4-18-2023

The Potential for Top-Down Control of the Corallivorous Gastropod Coralliophila Galea and Its Effect on Coral Reef Ecosystems

Tanya Y. Kamerman
Nova Southeastern University

NSUWorks Citation

Tanya Y. Kamerman. 2023. *The Potential for Top-Down Control of the Corallivorous Gastropod Coralliophila Galea and Its Effect on Coral Reef Ecosystems.* Master's thesis. Nova Southeastern University. Retrieved from NSUWorks, . (129)
https://nsuworks.nova.edu/hcas_etd_all/129.

Thesis of
Tanya Y. Kamerman

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

April 2023

Approved:
Thesis Committee

Committee Chair: Joana Figueiredo

Committee Member: Craig Dahlgren

Committee Member: David Gilliam

HALMOS COLLEGE OF ARTS AND SCIENCES

The potential for top-down control of the corallivorous gastropod *Coralliophila galea* and its effect on coral reef ecosystems

By

Tanya Y. Kamerman

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science

Nova Southeastern University

May 10, 2023

Contents

List of Figures IIIII

List of Tables IIIII

Abstract V

1.0 Introduction 1

2.0 Objectives 6

3.0 Methods 6

- **3.1 Site Selection** 6
- **3.2 Surveys** 12
- **3.3 Lobster Predation Studies** 14
- **3.4 Data Analysis** 146

4.0 Results 16

- **4.1 Lobster Snail Size Preference** 16
- **4.2 Coral Cover and Snail Density** 17
- **4.3 Depth** 20
- **4.4 Coral Diversity and Snail Density** 22
- **4.5 Snail Density and Fish Densities** 23
- **4.6 Coral Cover and Fish Densities** 24

5.0 Discussion 25

Appendix 31

Project Funding 33

Acknowledgments 33

References .... **Error! Bookmark not defined.**

List of Figures

Figure 1. *Coralliophila galea* on a) *Orbicella annularis* and b) after removal from colony to demonstrate the yellow operculum. 2

Figure 2. Images of newly killed coral tissue (circled in red) by *C. galea* on a) *Orbicella faveolata* and b) *Acropora palmata*. 3

Figure 3. *Coralliophila galea* (circled in red) on a) *Mycetophyllia ferox* (2 snails), b) *Agaricia agaricites* (1 snail), c) *Colpophyllia natans* (3 snails), d) *Montastraea cavernosa* (2 snails), e) *Orbicella faveolata* (8 snails), and f) *Orbicella annularis* (3 snails). 4

Figure 4a. Google Earth map of Bahamian survey area in the Exuma Cays and Eleuthera highlighting Exuma Cays Land and Sea Park. Sites marked in yellow. 9

Figure 4b. Google Earth map of Bahamian survey area in the Exuma Cays (left) showing locations of 8 study sites outside of Exuma Cays Land and Sea Park (right). All sites are shown in yellow. 10

Figure 4c. Google Earth map of Bahamian survey area in the Exuma Cays (left) showing locations of 4 study sites within the Exuma Cays Land and Sea Park (right). All sites are shown in yellow. 10

Figure 4d. Google Earth map of Bahamian survey area in Eleuthera (left) showing locations of 6 northern most study sites (right). All sites are shown in yellow. 11

Figure 4e. Google Earth map of Bahamian survey area in Eleuthera (left) showing locations of 3 southern most study sites (right). All sites are shown in yellow. 11

Figure 5. Study at Atlantis aquarium with two randomly selected *P. argus* and assorted sizes of *C. galea*; a) *P. argus* in 378 L system for trial, b) *P. argus* actively consuming *C. galea*, c) *C. galea* before placement, d) *C. galea* after study showing remaining *C. galea* ("consumed", "broken lip", and "intact" 15

Figure 6. Positive relationship between coral cover (cm²) and snail density per m². 18

Figure 7. Positive relationship between *D. labyrinthiformis* coral cover (cm²) and snail density per 30m² transect. 19

Figure 8. Slight positive relationship with *P. astreoides* coral cover (cm²) and snail density per 30m² transect. 20

Figure 9. Negative relationship between reef depth (m) and snail density per m². 21

Figure 10. Negative relationship between reef depth (m) and coral cover per m². 22

Figure 11. Positive relationship between damselfish density and snail density per site. (Note: Damselfish species included only the threespot damselfish (*Stegastes planifrons*) and yellowtail damselfish (*Microspathodon chrysurus*). 24

Figure 12. Positive relationship between average coral cover (cm²) and average number of damselfish per site. 25

List of Tables

Table 1. Exuma Cays and Eleuthera dive sites surveyed and total number of surveys for each type. (*Indicates reef sites inside the Exuma Cays Land and Sea Park.) 8

Table 2. Fish families recorded during AGRRA fish surveys. All species within families or listed species were recorded from the table below. (Modified from Table 5, AGRRA Protocols Version 5.4, Lang et al., 2010) 13

Table 3. Residuals of the test of association between snail presence (or absence) on individual coral colonies of each species. Residuals on the presence column >2 indicate the presence of snails occurs more often than expected on that coral species, while residuals <-2 indicate that the presence of snails on that coral species occurs less often than expected if there had been no association. Bold text represents coral species with the strongest association to snail presence or absence 17

Table 4. Comparison of the mean snail density and the calculated Simpson-Diversity Index of corals for all 20 study sites. (*Indicates sites within the Exuma Cays Land and Sea Park.) 23

Abstract

Corallivores are understood to be ecologically important. However, their effects on reef ecosystems are difficult to distinguish from the multiple anthropogenic stressors currently affecting reefs. The corallivorous muricid snail, *Coralliophila galea,* has been documented to have a strong negative impact on Caribbean coral reefs, including curtailing reef recovery following other stressors. Although the basic biology of *C. galea* is relatively well understood, the limited information on its predators prevents a complete understanding of predator-snail-coral relationships, which limits proper protection and conservation of coral reef ecosystems. To determine the impact predators of *C. galea* have on coral reef ecosystems, I assessed the relationships between the snails, their potential predators, and coral cover. Specifically, I determined if and to what extent spiny lobsters, *Panulirus argus,* naturally prey on *C. galea* and evaluated how concentrations of potential predators relate to snail densities, and how predators of *C. galea* indirectly affect coral cover via their impacts on snail densities. To do so, Atlantic and Gulf Rapid Reef Assessments (AGRRA) were conducted on a series of twenty Bahamian reefs to assess coral and other benthic cover, *C. galea* numbers, and numbers of potential predators of this corallivorous snail. Reef coral cover was inversely related to depth and directly related to *C. galea* site densities. Densities of *C. galea* was positively associated to the density of *Orbicella annularis* and *O. faveolata* and negatively associated to the density of *Porites astreoides*. *Porites astreoides* and *Diploria labyrinthiformis* coral cover also showed significance when analyzed individually to *C. galea* populations despite these two corals not being a common food source. Numbers of *P. argus* were too low to test its effect on snail densities. Their foraging behavior and level of interest of feeding on *C. galea* was examined in a controlled aquarium setting and revealed that while they will consume *C. galea* without size preference, it is still unclear to what extent in a wild setting this occurs. Fish densities did not reveal any additional significant associations except when analyzing Pomacentridae (damselfish). There was a positive relationship observed between damselfish and *C. galea* densities possibly indicating that either their predators are absent and/or that higher damselfish damage from "farming" on coral reefs attracts snails. Ultimately this study aided in understanding coral reef ecosystem dynamics and introduced new possible associations. Specifically, regarding important coral to snail relationships that may be aiding in settlement cues for *C. galea*, providing new data to potential *C. galea* predator options, and new fish populations that may provide clues to hidden coral reef dynamics.

Keywords: corallivory; Bahamas; fish surveys; coral survey; predation; lobster

1.0 Introduction

The gastropod *Coralliophila galea* (Dillwyn, 1823) (formerly *C. abbreviata* Lamarck 1816) is a natural predator of many scleractinian corals in the Western Atlantic and Caribbean (Miller, 1981). Current taxonomy places the genus *Coralliophila* in Coralliophilinae, a subfamily of Muricidae, which is a large diverse family of predatory marine neogastropod snails (Bouchet et al., 2005). Coralliophilines are small, ranging from 10 to 64 mm long when measured from the apex of the shell to the end of the operculum. Many researchers have recognized corallivores as ecologically important in reef communities through their potential ability to structure a coral reef ecosystem (Barnes, 1986; Birkeland & Lucas, 1990; Knowlton et al., 1990; Turner, 1994; Carpenter, 1997), and it has been documented that coral vulnerability to predators increases under added stressors such as lower salinity (Morton et al., 2002) and close proximity to algae (Wolf & Nugues, 2013). *Coralliophila galea* has been found to prefer stressed corals such as damaged or diseased colonies, to unstressed corals, greatly reducing recovery of a reef (Bright et al., 2015). Coral reefs have been declining globally over the past several decades because of both natural and anthropogenic factors (Clark & Edwards, 1995; Aronson & Precht, 2001; Becker & Mueller, 2001; Soong & Chen, 2003; Jackson et al., 2014). As a result, a concern exists that corallivores may further increase the demise of corals and reef ecosystems in the coming years.

The basic aspects of *C. galea* biology and ecology are relatively well understood. The species commonly occurs on *Acropora* spp. and *Orbicella annularis* (formerly *Montastraea annularis*); however, Miller (1981) observed 14 scleractinian corals with *C. galea* presence. This gastropod can be identified by its spiral ridges along the calcium carbonate shell and a bright yellow operculum (Knowlton et al., 1990) (Figure 1). It lacks jaws and a radula and instead utilizes enzymatic breakdown and proboscal pumping for consumption (Ward, 1965). Hayes (1989) believed it to be a protandrous hermaphrodite, although Baums et al. (2003a) suggested that either snail size at the time of the sex change must be influenced by the coral host or it may not be a protandrous hermaphrodite at all. Snail size appears to vary with the coral species on which the snail is feeding. Studies conducted in the Florida Keys demonstrated *C. galea* found on *Acropora cervicornis* and *Acropora palmata* to be larger (average 30.3 mm) and longer lived (Baums et al., 2003a; Johnston & Miller, 2007) relative to *C. galea* found on all other coral species (17.2-17.6 mm) (Johnston & Miller, 2007). Despite these size variations, Johnston et al.

(2012) found no genetic differentiation between snails on acroporids and those found on other coral hosts. Instead, gene flow is high throughout their geographic range. The ability of this species to maintain stable numbers despite the multitude of factors negatively impacting coral reefs is important to understand if their populations are to be controlled.

