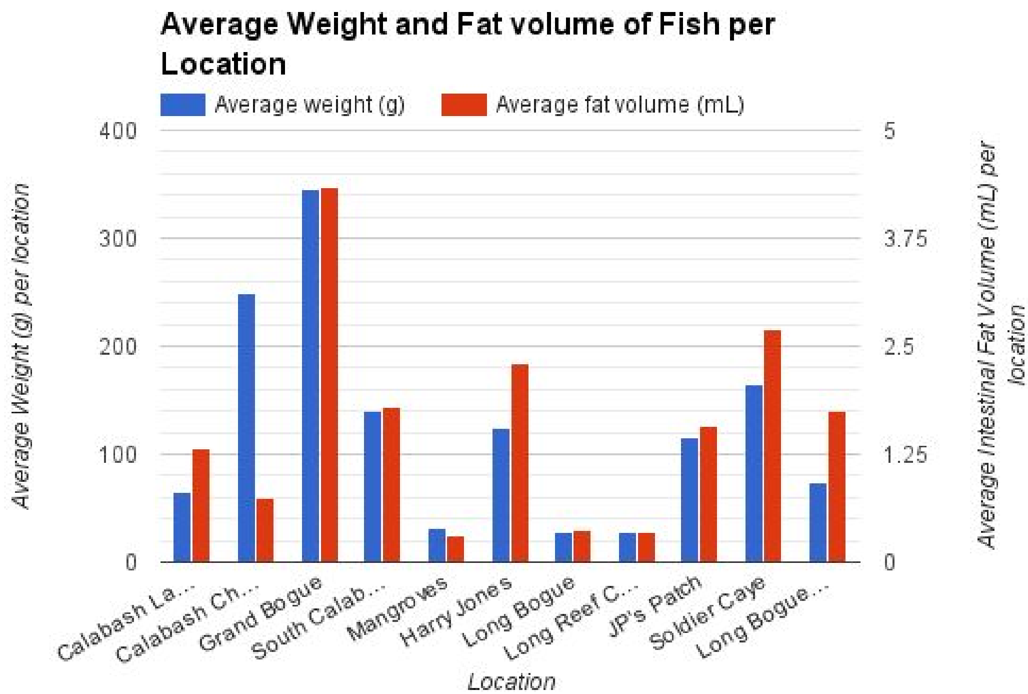


Figure XXIV: A comparison of the average weight and intestinal fat volume of lionfish at every location that was visited throughout the expedition. This relationship provides evidence for a factor driving lionfish growth and prosperity other than allometric growth, as fat does not necessarily increase with size.

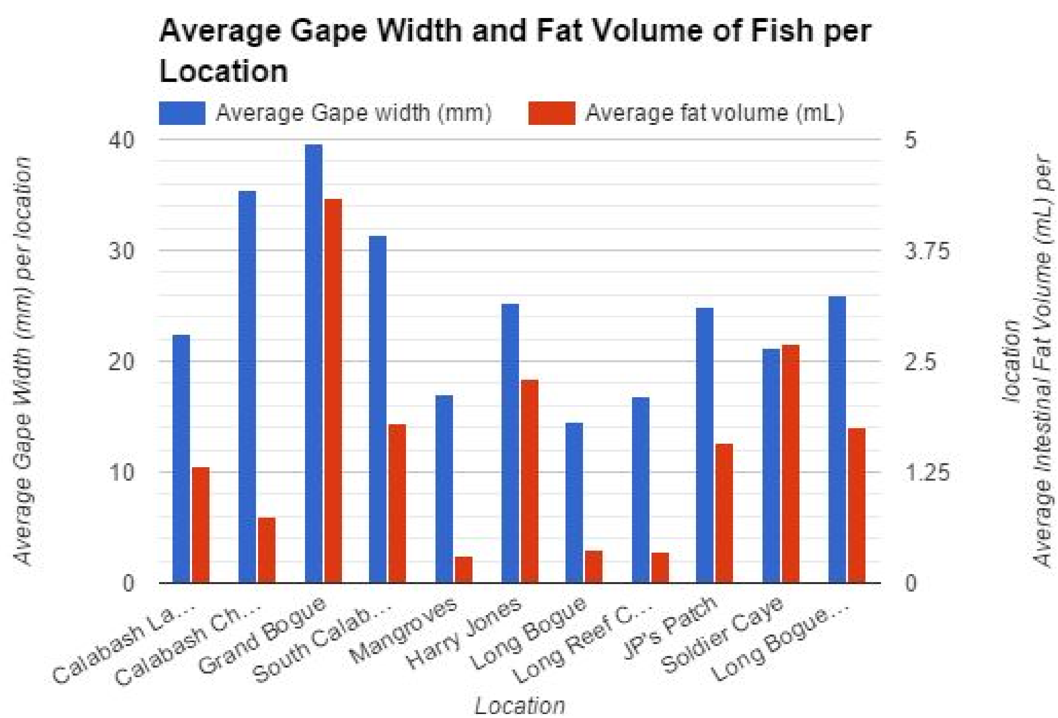


Figure XXV: A comparison of the average gape width and intestinal fat volume of lionfish at every location that was visited throughout the expedition. This relationship provides some evidence of a broadening (and more fatty) diet which grows along with the gape size. This hints that fatter lionfish are general found where fatter, more prosperous prey tend to thrive.

Figures XX and XXI display the variability of lionfish sex and development per location. While some locations appear to house prosperity for a certain sex at a certain timeframe, no hypothesizing is to be drawn from this data set, as it is lacking in size. The abnormal presence of certain categories at certain locations can only be attributed to chance, at this point.

Figures XXII and XXIII describe variance in prey data in accordance to the size of the predator's mouth. As described earlier, lionfish gape height/width is directly correlated to lionfish length and weight. The increase in prey size (and therefore the increase in prey variability for the lionfish) is also correlated to the increase in length and weight. See figures VII in the methods and XXVI below for adverse details regarding the observed flexibility of the lionfish diet.

Figure XXVI: A lionfish caught off the coast of Miami, Florida in 2012, whose stomach was found to contain 65 finfish and a shrimp. While figure VII demonstrates the potential prey size, this one is a more accurate representation of the effect the lionfish can have on a marine ecosystem. The fact that every prey item is still identifiable indicates that they had all been consumed within a short time period prior to capture.

As for the precise stomach content analysis (as seen in tables III and VI in appendix I), the results were generally as expected. Results showed either an empty stomach, one with digested, unidentifiable content, or one or many identifiable or quasi-identifiable fish. While these details were not the main focus of the study, it is worth mentioning that one specimen was found with some sea grass in its stomach, the habits of a herbivore within a carnivore. More specimen with this abnormality need to be found in order to draw hypotheses on the meaning of such deviation.

As for figures XXII and XXIII, the data suggests some trend that larger lionfish tend to gobble larger prey, but with a few abnormalities, as seen by the graph's less-than-optimal trendline. Further studies would be required on the precise increase in prey variability as a lionfish grows. For the moment, the data is insufficient to draw concrete conclusions, only some hypotheses.

Conclusion

It is important to recognize that this study's purpose was not to draw concrete conclusions regarding the predator's presence in the Caribbean, rather produce some testable hypotheses on quantifying their presence, as the precise metrics of their actions are still relatively unknown. Whether or not reef profile truly does affect the predator's prosperity can be tested, but there is now data that suggests a possible relationship. More data can be collected in order to determine if a lionfish's size coupled with the degree of reef structure where it was found can affect the amount of competition the lionfish faces. Whether or not all these previously mentioned factors truly will disturb prey variability is another generated testable hypothesis.

This field of study is still new. This research attempted to set some groundwork for future pioneers to build upon. The ideas for evidence regarding certain relationships are there, proof and further explanation are still required.

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Appendix I - Raw Data Tables

Table I: General Details of Captured Fish

YEAR	Lionfish #	Date of capture	Location of capture	Fish Name	Names of disectors
2014	1	13/01/2014	Calabash Lagoon	Wilk	Arjun, Elaine, Gillian
2014	2	13/01/2014	Calabash Lagoon	Julien	Serina, Agata, Linda
2014	3	13/01/2014	Calabash Lagoon	Ariele	Eric, Jacob, Stephanie
2014	4	13/01/2014	Calabash Lagoon	Rachel	Dominique, Anne-Marie, Emma
2014	5	13/01/2014	Calabash Lagoon	Ann	James, Orla
2014	6	13/01/2014	Calabash Lagoon	JP	Georges, Hilary, Erin
2014	7	13/01/2014	Calabash Channel	Rob	Courtney, Caitlin, Michael
2014	8	16/01/2014	Grand Bogue	Darwin	Annie, Emanuella
2014	9	16/01/2014	Grand Bogue	Sammy	Gillian, Agata, Emma
2014	10	16/01/2014	Grand Bogue	Brittany	Courtney, Caitlin
2014	11	16/01/2014	Grand Bogue	Chris	Elaine, Arjun, Orla, Michael
2014	12	16/01/2014	Grand Bogue	Sherington	Celia, Lucila, Georges
2014	13	17/01/2014	Grand Bogue	Quinn	Elaine, Linda, Emma
2014	14	17/01/2014	Grand Bogue	Diana	Serina, Caitlin, Courtney
2014	15	17/01/2014	Grand Bogue	Julie	Erin, Hilary, Annie
2014	16	17/01/2014	Grand Bogue	Nadia	JP
2014	17	17/01/2014	Grand Bogue	Emilie	Lucila, Stephanie, Emanuella
2014	18	17/01/2014	Grand Bogue	Melanie	Celia, Dominique
2014	19	17/01/2014	Grand Bogue	Nicholas	Michael, Jacob, Eric
2015	1	06/01/2015	Grand Bogue	Lola	Peter Q, Samantha
2015	2	06/01/2015	Grand Bogue	Big Momma	Julie, Nadia
2015	3	06/01/2015	Grand Bogue	Omar Jr.	Arièle, Julie, Nicolas
2015	4	06/01/2015	Grand Bogue	Little Jack	Ann, Rachel
2015	5	06/01/2015	Calabash Channel	Omar	Arièle, Nicolas
2015	6	06/01/2015	Grand Bogue	Princess Peacock	Émilie, Yara
2015	7	06/01/2015	Grand Bogue	Chelsea	Alec, Flordespina
2015	8	07/01/2015	South Calabash	Angelina	Sara, Danielle