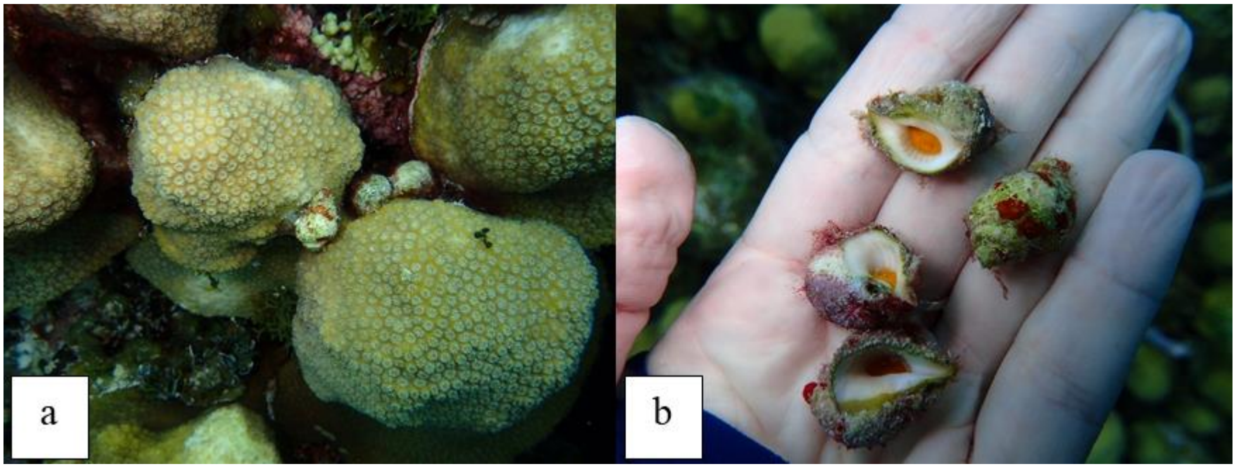

Figure 1. *Coralliophila galea* on a) *Orbicella annularis* and b) after removal from colony to demonstrate the yellow operculum.

Coralliophila galea consumption rates pose a significant threat to corals (Knowlton et al., 1990) and may be associated with other negative impacts through transmission of coral diseases (Williams & Miller, 2005; Sutherland et al., 2010; Gignoux-Wolfsohn et al., 2012). A snail can consume 0.4-6.5 cm² of *A. palmata* per day (Miller, 2001; Baums et al., 2003b); however, rates of consumption on *Orbicella* spp. were found to be comparatively low, ranging 0.13-0.88 cm² snail^{-1} day^{-1} (Baums et al., 2003b). Snail feeding patterns also seem to differ depending upon the prey species. Acroporids tend to show more obvious damage with *C. galea* aggregating towards the middle of the colony (Figure 2). On other coral species such as *Orbicella* spp. and *Agaricia* spp., snails generally gather along the colony edges and cause minimal tissue damage (Hayes, 1990; Baums et al., 2003b). These consumption rates and feeding patterns can be particularly devastating for acroporids following hurricanes exemplified by Hurricane Allen in 1980 and Hurricane Georges in 1998. Following Hurricane Allen, *A. cervicornis* colonies decreased 100-fold, while *C. galea* numbers remained relatively unchanged (Knowlton et al., 1981; 1990). Following Hurricane Georges, *A. palmata* colonies decreased by 75% while snail-infested colonies doubled, and snail numbers increased per colony (Baums et al., 2003a). Regardless of the additional stressors corals are facing, these high consumption rates suggest that corals are not able to grow at a rate that allows them to survive this extent of consumption (Baums et al., 2003a; 2003b).

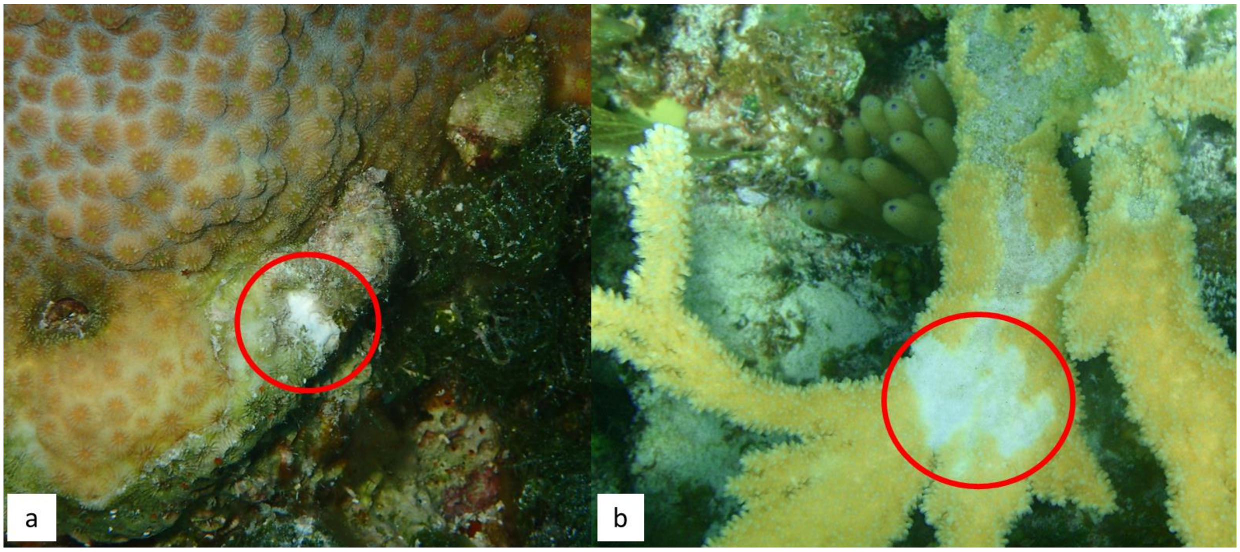

Figure 2. Images of newly killed coral tissue (circled in red) by *C. galea* on a) *Orbicella faveolata* and b) *Acropora palmata.*

Lacking an understanding of how *C. galea* numbers can be controlled limits our ability to provide conservation and protection plans for coral reef ecosystems. *Coralliophila galea* densities may be controlled by manual removal, which allows targeted focus by divers and has been effective in some areas such as the Florida Keys (Williams et al., 2011). This process is time consuming, snails can be easily missed (Figure 3), and restricts efforts to readily accessible reef sites. Snails could also be removed by natural predators, which maintain reduced snail density levels through top-down control and thus help restore a balanced ecosystem, as it has been documented for other species (Shears & Babcock, 2002; Worm & Myers, 2003; Mumby et al., 2006). Such a natural control would ideally provide the most effective method for restoring the coral reef ecosystem balance. Understanding natural predators of *C. galea* may not only be beneficial as a natural corallivore control but may also identify key reef species that need to be focused upon when determining fishing regulations, potential coral restoration sites, and Marine Protected Areas (MPAs).

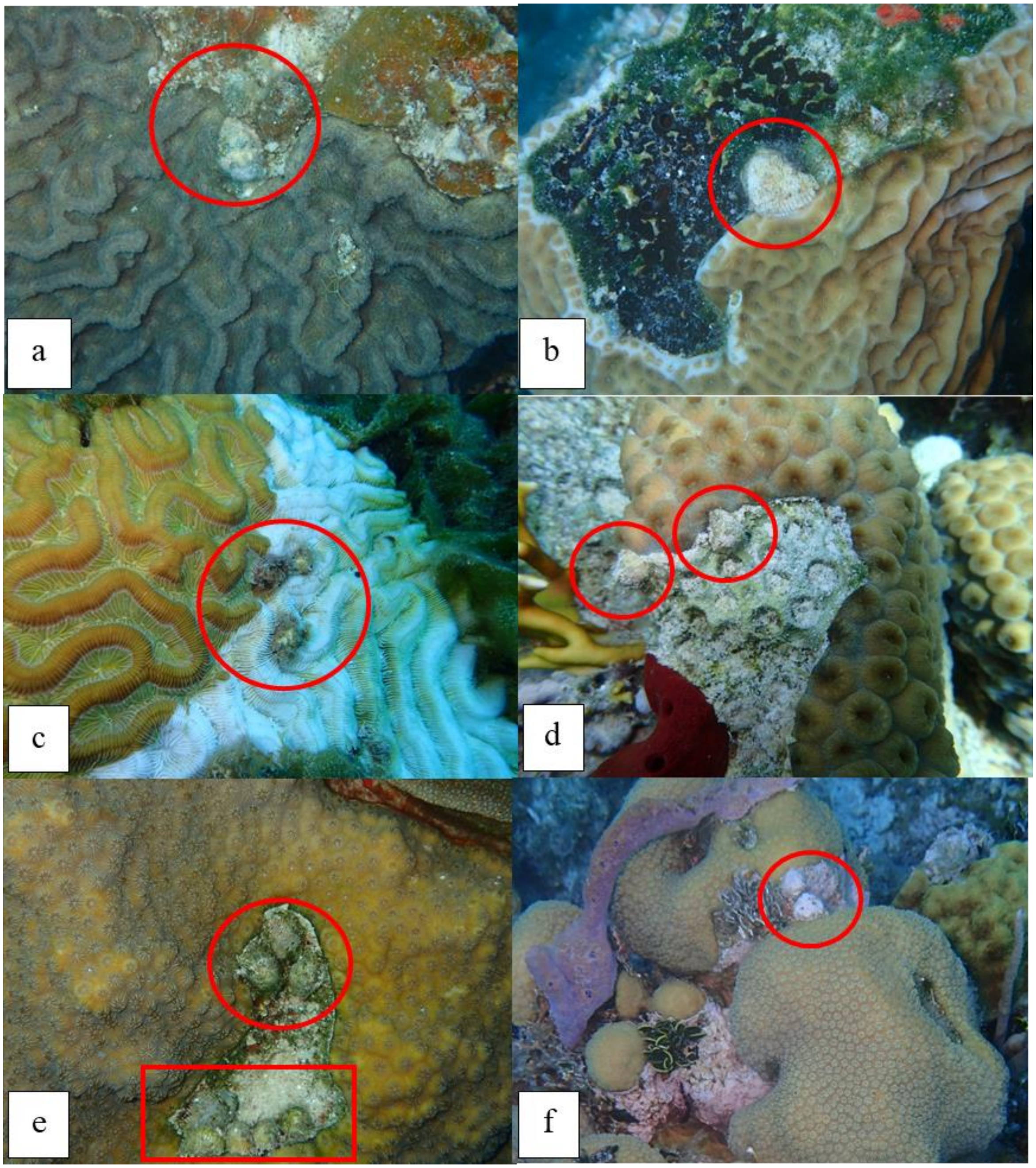

Figure 3. *Coralliophila galea* (circled in red) on a) *Mycetophyllia ferox* (2 snails), b) *Agaricia agaricites* (1 snail), c) *Colpophyllia natans* (3 snails), d) *Montastraea cavernosa* (2 snails), e) *Orbicella faveolata* (8 snails), and f) *Orbicella annularis* (3 snails).

The higher abundance of large predators and herbivorous fishes within marine protected areas (MPA) has been shown to have a positive impact on coral density and recruitment (Mumby et al., 2006). An example of a working MPA is the Exuma Cays Land and Sea Park (ECLSP) in The Bahamas. This is a large 456 km^2 MPA that was designated in 1958 and has been successfully enforced since 1986 through consistent park monitoring and reporting of illegal activity from boaters within the park. Decreased fishing in the park had a particularly significant positive impact in coral recruitment (Mumby et al., 2007). Additionally, fishing mortality of a potential predator of *C. galea*, the spiny lobster, *Panulirus argus,* was 47-98% lower within the ECLSP (Lipcius et al., 2001). This park was a main area of interest for this research and as many reef sites as possible were assessed within the ECLSP to compare to Bahamian reefs in unprotected areas.