2015	9	07/01/2015	Mangroves	Little Cindy-Lou	Alessya, Gwendolyne
2015	10	07/01/2015	South Calabash	Pedra	Julien, Peter W
2015	11	07/01/2015	Harry Jones	Nacho	Arièle, Nicolas
2015	12	07/01/2015	South Calabash	Katalina	Melanie, Diana
2015	13	07/01/2015	Harry Jones	Big Bertha	Alex, Brittany
2015	14	07/01/2015	Harry Jones	Tiny Tim	Alex, Brittany
2015	15	07/01/2015	Harry Jones	Harriette	Evan, Roberto
2015	16	08/01/2015	Long Bogue	Alex	Julie, Alec, Flordespina
2015	17	08/01/2015	Long Reef Channel	Bubba	Émilie, Yara
2015	18	08/01/2015	Long Bogue	Chloe	Alec, Flordespina
2015	19	08/01/2015	Long Bogue	Morgan	Alec, Flordespina
2015	20	08/01/2015	Long Reef Channel	Sandy	Émilie, Yara
2015	21	08/01/2015	Long Reef Channel	DJ Ded Fysh	Julie, Nadia
2015	22	08/01/2015	Long Bogue	Lil Poison	Julie, Nadia
2015	23	08/01/2015	Long Reef Channel	Taco	Ann, Rachel
2015	24	08/01/2015	Long Reef Channel	Blue Lagoon	Ann, Rachel
2015	25	08/01/2015	Long Bogue	Dog	Peter Q, Samantha
2015	26	08/01/2015	Long Reef Channel	Pesche	Peter Q, Samantha
2015	27	10/01/2015	JP's Patch	Fat Albert	Alex, Brittany
2015	28	10/01/2015	Soldier Caye	Baby Girl	Sara, Danielle
2015	29	10/01/2015	Soldier Caye	Lt. Dan	Evan, Peter W
2015	30	10/01/2015	JP's Patch	Sammy	Alessya, Gwendolyne
2015	31	10/01/2015	JP's Patch	Harold	Julien, Roberto
2015	32	10/01/2015	JP's Patch	Kumar	Julien, Roberto
2015	33	10/01/2015	JP's Patch	Lila	Peter Q, Samantha
2015	34	10/01/2015	JP's Patch	Tammy-Lee	Evan, Peter W
2015	35	10/01/2015	JP's Patch	Cleopatra	Melanie, Diana
2015	36	10/01/2015	JP's Patch	Jamila	Arièle, Nicolas
2015	37	10/01/2015	JP's Patch	Albert	Sara, Danielle

2015	38	10/01/2015	JP's Patch	Matilda	Melanie, Diana
2015	39	10/01/2015	JP's Patch	Zoe	Alec , Flordespina
2015	40	10/01/2015	JP's Patch	Evan	Evan, Peter W
2015	41	10/01/2015	JP's Patch	Tiny	Émilie, Yara
2015	42	10/01/2015	JP's Patch	Tigger	Ann, Rachel
2015	43	11/01/2015	Long Bogue Caye	Sally	Sara, Danielle
2015	44	11/01/2015	Long Bogue Caye	Chantelle	Alessya, Gwendolyne
2015	45	11/01/2015	Long Bogue Caye	Melissa	Melanie, Diana
2015	46	11/01/2015	Long Bogue Caye	Yara	Émilie, Yara
2015	47	11/01/2015	Long Bogue Caye	Priscilla	Ann, Rachel
2015	48	11/01/2015	Long Bogue Caye	Face Crusher	Ann, Rachel
2015	49	11/01/2015	Long Bogue Caye	Clarice	Arièle, Nicolas
2015	50	11/01/2015	Long Bogue Caye	Hurtubise	Alex, Brittany
2015	51	11/01/2015	Long Bogue Caye	Ass Kicker	Evan, Peter W
2015	52	11/01/2015	Long Bogue Caye	Jarhead	Julien, Roberto