Coralliophila galea has only a few documented predators: the spiny lobster *Panulirus argus* (Baums 2003a; Kamerman, personal observation 2014), snapping shrimp *Synalpheus fritzmuelleri* (Goldberg, 1971), and the muricid rock snail *Thais deltoidea* (Sharp & Delgado, 2015). Other invertebrates, such as the common octopus, *Octopus vulgaris*, and some fishes, including members of Ostraciidae (trunkfish), Tetraodontidae (pufferfish), and Labridae (hogfish), may also consume the snail, as their known diets include other gastropods. Similar corallivores belonging to the Indo-Pacific genus *Drupella* are preyed upon by fish species of the families Balistidae and Labridae (McClanahan, 1994). *Coralliophila galea* may thus have similar predators as well. This may be important as numbers of *Drupella* and another corallivore, the crown-of-thorns sea star, *Acanthaster planci*, appear to increase when their natural predators are overfished (Turner, 1994; Sweatman, 2008; Armstrong, 2009).

The limited information on known predators of *C. galea* prevents a complete understanding of prey-predator relationships, which limits our ability to properly protect and conserve coral reef ecosystems. Given the current status of corals reefs, efforts to help reef recovery through MPAs or restoration may be futile if predators of *C. galea* and *C. galea* densities themselves are overlooked. To help achieve the most effective conservation plan for coral reefs, an ecological top-down approach must be studied to evaluate the effect that predators of *C. galea* on a reef may have to help improve reef conservation efforts. While results vary on other corallivore prevalence, such as *Acanthaster planci,* when predators are reduced (Sweatman, 2008; Mendonça et al., 2010), the impact from reduced predators of *C. galea* has yet to be determined. Miller et al. (2002) found no differences in *C. galea* densities between no-take reserves and sites outside reserve areas, indicating that decreased fishing pressure does not impact the corallivore. However, no surveys focused specifically on potential predators of the gastropod. The aim of this research was to help future coral reef conservation by further understanding how ecological changes caused by *C. galea* can affect conservation efforts and identify potential ways to control the corallivore.

2.0 Objectives

The aim of this research was to better understand the impacts of *Coralliophila galea* on coral reef environments and determine any potential predators for the corallivore. The predator-prey dynamic between key fish, invertebrates, coral species and *C. galea* is important in order to understand key relationships in a healthy coral reef ecosystem and therefore provide better future conservation efforts. This was accomplished in the following ways:

1) Determine if the spiny lobster, *Panulirus argus,* has a size preference for *C. galea.*
2) Determine if *C. galea* density was associated with coral cover and/or individual coral species.
3) Evaluate the relationship between depth, coral cover, and *C. galea* density.
4) Evaluate the relationship between coral diversity and *C. galea* density.
5) Determine if fish densities were associated with *C. galea* density.
6) Determine if fish densities were associated with coral cover.

3.0 Methods

3.1 Site Selection

To assess these research questions, 20 Bahamian reefs, 12 in the Exuma Cays and 8 in south Eleuthera, were surveyed between October 2015 to November of 2017 (Figure 4a-e). The Exuma Cays reef sites were located both within the ECLSP and outside the park. All the reef sites were accessed from a live-a-board charter dive boat, Aquacat, based in Nassau, The Bahamas. This charter conducted week-long trips to both areas regularly. The study sites were chosen from among the most frequented sites to ensure adequate dive time was available for data collection. My previous assessments conducted at these sites, entailing over 100 dives in one year, provided me with sufficient background information regarding the presence of *C. galea* to ensure these questions could be adequately addressed. Each site was surveyed using Atlantic and Gulf Rapid Reef Assessment (AGRRA v5) protocols including coral and fish species data collection (www.agrra.org). Additionally, 30 m^2 (30 m x 1 m) "tally" surveys were conducted at each site where all coral species ≥ 4 cm were counted, or tallied, to get a broader understanding of coral cover, coral diversity, and snail density on each site. Due to time constraints on each site, fish surveys were done by the Perry Institute for Marine Science (PIMS). The sites surveyed by PIMS were performed within the same time frame as my data collection and chosen based on field logistics to coincide with their research. Of the 20 dive sites, 15 were surveyed by PIMS. The remaining five were not included in fish analyses (Table 1). All three survey types were used to generate data collection appropriate for the posed research questions.

Table 1. Exuma Cays and Eleuthera dive sites surveyed and total number of surveys for each type. (*Indicates reef sites inside the Exuma Cays Land and Sea Park.)

	Reef Site	Avg. Depth (m)	Latitude	Longitude	Coral	Tally	Fish
Exuma Cays	Barracuda Shoals	6.3	24°45'41.76"N	76°50'33.06"W	4	3	n/a
	Blacktip Reef	19.0	24°41'23.82"N	76°48'2.16"W	4	3	6
	Crab Mountain	14.8	24°46'47.28"N	76°48'52.74"W	4	3	6
	Danger Reef*	13.6	24°29'55.79"N	76°31'54.67"W	5	3	8
	Dog Rocks	11.8	24°52'48.78"N	76°47'30.42"W	4	3	n/a
	Flat Rock Reef	4.3	24°45'23.04"N	76°49'48.48"W	4	4	n/a
	Hammerhead Gulch	8.1	24°39'59.28"N	76°49'3.18"W	4	3	n/a
	Jeep Reef*	7.9	24°21'2.04"N	76°35'21.36"W	4	3	8
	Lobster No Lobster	8.0	24°46'51.06"N	76°50'15.00"W	4	4	7
	Parrotfish Reef*	4.8	24°25'32.58"N	76°41'13.32"W	5	3	7
	Pillar Wall	14.9	24°44'17.82"N	76°48'16.32"W	4	3	6
	Three Peaks*	11.9	24°25'46.14"N	76°41'6.00"W	4	3	7
Eleuthera	Cave Rock	10.8	24°48'41.64"N	76°20'54.24"W	5	3	n/a
	Cut 'n Run	19.7	24°49'2.21"N	76°21'15.08"W	4	3	7
	Cut Through City	18.4	24°47'34.80"N	76°20'11.40"W	4	3	6
	Jake's Hole	6.5	24°40'36.36"N	76°13'0.48"W	4	4	7
	Monolith Wall	18.4	24°47'10.92"N	76°20'0.78"W	4	3	4
	Premo Wall	19.7	24°46'51.48"N	76°19'49.56"W	4	3	6
	Split Coral Head	11.9	24°45'27.90"N	76°17'52.14"W	4	3	9
	Tunnel Rock	7.2	24°48'54.90"N	76°20'58.56"W	4	4	6

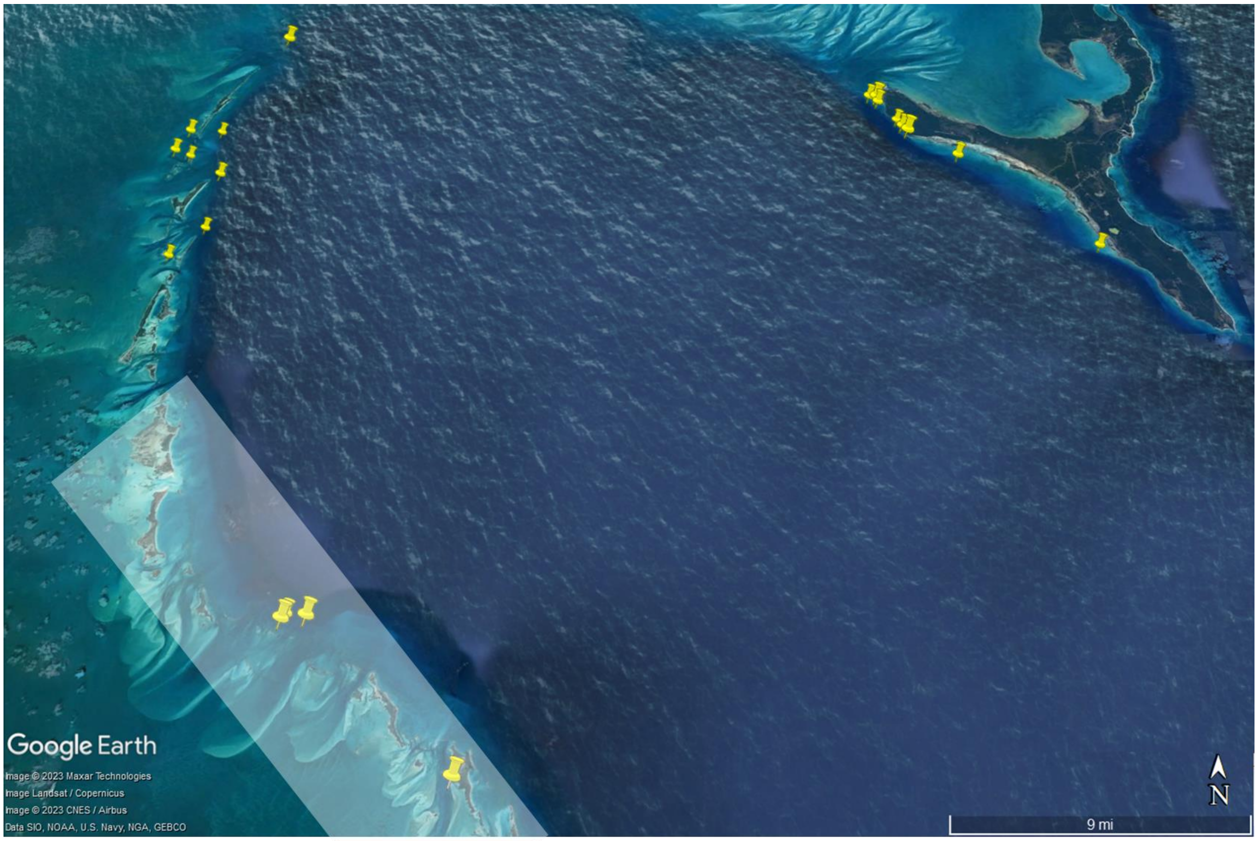

Figure 4a. Google Earth map of Bahamian survey area in the Exuma Cays and Eleuthera highlighting Exuma Cays Land and Sea Park. Sites marked in yellow.

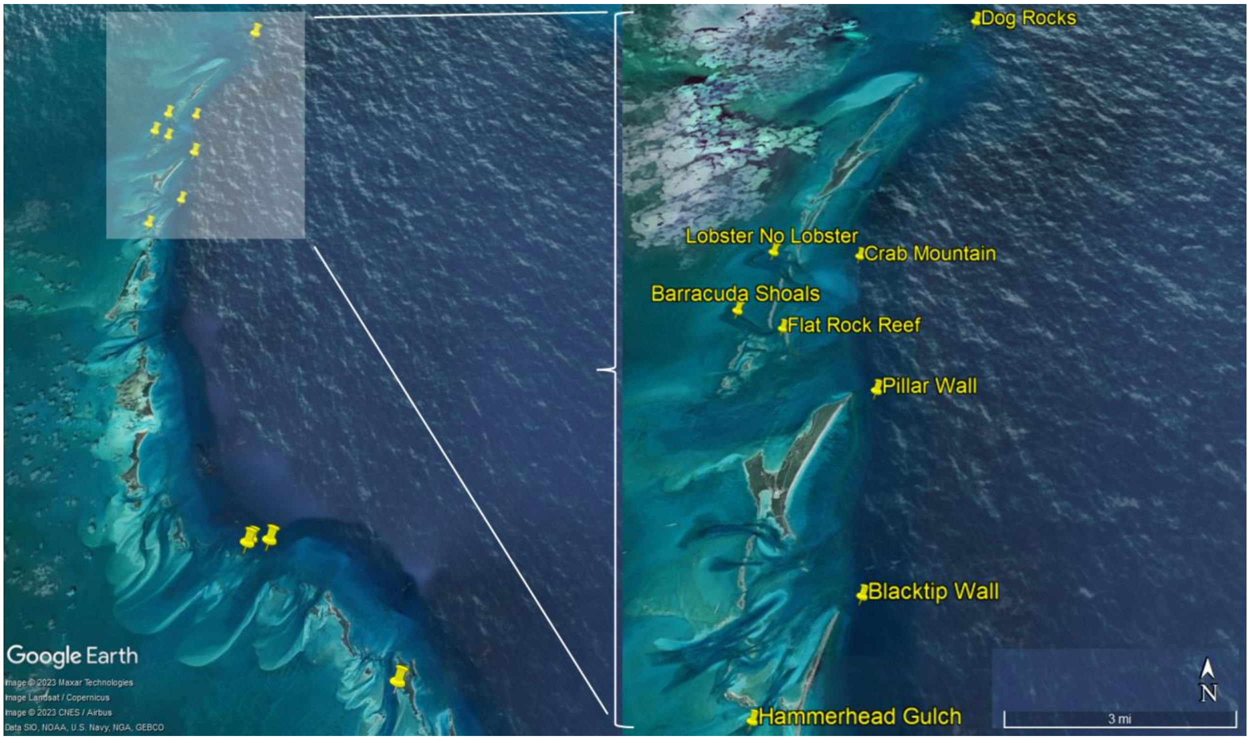

Figure 4b. Google Earth map of Bahamian survey area in the Exuma Cays (left) showing locations of 8 study sites outside of Exuma Cays Land and Sea Park (right). All sites are shown in yellow.

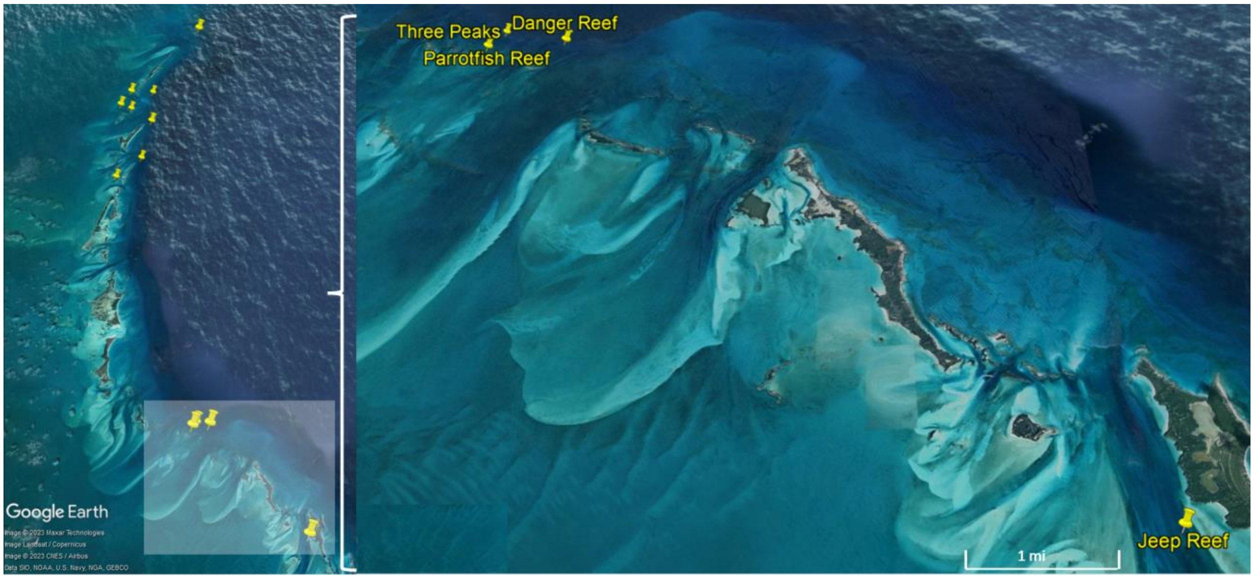

Figure 4c. Google Earth map of Bahamian survey area in the Exuma Cays (left) showing locations of 4 study sites within the Exuma Cays Land and Sea Park (right). All sites are shown in yellow.

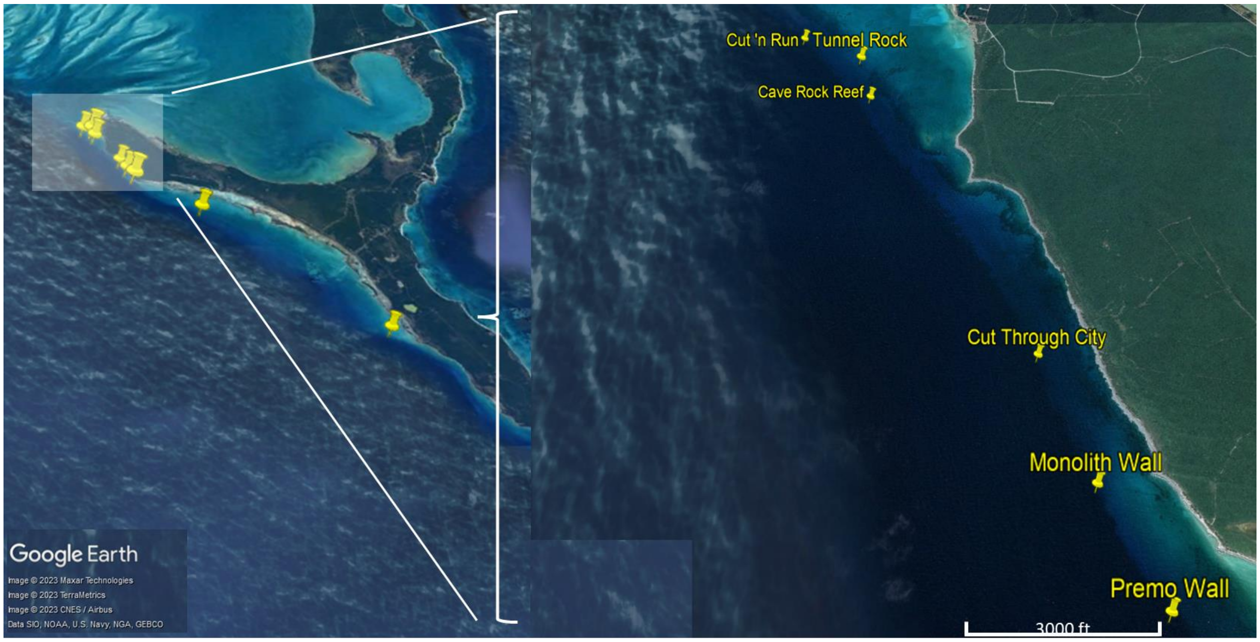

Figure 4d. Google Earth map of Bahamian survey area in Eleuthera (left) showing locations of 6 northern most study sites (right). All sites are shown in yellow.

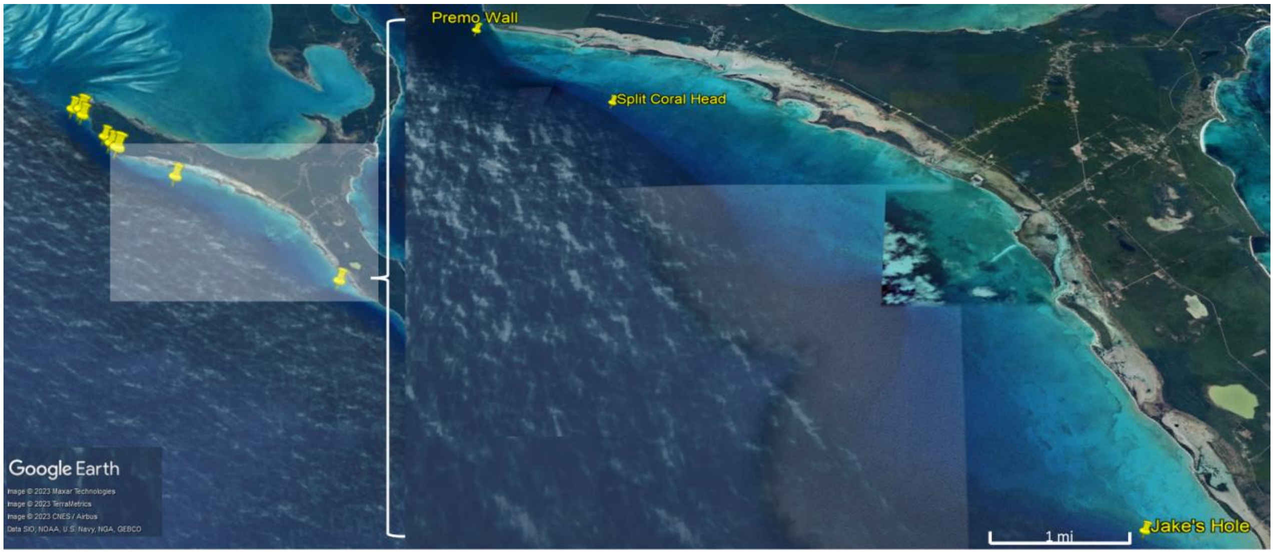

Figure 4e. Google Earth map of Bahamian survey area in Eleuthera (left) showing locations of 3 southern most study sites (right). All sites are shown in yellow.

3.2 Surveys

To assess potential *C. galea* predator densities, densities of *C. galea*, and coral cover, I conducted site surveys. These included AGRRA (coral and fish types), and tally surveys via SCUBA. Data was recoded *in situ* on dura copy waterproof laser paper™ on a clipboard.

Coral surveys were conducted along a 10-m survey line using a 10-m lead line rope marked at 10-cm intervals by color coded cable ties. These surveys focused on *C. galea* densities, coral cover calculated from length, width and height and percent mortality of each colony. The survey covered 10 m^2—0.5 m on either side of the 10-m line. All corals ≥4cm were identified to species and measured to the nearest 5 cm for corals greater than 50 cm and to the nearest 1 cm for corals less than 50 cm. Each colony was measured for total length, width and height, recorded for any bleaching or paleness, and examined for percent of mortality including disease, predation, and spatial competitors. All *C. galea* were counted and recorded on each coral colony. A final pass along the line was used to document any *P. argus*.

Fish surveys provided identifications and estimates of the abundance and sizes of potential fish predators of *C. galea*. Fish surveys were performed following AGRRA protocols by PIMS staff. Ideally, a minimum of six surveys were performed per reef site. However, due to the required assistance of PIMS to collect fish data, some of my study sites were not specifically assessed. These surveys did not require the same start point due to the greater number of surveys and the mobile nature of fish on a reef. Fish surveys were chosen haphazardly along the reef using a 30 m transect tape, which were swum out from a starting point while simultaneously recording data on the fishes that pass across or along the line. Data was recorded on all fish grouping presented in Table 2 following AGRRA protocols and to accommodate all potential species believed to potentially impact *C. galea* numbers. All other taxa were disregarded.