Table II: Morphological Measurements of Captured Lionfish

Fish Name	Total length (cm)	Standard length (cm)	Gape height (mm)	Gape width (mm)	Weight (g)	Intestinal fat volume (ml)
Wilk	11.6	8	18	14	15	0.5
Julien	12	8	28	26	60	2.1
Ariele	12.5	9.5	18	18	15	0.5
Rachel	9	7.2	17	15	9	0.5
Ann	17	13	20	25	56	1.5
JP	25	19	32	37	232	2.8
Rob	21.2	16.3	35	31	100	1
Darwin	30	25	38	40	434	30
Sammy	31	23.7	40	34	319	0
Brittany	30	24	46	41	219	0
Chris	37	29.5	55	53	688	0
Sherington	33	25	48	50	511	3.5
Quinn	31.4	23.8	48	40	406	7
Diana	28	21	40	34	235	0
Julie	27.5	21.5	40	40	245	3.5
Nadia	28	22	45	41	307	0

Emilie	29	22.5	45	41	328	0.5
Melanie	36	28	60	50	553	12
Nicholas	33	26	47	47	562	11
Lola	30	25.5	45	40	318	3.6
Big Momma	32	25.5	45	49	429	1.5
Omar Jr.	9.4	7	18	0.9	9	0.25
Little Jack	26.5	21	45	38	256	3
Omar		23	50	40	400	0.5
Princess Peacock	22.7	17.5	37	35	17.6	1.5
Chelsea	31.1	25.2	55	41	379	0.75
Angelina	19.5	14.3	29	27	68	0.5
Little Cindy-Lou	15.8	11.7	19	17	31	0.3
Pedra	20.9	15.6	29	30	90	1.1
Nacho	25	19.5	40	35	193	4
Katalina	26	19.5	44	37	265	3.8
Big Bertha	23	16	28	25	119	1.85
Tiny Tim	12.5	10	25	11	10	0
Harriette	26	19.5	40	30	176	3.4
Alex	13.2	9.6	15	10	19	0.5
Bubba	22.3	17.4	33	30	11.3	1.1
Chloe	17.2	12.4	25	22	53	
Morgan	15.5	11.8	25	18	38	0.5
Sandy	10.3	8	8	10	13	0.2
DJ Ded Fysh	15.6	11.4	20	16	33	
Lil Poison	10.2	7.7	10	10	8	0.5
Taco	19	15	12	20	78	0.5
Blue Lagoon	11	9	5	10	15	0
Dog	13.3	9	15	13	23	0
Pesche	13.5	9.5	20	15	21	0
Fat Albert	28	21	42	34	223	7.7
Baby Girl	18.9	14.2	12.8	12.5	75	0.4
Lt. Dan	28	22	50	30	256	5
Sammy	27	21	46	36	248	2.3

Harold	22.4	17.4	34	20	121	1
Kumar	22.5	17	40	20	128	2.8
Lila	22.5	17.5	30	25	111	0.5
Tammy-Lee	21	16	30	25	97	1
Cleopatra	12	10	19	18	18	0.3
Jamila	30	23	45	40	359	4
Albert	23.2	17.8	40	31	131	1.2
Matilda	14.5	11	27	20	31	0.5
Zoe	19.3	14.6	38	25	70	0.5
Evan	15.8	11.6	35	25	40	0
Tiny	11.9	9	15	15	13	0.3
Tigger	13	10	20	15	21	0
Sally	23	17.2	35	35	147	1.3
Chantelle	23.5	17.9	37	32	127	3.5
Melissa	18.3	13.5	29	30	18.3	1
Yara	16.1	12.3	25	20	28	0.7
Priscilla	12	8.5	10	15	12	0
Face Crusher	17	13	20	25	63	0.25
Clarice	15	11	20	25	24	0
Hurtubise	18	13.5	23	25	63	0.5
Ass Kicker	14.5	11	30	15	27	0.2
Jarhead	26.5	20.5	40	37	228	

Note: Bubba’s weight is recorded in red as the validity of this measurement is questionable. It was nevertheless used in the analysis, considered an outlier.