Table 2. Fish families recorded during AGRRA fish surveys. All species within families or listed species were recorded from the table below. (Modified from Table 5, AGRRA Protocols Version 5.4, Lang et al., 2010)

TAXON			
PREDATORS		**GRAZERS**	
FAMILY	**SPECIES OR COMMON NAME**	**FAMILY**	**SPECIES OR COMMON NAME**
Balistidae	Triggerfish	Acanthuridae	Surgeonfish
Carangidae	*Caranyx ruber*	Chaetodontidae	Butterflyfish
	Trachinotus falcatus	Haemulidae	Grunts
Diodontidae	Porcupinefishes	Pomacanthidae	Angelfish
Kyphosidae	*Kyphosus spectator*	Pomacentridae	*Microspathodon chrysurus*
Labridae	Wrasses		*Stegastes planifrons*
Lutjanidae	Snappers	Scaridae	Parrotfish
Muraenidae	Morays	Sparidae	Porgies
Monacanthidae	Filefishes		
Ostraciidae	Trunkfish		
Scorpaenidae	*Pterois* spp.		
Serranidae	*Epinephelus* sp.		
	Cephalopholis sp.		
	Mycteroperca sp.		
Sphyraenidae	*Sphyraena barracuda*		
Tetraodontidae	Pufferfishes		

Tally surveys provided a broader understanding of coral cover by species, coral diversity, and snail densities. A 30 m² (30 m x 1 m) transect was swum out at randomly chosen start points to ensure the majority of 30 m² was on top of the reef. All corals >4 cm were recorded by tallying each species. Any corals found with *C. galea* present was measured (LxWxH), recorded for total number of snails, and any mortality.

The invertebrate species believed to prey upon *C. galea* were *P. argus* (Baums 2003a; Kamerman, personal observation 2014), *S. fritzmuelleri* (Goldberg, 1971), and *T. deltoidea* (Sharp & Delgado, 2015). *Panulirus argus* was recorded during surveys; however, because other potential invertebrate predators are either found in low numbers (*T. deltoidea*), cryptic (*S. fritzmuelleri*) or nocturnal (*Octopus* spp.), they were not observed reliably enough, and no data was analyzed in regard to those species. Night dives were performed, when possible, but frequent night dives on all reef sites was not feasible due to charter operations.

Coral colony area, coral cover and coral diversity were calculated as follows:

$$Coral\ Colony\ Area\ (A) = \left(\pi * \frac{L}{2} * \frac{W}{2}\right) * \%\ Live\ Tissue$$

$$Coral\ Cover\ (CC) = \frac{\Sigma A\ per\ transect}{(Survey\ Length)}$$

$$Simpson\ Diversity\ Index = \frac{\Sigma n(n-1)}{N(N-1)}$$

Where L is the length, W is the width, n is the total number of corals per species, and N is the total number of corals of all species.

3.3 Lobster Predation Studies

To help understand predator-prey relationships of *C. galea*, the potential size preference of one of its most likely predators, the spiny lobster *P. argus*, was assessed. Lobsters were held in Atlantis Paradise Island, Bahamas aquarium holding systems and offered *C. galea* for up to one hour per trial. All lobsters were monitored to observe *C. galea* consumption in isolated and controlled settings.

P. argus were collected by Atlantis Paradise Island, Bahamas aquarium staff and held indoors within a 6 m circular 22,712 L open system with sand filtration and ozonation until time of experiments. Two 378 L systems, also equipped with sand filtration and ozonation, were used for experiments. Water parameters including salinity, pH, ammonia, and nitrite levels, were monitored on all systems by Atlantis aquarist staff to ensure optimal water quality. Due to the short duration of each trial and the nature of the open systems, water changes were not required. The *C. galea* collected from reefs in the Exuma Cays and Eleuthera ranged from 5 mm to over 25 mm. All snails were transported in 45 L coolers with air bubblers for oxygenation. One hundred percent water changes were performed daily until collection arrival to Atlantis facilities. Snails were placed in each system to start and allowed 15 minutes to acclimate before introducing the *P. argus* individuals. Two *P. argus* were subsequently transferred to each of the two, 378 L systems for each trial and observed for up to one hour then returned to the main 22,712 L system at the end of each experiment. Snails and any fragments were then collected and recorded as “intact”, “broken lip”, or “consumed”. “Broken lip” snails were ultimately combined with “intact” snails and considered uneaten for analysis. Thirteen total trials were performed consisting of 30 total *C. galea* in each trial (Figure 5). No evening trials were performed due to the consumption of *C. galea* during daylight hours. The number and sizes of the *C. galea* snails included per trial were as follows:

- ten 5-10 mm
- ten >10-20 mm
- five >20-25 mm
- five >25 mm

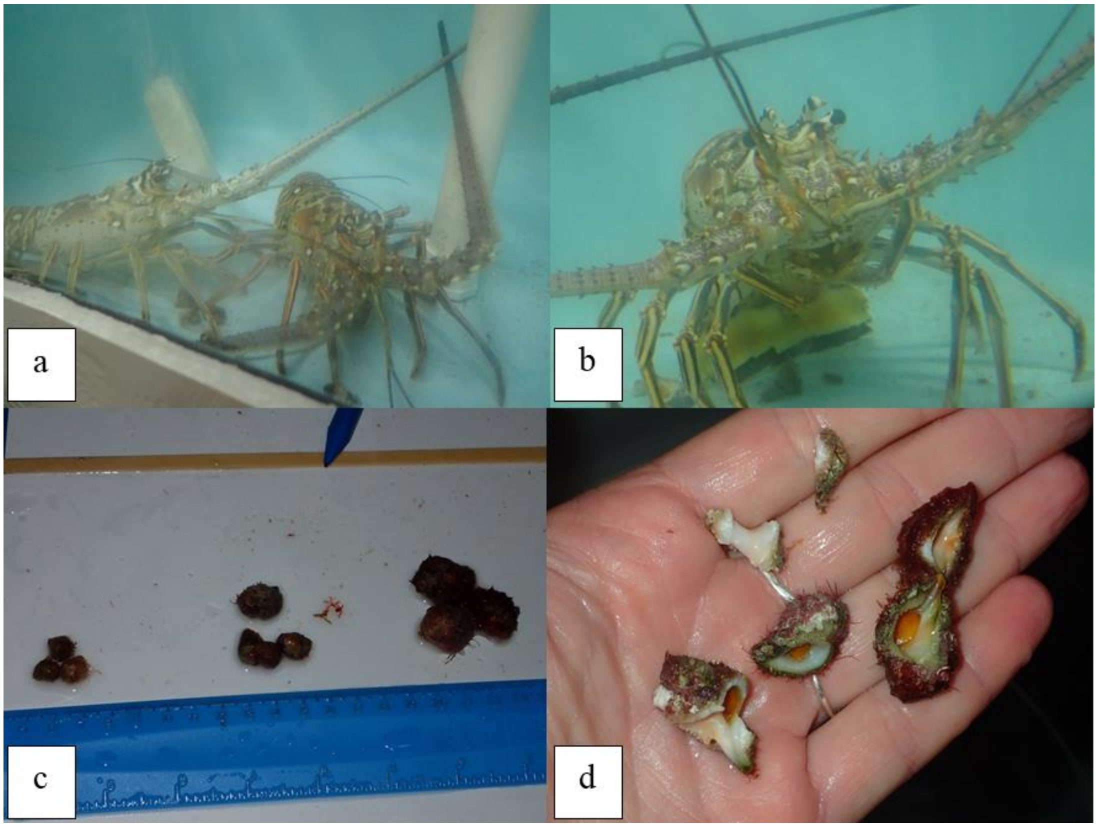

Figure 5. Study at Atlantis aquarium with 2 randomly selected *P. argus* and assorted sizes of *C. galea*; a) *P. argus* in 378 L system for trial, b) *P. argus* actively consuming *C. galea*, c) *C. galea* before placement, d) *C. galea* after study showing remaining *C. galea* (“consumed”, “broken lip”, and “intact”).

3.4 Data Analysis

To analyze if *P. argus* had a size preference of *C. galea*, a Chi-square contingency test of association was performed looking at the number of snails consumed vs. uneaten for each of the four size categories. Not enough lobsters were found on the surveys to analyze any relationship between *P. argus* and snail densities on a reef, therefore no further analyses were performed.

To determine if coral species were associated with the presence or absence of snails, a test of association (Fisher exact test) was used. To assess the relationship between coral cover and snail density a correlation was used. Correlations were also used to assess if the coral cover of each species was related to snail density.

To determine how snail density changed with depth and with coral cover, a non-parametric regression and an exponential model were used, respectively.

The relationship between coral diversity (calculated using the Simpson Diversity Index) and snail density was analyzed through a Kendall rank correlation.

To evaluate the relationship between fish density and snail density, fish families were first grouped into the categories of predatory or grazer fish. Model II regressions were used to assess if the density of predator and grazing fish were related to snail density. To assess if the density of each fish family was related to snail density, linear regressions were used. To assess the relationship between fish density and coral cover, fish families were also first grouped as predators or grazers. Correlations were used to test if fish density of predator and grazer fish was related to coral cover. Correlations were also used to test the relationship between coral cover and density of each fish family.

All statistical analyses were performed in R Studio.

4.0 Results

4.1 Lobster Snail Size Preference

No significant association was found between snail size and the likelihood of being predated by lobster from the aquarium studies, indicating that the lobster has no size preference for the snails (df=2, X^2=0.84783, p-value=0.6545).

4.2 Coral Cover and Snail Density

There was a significant association between the presence or absence of *C. galea* snails on individual colonies of multiple coral species (Fisher exact test, $p<5\times10^{-4}$). Snails were more likely present on *Orbicella annularis* and *O. faveolata* colonies and more commonly absent from *Porites astreoides* colonies (Table 3).

Table 3. Residuals of the test of association between snail presence (or absence) on individual coral colonies of each species. Residuals on the presence column >2 indicate the presence of snails occurs more often than expected on that coral species, while residuals < -2 indicate that the presence of snails on that coral species occurs less often than expected if there had been no association. Bold text represents coral species with the strongest association to snail presence or absence.

Coral Species	Absent	Present
Acropora cervicornis	-0.52520044	3.22428055
Agaricia agaricites	0.0162769	-0.09994337
Colpophyllia natans	-0.60633773	3.722394
Diploria labyrinthiformis	-0.14549597	0.89322057
Isophyllia sinuosa	-0.31365963	1.92560132
Madracis decactis	0.36129122	-2.21801841
Montastraea cavernosa	0.80412689	-4.9366499
Mycetophyllia spp.	0.2758275	-1.69334445
Orbicella annularis	**-3.26204582**	**20.02616548**
Orbicella faveolata	**-3.4788723**	**21.3572942**
Porites astreoides	**2.15804518**	**-13.24854775**
Porites porites	0.91797991	-5.63560987
Solenastrea bournoni	0.48585345	-2.98272376
Scolymia cubensis	-0.14854392	0.91193238
Stephanocoenia intersepta	0.43886957	-2.69428299

On a reef, *C. galea* density was highly correlated to coral cover (cm^2) per m^2 ($p=0.01917$, $tau=0.1959$) (Figure 6). When coral species cover was analyzed, *D. labyrinthiformis* colonies ($p=0.006$, $rho=0.53$) (Figure 7) were found to be positively correlated with snail density. The coral cover of *P. astreoides* was also significantly positively correlated to snail density but to a much lesser extent ($p=0.025$, $tau=0.08$), with the slope of the relationship nearly zero (Figure 8).