Table III: Development, Maturity and Diet of Captured Lionfish

Fish Name	Gender (M / F)	Gonad stage	Stomach content description
Wilk	M	Immature	One 1.8cm fish and assorted pieces of other fish
Julien	M	Spawning capable	No stomach content
Ariele	No gonads found	NA	Unidentified content
Rachel	No gonads found	NA	Unidentified content
Ann	F	Spawning capable	Partially digested fish, small vertebrae
JP	M	Spawning capable	Unidentified content

Rob	M	Spawning capable	No stomach content
Darwin	M	Spawning capable	No stomach content
Sammy	F	Spawning capable	No stomach content
Brittany	F	Developing	Small fish (4.4cm length)
Chris	M	Spawning capable	Small sand diver ? (2.5cm length)
Sherington	M	Spawning capable	Unidentified content
Quinn	M	Spawning capable	Shrimp (3.8cm), 4 fish (3.6cm; 2.4cm; 2.2cm; 1.8cm)
Diana	F	Spawning capable	8 fish (1cm; 1.3cm; 1.5cm; 1.6cm; 2cm; 2cm; 2.8cm; 3cm)
Julie	F	Spawning capable	7 fish (2cm; 3cm; 3cm; 4cm; 4cm; 4.5cm; 5cm)
Nadia	F	Spawning capable	16 fish (5.2cm fish; all others are 1-2cm)
Emilie	F	Actively Spawning	3 fish (5cm; 5cm; 6.5cm)
Melanie	F	Developing	Unidentified fish
Nicholas	M	Spawning capable	No stomach content
Lola	F	Early developing	3 fish (4cm; 5cm; 5cm; total weight = 3g)
Big Momma	F	Actively Spawning	2 fish (3cm; 3.5cm; total weight = <1g)
Omar Jr.	M	Undeveloped	Undetermined
Little Jack	M	Spawning Capable	1 fish (7cm; total weight = 10g)
Omar	M	Spawning Capable	Small live fish (goby?) (5cm; total weight = 2g)
Princess Peacock	F	Early developing	1 fish (goby?) (1cm; total weight = <1g)
Chelsea	F	Developing	Undetermined
Angelina	F	Early developing	Digested fish (total weight = <1g)
Little Cindy-Lou	F (hypothesis)	Early developing	Digested fish (total weight = <1g)
Pedra	F	Early developing	Digested fish
Nacho	F	Developing	Undetermined
Katalina	F	Spawning Capable	Digested fish
Big Bertha	F	Early developing	Empty
Tiny Tim	Unknown	Unknown	Undetermined
Harriette	F	Early developing	1 fish (3.5cm), sea grass (5cm)
Alex	Unknown	Unknown	Unknown
Bubba	F	Early developing	1 fish (1.8cm; total weight = <1g)

Chloe	F	Developing	Partly digested fish
Morgan	Lost in Battle	Unknown	Unidentifiable
Sandy	Unknown	Unknown	1 fish (1.8cm; total weight = <1g)
DJ Ded Fysh	F	Early developing	Unidentifiable (total weight = <1g)
Lil Poison	Unknown	Unknown	Unidentifiable (total weight = <1g)
Taco	M	Spawning Capable	Unidentifiable
Blue Lagoon	Unknown	Unknown	Unidentifiable
Dog	Unknown	Early developing	Unidentifiable (total weight = <1g)
Pesche	M	Immature	Unidentifiable (total weight = <1g)
Fat Albert	M	Spawning Capable	Empty
Baby Girl	F	Early developing	Empty
Lt. Dan	M	Spawning Capable	1 fish (total weight = <1g)
Sammy	M	Intermediate Development	Unidentifiable (total weight = <1g)
Harold	M	Spawning Capable	Empty
Kumar	M	Spawning Capable	Empty
Lila	F	Early developing	Unidentifiable
Tammy-Lee	F	Developing	1 fish (total weight = 4g)
Cleopatra	F	Developing	1 fish (total weight = <1g)
Jamila	F	Developing	Juvenile Conch
Albert	M	Spawning Capable	1 fish (total weight = <1g)
Matilda	F	Developing	Empty
Zoe	F	Developing	Unidentifiable
Evan	Unknown	Early developing	Unidentifiable
Tiny	Unknown	Early developing	1 fish (0.9cm; total weight = <1g)
Tigger	Unknown	Early developing	Unidentifiable
Sally	F	Developing	Empty
Chantelle	F	Spawning Capable	2 fish (1 Brown Chromis) (9.4cm; 4.2cm; total weight = 10g)
Melissa	F	Developing	1 digested fish (total weight = <1g)
Yara	F	Developing	Empty
Priscilla	Unknown	Early developing	Unidentifiable (total weight = <1g)
Face Crusher	F	Developing	Unidentifiable (total weight = <1g)
Clarice	M	Immature	Empty
Hurtubise	F	Developing	3 fish

Ass Kicker	F	Developing	Empty
Jarhead	M	Spawning Capable	Goby in mouth, Fish in stomach

Note: Referring to stomach content as “unidentifiable” indicates a digested mass that is now beyond not only species recognition, but recognition of the number of prey items.

Table IV: Average Lionfish Measurements by Capture Location

Location	Average Standard Length (cm)	Standard error	Average Gape width (mm)	Average weight (g)	Average fat volume (mL)
Calabash Lagoon	10.78333333	1.847596036	22.5	64.5	1.316666667
Calabash Channel	19.65	3.35	35.5	250	0.75
Grand Bogue	22.98333333	1.145415699	39.71666667	345.3111111	4.338888889
South Calabash	16.46666667	1.562405553	31.33333333	141	1.8
Mangroves	11.7	0	17	31	0.3
Harry Jones	16.25	2.24072161	25.25	124.5	2.3125
Long Bogue	10.1	0.877496439	14.6	28.2	0.375
Long Reef Channel	11.71666667	1.519740475	16.83333333	28.55	0.36
JP's Patch	15.49285714	1.220631447	24.92857143	115.0714286	1.578571429
Soldier Caye	18.1	3.9	21.25	165.5	2.7
Long Bogue Caye	13.84	1.155104613	25.9	73.73	1.745

Table V: Gonad Development and Maturity by Location

	Males		Females					
Location	Immature	Spawning Capable	Early Developing	Developing	Spawning Capable	Actively Spawning	Unknown	Total
Calabash Lagoon	1	2	0	0	1	0	2	6
Calabash Channel	0	2	0	0	0	0	0	2
Grand Bogue	1	6	2	3	4	2	0	18
South Calabash	0	0	2	0	1	0	0	3
Mangroves	0	0	1	0	0	0	0	1

Harry Jones	0	0	2	1	0	0	1	4
Long Bogue	0	0	1	0	0	0	5	6
Long Reef Channel	1	1	2	0	0	0	1	5
JP's Patch	1	4	1	4	0	0	3	13
Soldier Caye	0	1	1	0	0	0	0	2
Long Bogue Caye	1	1	0	6	1	0	1	10
Total	5	17	12	14	7	2	13	70

Table VI: Prey Data

Fish Name	Gape height (mm)	Gape width (mm)	Stomach content description	Intestinal fat volume (ml)	Average Prey Size (cm)	Maximum Prey Size (cm)
Wilk	18	14	One 1.8cm fish and assorted pieces of other fish	0.5	N/A	1.8
Julien	28	26	No stomach content	2.1	0	0
Ariele	18	18	Unidentified content	0.5	N/A	N/A
Rachel	17	15	Unidentified content	0.5	N/A	N/A
Ann	20	25	Partially digested fish, small vertebrae	1.5	N/A	N/A
JP	32	37	Unidentified content	2.8	N/A	N/A
Rob	35	31	No stomach content	1	N/A	N/A
Darwin	38	40	No stomach content	30	N/A	N/A
Sammy	40	34	No stomach content	0	N/A	N/A
Brittany	46	41	Small fish (4.4cm length)	0	4.4	4.4
Chris	55	53	Small sand diver ? (2.5cm length)	0	2.5	2.5
Sheringto n	48	50	Unidentified content	3.5	N/A	N/A
Quinn	48	40	Shrimp (3.8cm), 4 fish (3.6cm; 2.4cm; 2.2cm; 1.8cm)	7	2.8	3.8