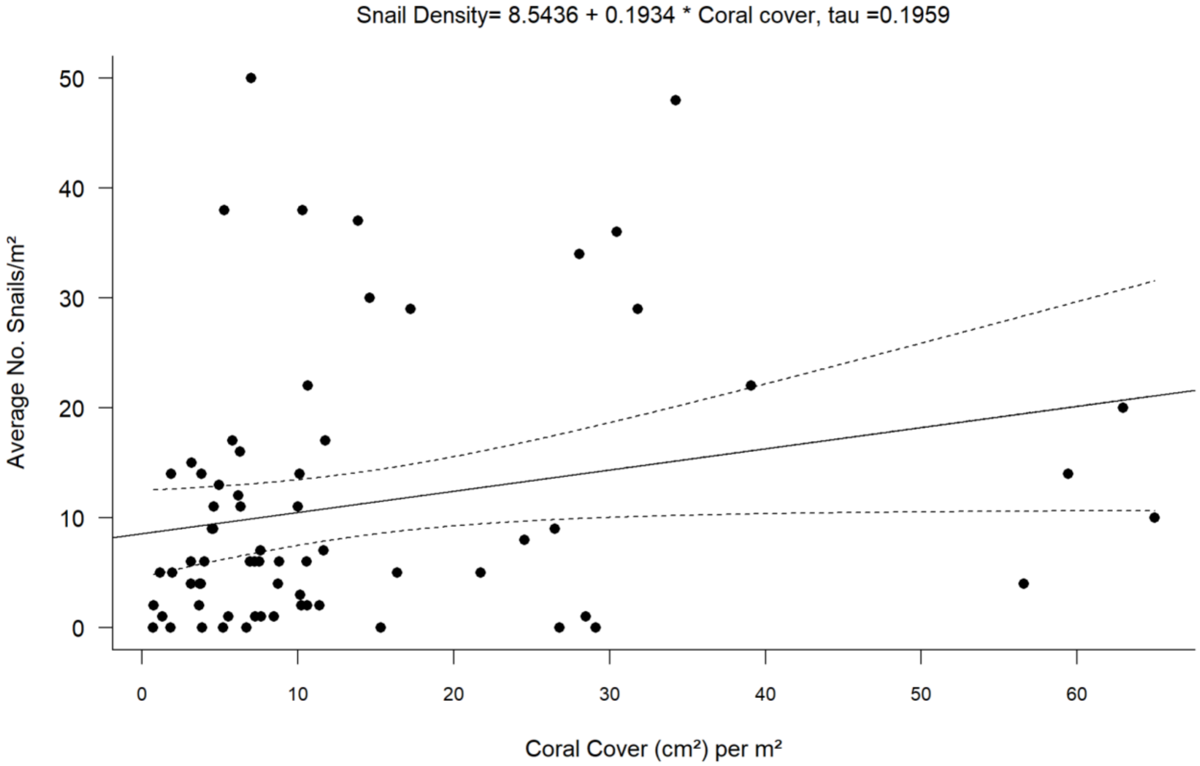

Figure 6. Positive relationship between coral cover (cm2) and snail density per m².

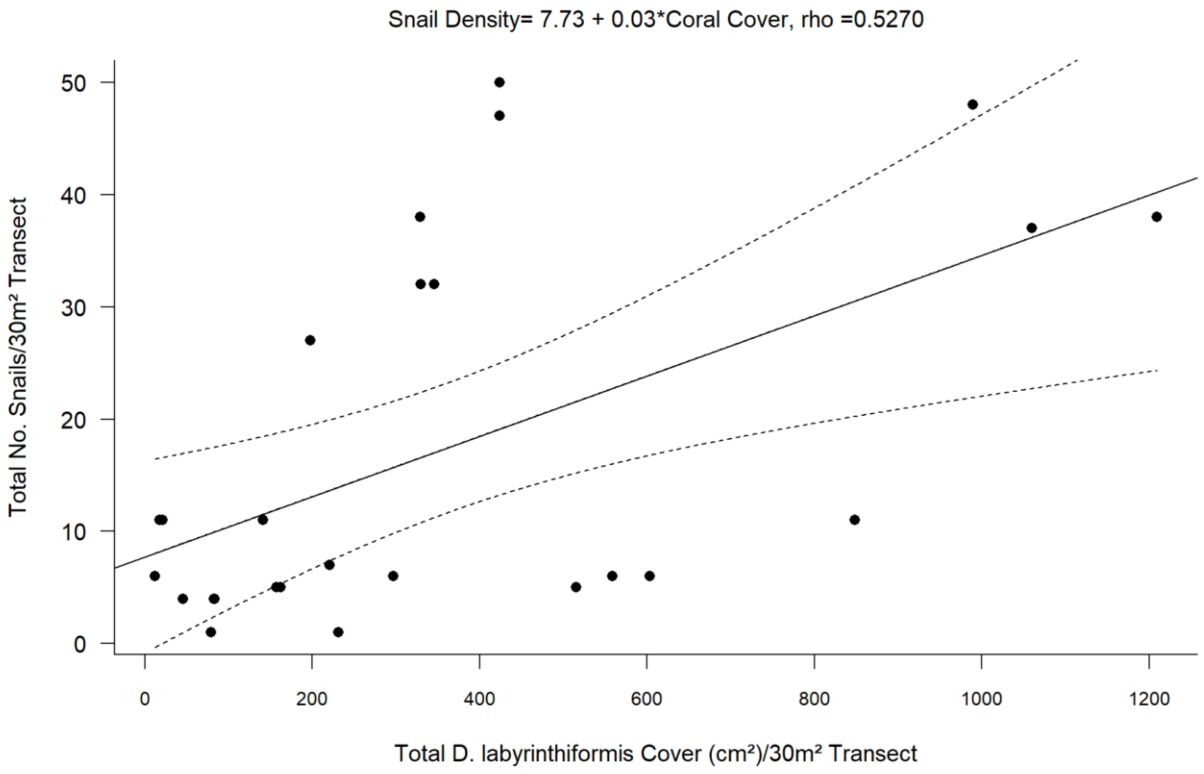

Figure 5. Positive relationship between *D. labyrinthiformis* coral cover (cm²) and snail density per 30m² transect.

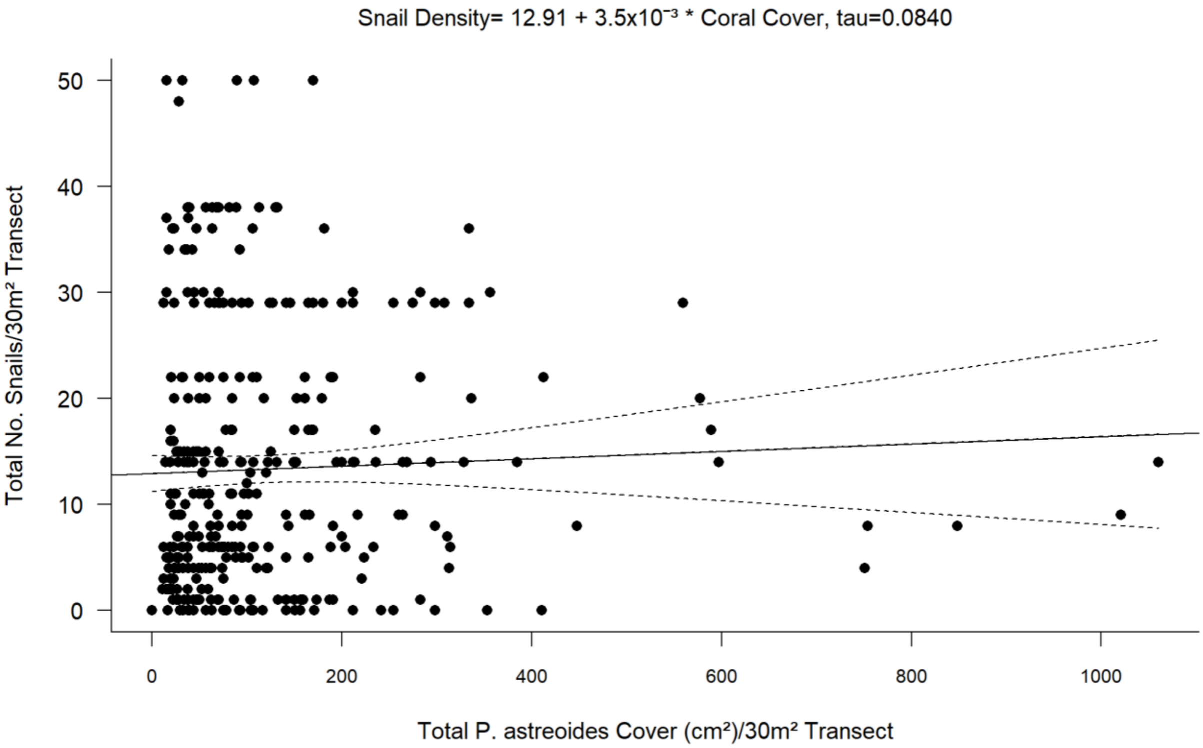

Figure 6. Slight positive relationship with *P. astreoides* coral cover (cm²) and snail density per 30m² transect.

4.3 Depth

The density of *C. galea* was inversely related to depth ($p=2x10^{-16}$) (Figure 9). However, since snail density was highly correlated with coral cover per 30m² transect (p=0.01917, tau=0.1959), this relationship is likely explained by the fact that live coral cover also decreases significantly with depth (exponential model: Coral Cover=53.5*exp(-0.1*Depth), (p<0.001)) (Figure 10).

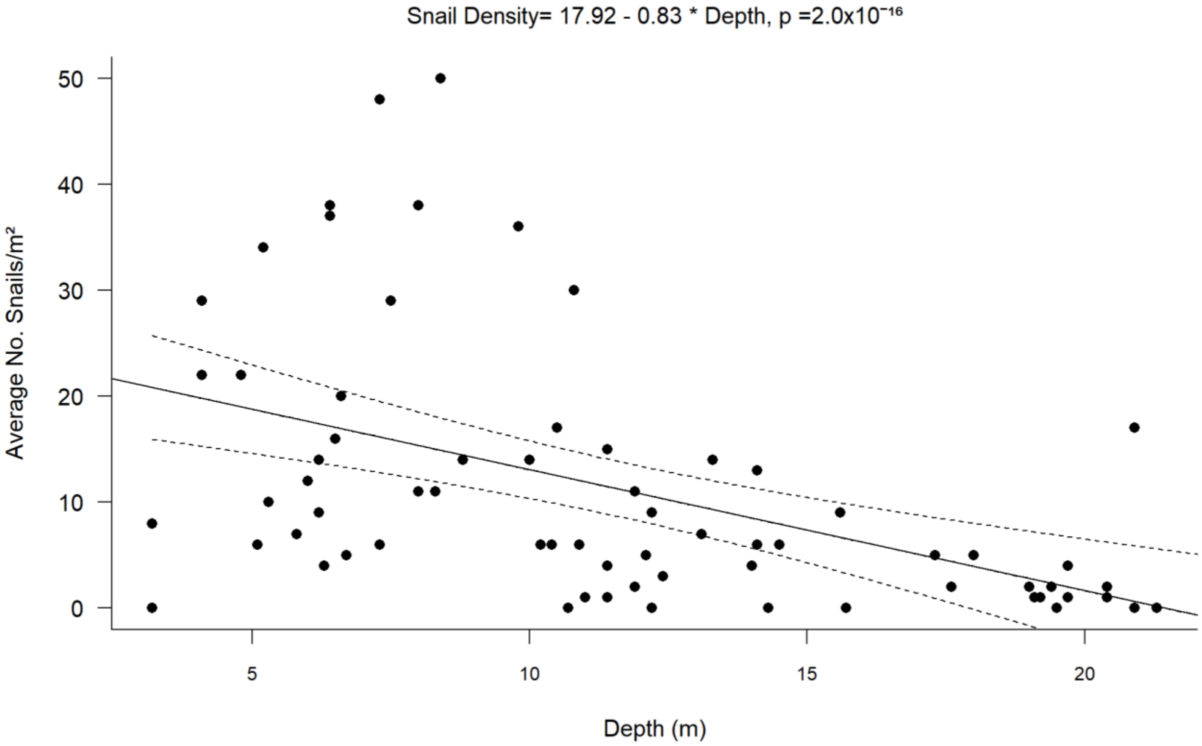

Figure 7. Negative relationship between reef depth (m) and snail density per m².

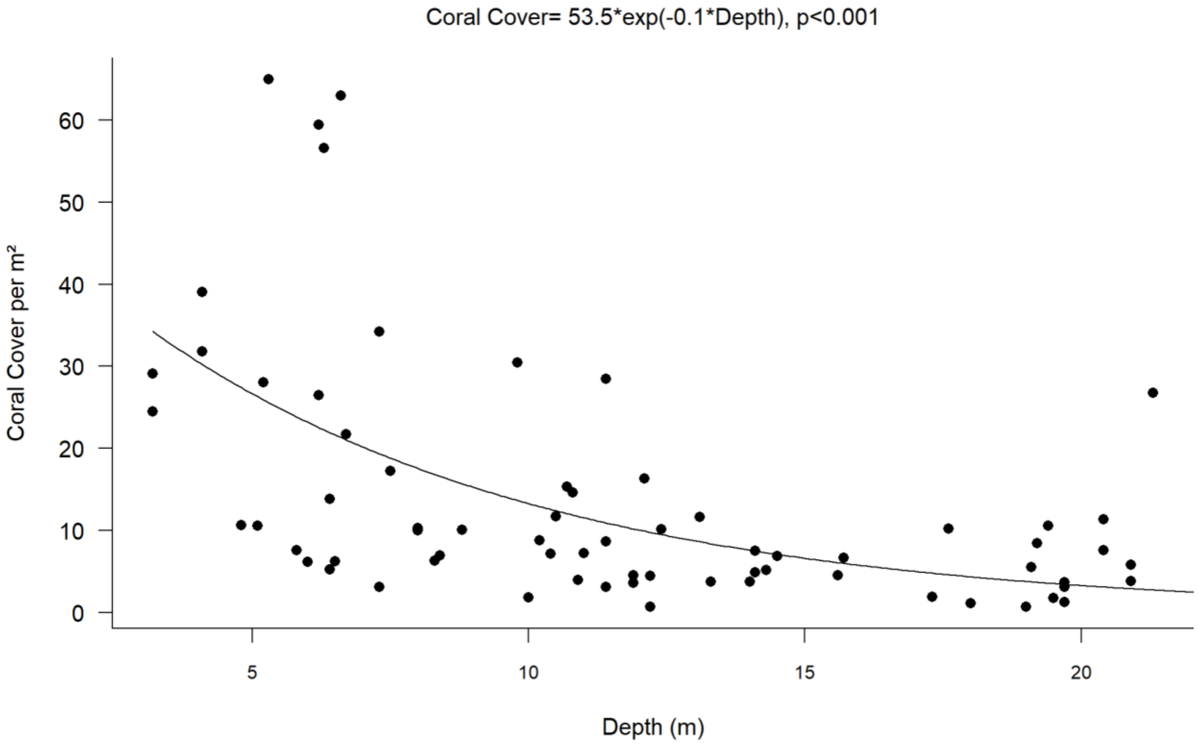

Figure 8. Negative relationship between reef depth (m) and coral cover per m².

4.4 Coral Diversity and Snail Density

Coralliophila galea density and coral diversity were not significantly correlated (p=0.09969, tau=-0.1383) (Table 4).

Table 4. Comparison of the mean snail density and the calculated Simpson-Diversity Index of corals for all 20 study sites. (*Indicates sites within the Exuma Cays Land and Sea Park.)

Site Name	Location	Mean Snail Density (±SE)	Mean No. Coral Species (±SE)	Simpson-Diversity Index
Barracuda Shoals	Exuma	14.7 (±1.3)	12.1 (±0.3)	0.307
Blacktip Wall	Exuma	6.2 (±1.0)	16 (±0.6)	0.165
Crab Mountain	Exuma	12.8 (±1.2)	17.2 (±0.6)	0.155
Danger Reef*	Exuma	9.0 (±1.2)	18.4 (±0.4)	0.134
Dog Rocks	Exuma	9.5 (±0.7)	16.4 (±0.1)	0.188
Flat Rock Reef	Exuma	30.2 (±2.5)	11.8 (±0.3)	0.302
Hammerhead Gulch	Exuma	24.1 (±2.9)	15.4 (±0.2)	0.215
Jeep Reef*	Exuma	15.0 (±1.2)	16 (±0.2)	0.165
Lobster No Lobster	Exuma	35.2 (±2.8)	14.2 (±0.3)	0.301
Parrotfish Reef*	Exuma	20.0 (±1.7)	11.6 (±0.1)	0.207
Pillar Wall	Exuma	4.6 (±0.6)	18.5 (±0.6)	0.163
Three Peaks*	Exuma	4.6 (±0.5)	19.4 (±0.8)	0.131
Cave Rock	Eleuthera	15.7 (±1.2)	18.7 (±0.4)	0.118
Cut'n Run	Eleuthera	2.0 (±0.5)	13.2 (±0.2)	0.140
Cut Through City	Eleuthera	5.0 (±0.9)	15.8 (±0.3)	0.150
Jake's Hole	Eleuthera	40.0 (±2.8)	16 (±0.2)	0.164
Monolith Wall	Eleuthera	6.2 (±0.8)	15.7 (±0.1)	0.148
Premo Wall	Eleuthera	0.5 (±0.0)	16 (±0.4)	0.111
Split Coral Head	Eleuthera	41.6 (±2.2)	17.6 (±0.2)	0.154
Tunnel Rock	Eleuthera	26.6 (±1.5)	17.3 (±0.3)	0.194

4.5 Snail Density and Fish Densities

Average snail density per site was not significantly explained by the presence of predator nor grazer fish (Model II Regression grazers: p=0.32, predators: p=0.5). Damselfish abundance was the only fish grouping found to be a significantly good predictor of snail density (Linear Regression, p=0.01431) (Figure 11).

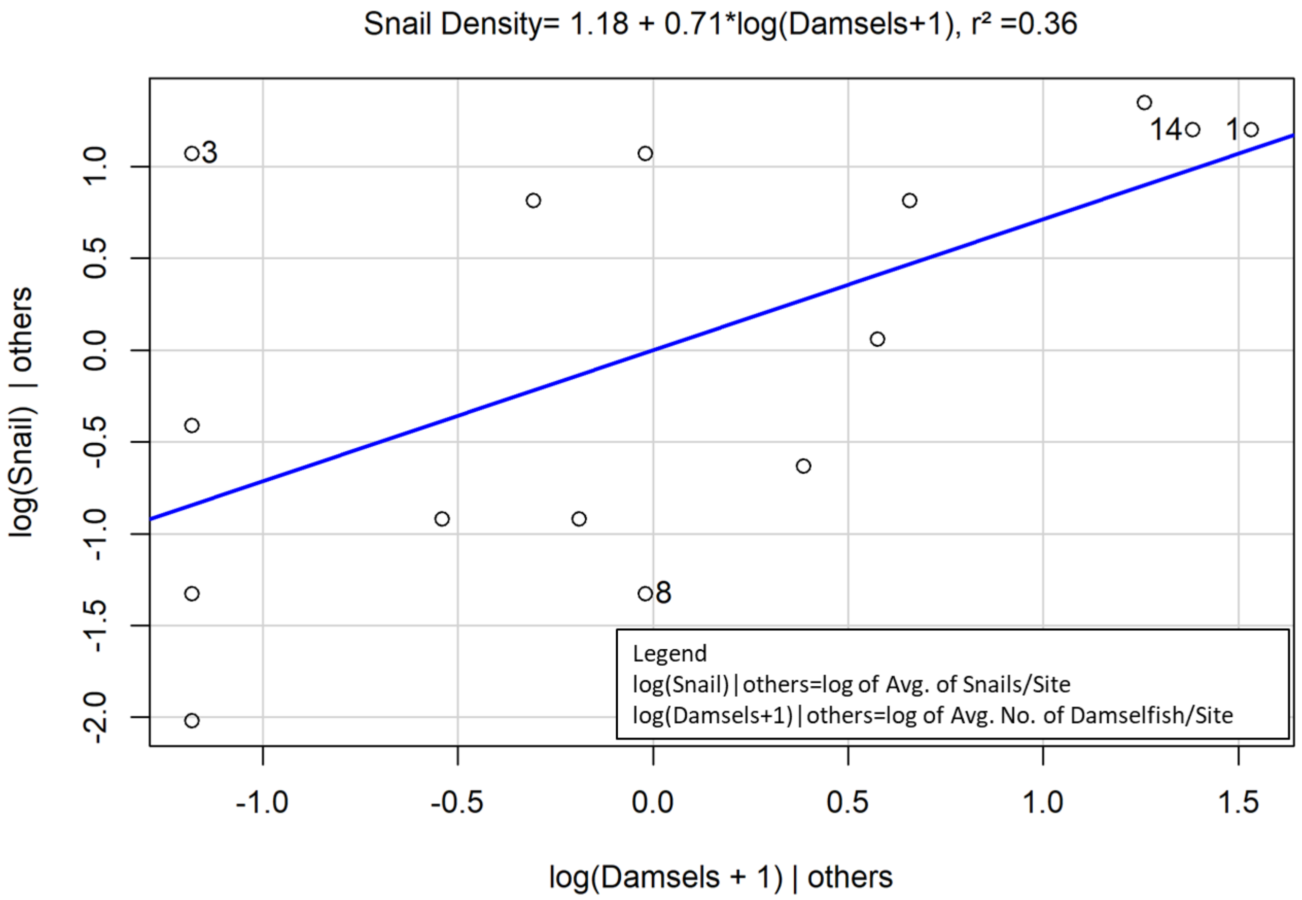

Figure 9. Positive relationship between damselfish density and snail density per site. (Note: Damselfish species included only the threespot damselfish (*Stegastes planifrons*) and yellowtail damselfish (*Microspathodon chrysurus*).