Diana	40	34	8 fish (1cm; 1.3cm; 1.5cm; 1.6cm; 2cm; 2cm; 2.8cm; 3cm)	0	1.9	3
Julie	40	40	7 fish (2cm; 3cm; 3cm; 4cm; 4cm; 4.5cm; 5cm)	3.5	3.6	5
Nadia	45	41	16 fish (5.2cm fish; all others are 1-2cm)	0	1.3-2.9	5.2
Emilie	45	41	3 fish (5cm; 5cm; 6.5cm)	0.5	5.5	6.5
Melanie	60	50	Unidentified fish	12	N/A	N/A
Nicholas	47	47	No stomach content	11	0	0
Lola	45	40	3 fish (4cm; 5cm; 5cm; total weight = 3g)	3.6	4.7	5
Big Momma	45	49	2 fish (3cm; 3.5cm; total weight = <1g)	1.5	3.25	3.5
Omar Jr.	18	0.9	Undetermined	0.25	N/A	N/A
Little Jack	45	38	1 fish (7cm; total weight = 10g)	3	7	7
Omar	50	40	Small live fish (goby?) (5cm; total weight = 2g)	0.5	5	5
Princess Peacock	37	35	1 fish (goby?) (1cm; total weight = <1g)	1.5	1	1
Chelsea	55	41	Undetermined	0.75	N/A	N/A
Angelina	29	27	Digested fish (total weight = <1g)	0.5	N/A	N/A
Little Cindy-Lou	19	17	Digested fish (total weight = <1g)	0.3	N/A	N/A
Pedra	29	30	Digested fish	1.1	N/A	N/A
Nacho	40	35	Undetermined	4	N/A	N/A
Katalina	44	37	Digested fish	3.8	N/A	N/A
Big Bertha	28	25	Empty	1.85	0	0
Tiny Tim	25	11	Undetermined	0	N/A	N/A
Harriette	40	30	1 fish (3.5cm), sea grass (5cm)	3.4	4.25	3.5
Alex	15	10	Unknown	0.5	N/A	N/A
Bubba	33	30	1 fish (1.8cm; total weight = <1g)	1.1	1.8	1.8
Chloe	25	22	Partly digested fish		N/A	N/A

Morgan	25	18	Unidentifiable	0.5	N/A	N/A
Sandy	8	10	1 fish (1.8cm; total weight = <1g)	0.2	1.8	1.8
DJ Ded Fysh	20	16	Unidentifiable (total weight = <1g)		N/A	N/A
Lil Poison	10	10	Unidentifiable (total weight = <1g)	0.5	N/A	N/A
Taco	12	20	Unidentifiable	0.5	N/A	N/A
Blue Lagoon	5	10	Unidentifiable	0	N/A	N/A
Dog	15	13	Unidentifiable (total weight = <1g)	0	N/A	N/A
Pesche	20	15	Unidentifiable (total weight = <1g)	0	N/A	N/A
Fat Albert	42	34	Empty	7.7	0	0
Baby Girl	12.8	12.5	Empty	0.4	0	0
Lt. Dan	50	30	1 fish (total weight = <1g)	5	N/A	N/A
Sammy	46	36	Unidentifiable (total weight = <1g)	2.3	N/A	N/A
Harold	34	20	Empty	1	0	0
Kumar	40	20	Empty	2.8	0	0
Lila	30	25	Unidentifiable	0.5	N/A	N/A
Tammy-Lee	30	25	1 fish (total weight = 4g)	1	N/A	N/A
Cleopatra	19	18	1 fish (total weight = <1g)	0.3	N/A	N/A
Jamila	45	40	Juvenile Conch	4	N/A	N/A
Albert	40	31	1 fish (total weight = <1g)	1.2	N/A	N/A
Matilda	27	20	Empty	0.5	0	0
Zoe	38	25	Unidentifiable	0.5	N/A	N/A
Evan	35	25	Unidentifiable	0	N/A	N/A
Tiny	15	15	1 fish (0.9cm; total weight = <1g)	0.3	0.9	0.9
Tigger	20	15	Unidentifiable	0	N/A	N/A
Sally	35	35	Empty	1.3	0	0

Chantelle	37	32	2 fish (1 Brown Chromis) (9.4cm; 4.2cm; total weight = 10g)	3.5	6.8	9.4
Melissa	29	30	1 digested fish (total weight = <1g)	1	N/A	N/A
Yara	25	20	Empty	0.7	0	0
Priscilla	10	15	Unidentifiable (total weight = <1g)	0	N/A	N/A
Face Crusher	20	25	Unidentifiable (total weight = <1g)	0.25	N/A	N/A
Clarice	20	25	Empty	0	0	0
Hurtubise	23	25	3 fish	0.5	N/A	N/A
Ass Kicker	30	15	Empty	0.2	0	0
Jarhead	40	37	Goby in mouth, Fish in stomach	10	N/A	N/A

Appendix II - Details of hunting locations

Map III: Location of Capture Sites

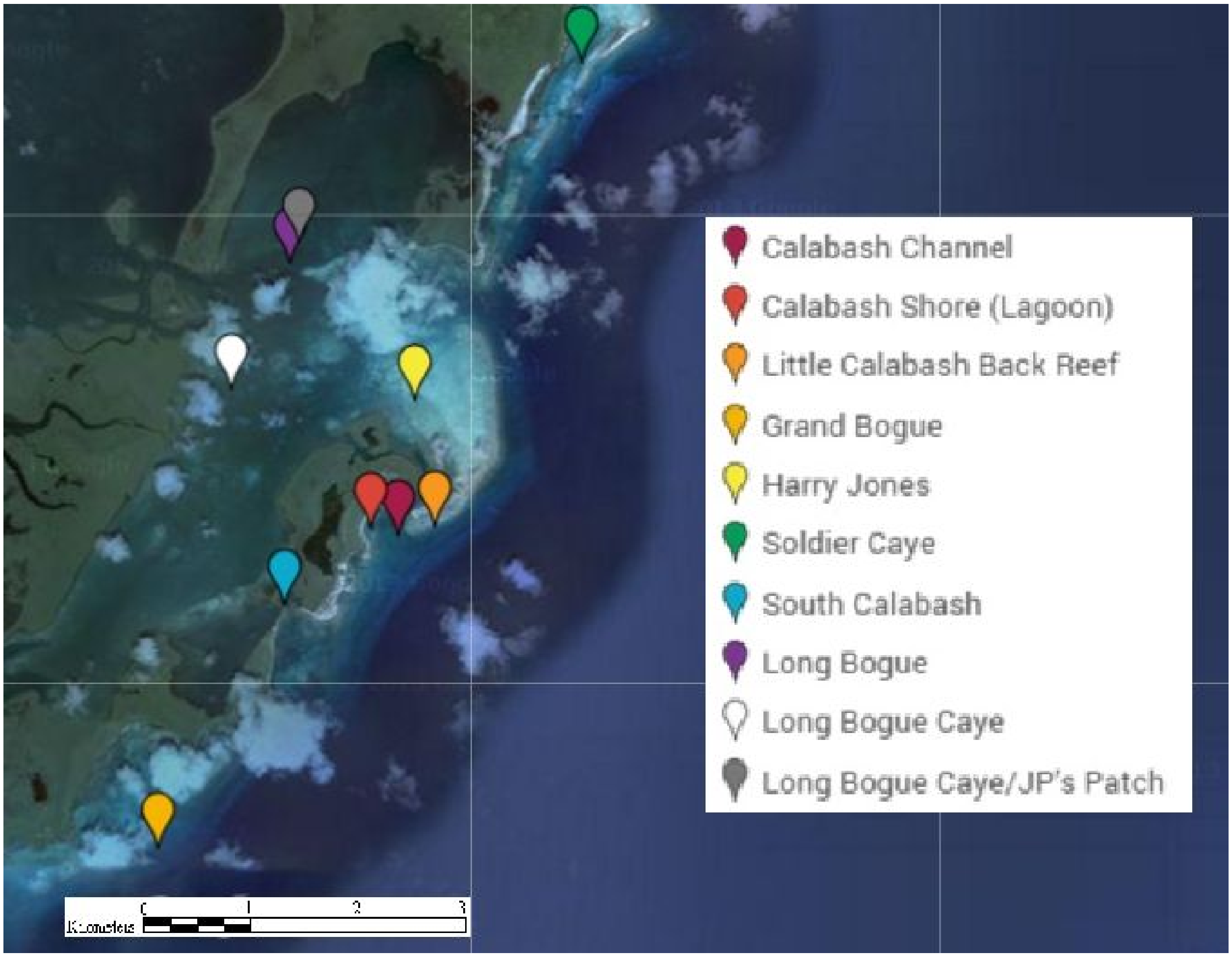

Table VII: Details of Capture Sites

REEF site #	Site name	Comment	Coordinates
55030023	Calabash Wall (Blackbird Caye) - Same as Calabash Channel		N17˚16’47.93” W87˚48’34.56”
55030080	Calabash Shore		N17˚16’50” W87˚48’44”
55030081	Little Calabash Back Reef		N17˚16’51.23” W87˚48’22.05”
55030005	Grand Bogue	Misspelled as Grand Boque in REEF database	N17˚15’7.344” W87˚49’55.668”
55030082	Turneffe Lagoon	Report as Grand Bogue	
55030083	Harry Jones (Blackbird Caye)		N17˚17’32” W87˚48’29”
55030024	Soldier Caye (Blackbird Caye) - Patch Reef		N17˚19’20.5” W87˚47’33.1”
55030095	South Calabash		N17˚16’25.6” W87˚49’13.0”
55030094	Long Bogue	N17˚17’25.9274” W87˚49’05.56”	N17˚18’16.3” W87˚49’11.4”
55030094	Long Bogue Island Patch Reef	Report as Long Bogue	N17˚17’35.3” W87˚49’31.0”
55030094	Long Bogue Behind Island - JP's patch		N17˚18’22.4” W87˚49’08.1”