4.6 Coral Cover and Fish Densities

No significant relationship was found between coral cover and grazing fish populations (p=0.1059) nor predatory fish (p=0.2091). Damselfish abundance was the only fish species highly correlated to coral cover (p=6.4x10^{-4}, r=0.8197) (Figure 12).

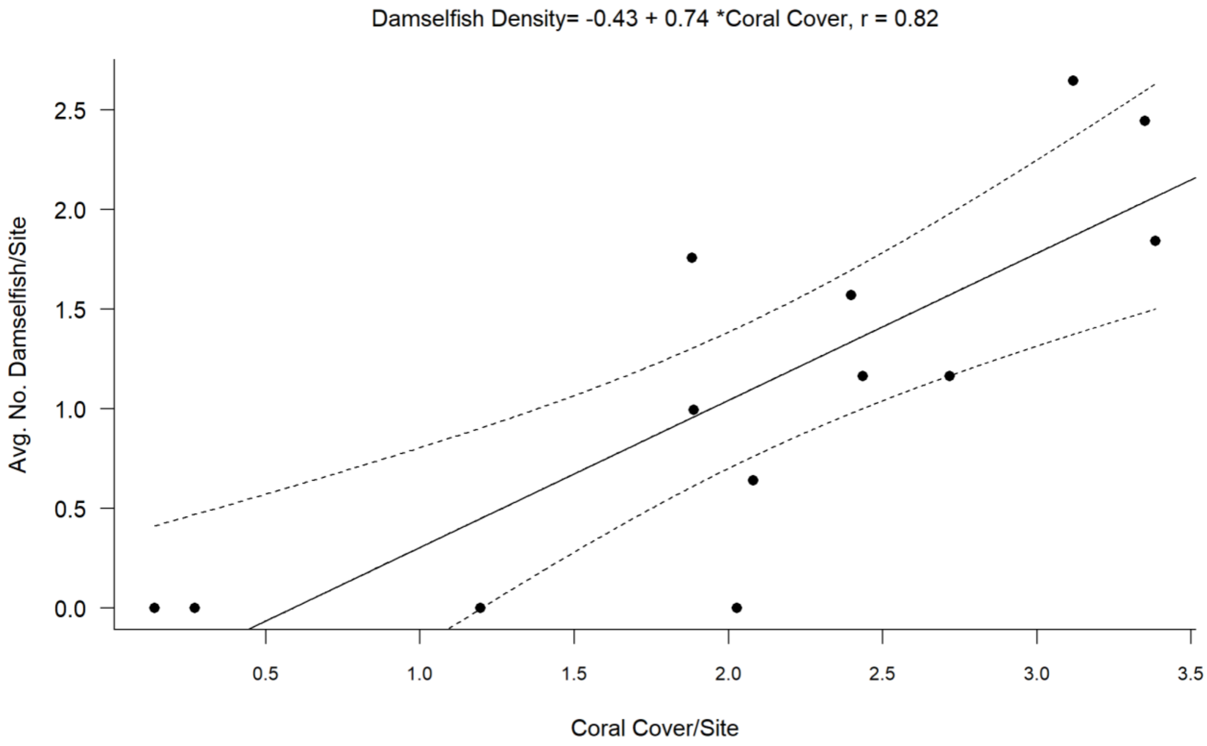

Figure 10. Positive relationship between average coral cover (cm²) and average number of damselfish per site.

5.0 Discussion

The purpose of this study was to contribute to the understanding of the predator-snail-coral relationship on coral reefs. Data from 20 Bahamian reef sites was used to analyze fish and lobster populations, *C. galea* density on a reef and on individual coral species, and coral cover. While the potential predatory impact of *Panulirus argus* on the snails was the focus at the start of this study, the only conclusion that was able to be ascertained through the aquarium studies was their lack of preference for a specific snail size. *Panulirus argus* numbers were small throughout all study sites preventing any analysis of their impacts on *C. galea* densities. There was a significant relationship between coral cover and *C. galea* density. The coral species found to have the strongest association to *C. galea* density included *Orbicella annularis* and *O. faveolata,* with snails being present on colonies of these species more often than expected. This indicates they are a likely food source. *Coralliophila galea* density was also directly related to *Diploria* *labyrinthiformis'* and *P. astreoides'* coral cover. Grazer and predatory fish populations were not significantly related to snail density. However, damselfish alone (*Stegastes planifrons* and *Microspathodon chrysurus*) showed a strong direct relationship with both coral cover on reef sites and *C. galea* density.

The potential for *P. argus* predation on *C. galea* was examined in both a wild and controlled aquarium environment. *Panulirus argus* was confirmed to feed on *C. galea* snails and had no preference for their size; however, I was unable to find enough *P. argus* on the reef to assess if this species could top-down control the snails. *Panulirus argus* was expected to have high potential for predation of *C. galea*. Cox et al. (1997) found that gastropods alone make up nearly 50% of *P. argus'* diet. Unfortunately, collecting sufficient data on *P. argus'* presence on each reef site proved challenging. The low sample size from only seven out of the 20 sites resulted in 15% of surveys with any recorded *P. argus*. Supplemental data was used from PIMS field work during the same time frame, however the numbers still proved to be insufficient to test associations. This could be attributed to lack of focused surveys or could just indicate that *P. argus* numbers are considerably lower than what was initially believed. *Panulirus argus'* impact on *C. galea* densities cannot be completely disregarded at this time and further studies should be performed. However, *P. argus* feeding trials performed here helped determine they will consume *C. galea* opportunistically without preference in size. Previously conducted field surveys had found that lobsters preferred smaller snails; specifically, the mean snail size increased from an average of 17.87 ±4.91mm to 19.28 ±5.45mm where higher *P. argus* densities were recorded (Shaver et al., 2020). However, both snail size averages fall into one of my size categories (10-20mm) indicating the size grouping used in this study may be too broad. Anecdotally, the limiting factor for *P. argus* to consume the snail seemed to relate to difficulties in cracking a *C. galea* outer shell. Often the lip of the shell was broken only, and after several minutes the lobster would drop the snail and search for other prey items. Based on the optimal foraging theory (MacArthur & Pianka, 1966), the energy required to consume *C. galea* vs. the energy received by consuming it may not be sufficient for *P. argus* to preferably consume it. Considering Shaver et al. (2020) did find that *P. argus* preyed on *C. galea* in the Florida Keys, my findings may, once again, simply reflect low densities of the lobster in the sites surveyed. Further studies are required to determine whether *P. argus* consistently consume *C. galea* in the wild reef ecosystems when potentially easier prey items are present.

The density of *C. galea* decreased with depth, and was directly related to coral cover, but not with coral diversity. The observed decreased *C. galea* densities with depth is likely an artifact of its strong direct relationship with coral cover, which also decreased with depth. Settlement cues may be involved to draw *C. galea* to coral reefs, but a higher coral diversity does not seem to influence their density. Since *C. galea* has been found on at least 25 different scleractinian species (Appendix 1), it is possible that a highly diverse reef is simply not required for the snails to find an adequate food source.

Snail density was positively related to the cover of *P. astreoides* and *D. labyrinthiformis*, but the significance was much higher in the latter. *Porites astreoides* was by far the most prevalent coral species, representing nearly 30% of the corals observed (Appendix 2), and was ubiquitous on all reef sites surveyed. Despite this coral's dominant presence, less than 0.25% of total *C. galea* was found on this species. The large number of *P. astreoides* colonies on all reef sites studied could explain why, despite not being a common food source for the snail, it was a good predictor of snail density. This coral species could simply be an indicator of high coral cover that, along with other coral-associated invertebrates, ultimately attracts settlement of *C. galea* (Stella et al., 2011). In contrast, snails were not found to be associated to the presence of *Diploria labyrinthiformis,* but *D. labyrinthiformis* cover was found to be a very good predictor of *C. galea* density despite its considerably lower contribution to coral cover (1.5%, Table 5). It is possible that this relationship is simply an artifact of a possible strong relationship between *D. labyrinthiformis* and coral cover. This species usually occurs in low density, has a slow growth rate (0.35±0.06 cm/yr) (Ghiold & Enos, 1982) and a low settlement success (Smith, 1992). Despite the lower settlement success, Smith (1992) noted that once settlement occurs, *D. labyrinthiformis* had lower mortality than other prominent coral species. In other words, *D. labyrinthiformis'* ability to settle and grow on a reef may make it a good proxy for coral cover and health, which should boost *C. galea* settlement.

The strong positive associations between *Orbicella faveolata* and *O. annularis* colonies and *C. galea* density suggest these are preferential food for the snail. Of the thirty-nine coral species documented, fifteen hosted *C. galea* snails within the study area. Within these fifteen, over 80% of all snails were found on *O. faveolata* and *O. annularis* (Appendix 2). This positive association is not entirely surprising based on anecdotal evidence in the field that these two species are a preferred food source for *C. galea*. *Coralliophila galea* were consistently found along the edges of healthy tissue or inside tight crevices the corals naturally form which is consistent with other studies (Hayes, 1990; Baums et al., 2003b). It is possible that the crevices provide for a more protected habitat allowing for the snail to go relatively unnoticed from potential predators. This could also help explain why *C. galea* density on orbicellids was higher than other many other coral species.

The main fish families suspected to have an impact on *C. galea* as predators included Balistidae (triggerfish), Labridae (wrasses), and Tetraodontidae (pufferfish). However, these families, or any other predatory fish families, were not seen to have any significant relationship with *C. galea* abundance. One study did find that the presence of *P. argus* and the black margate (*Anisotremus surinamensis*) helped control *C. galea* numbers (Shaver et al., 2020). However, in this study, neither species was observed at high density (*P. argus*) or seen at all (*A. surinamensis*). The difference in results for these studies may simply be an indicator of differences in fish populations between the Florida Keys and The Bahamas. An unexpected finding related to fish populations, however, was observed regarding Pomacentridae, or damselfish (*Stegastes planifrons* and *Microspathodon chrysurus*). The positive relationship between damselfish and snail density may be explained by this species' algae "farming". It is well documented that damselfish often "farm" on corals forming algal mats or "gardens" (Gibson et al., 2001; Hata et al., 2010). This damages the coral they are farming causing the coral to become stressed. Since stressed corals are known to attract *C. galea* in a higher frequency than healthy or non-stressed corals (Bright et al., 2015), it is possible that the "farming" technique of damselfish allows for a higher stress rate amongst corals which then leads to greater *C. galea* densities on a reef. It is also worth noting that there was a significant positive association between damselfish and coral cover possibly indicating that both damselfish and *C. galea* have similar cues/associations/dependence on corals leading them to high coral cover reefs. One study in the Great Barrier Reef found the most preferred coral species for damselfish habitat were also the most commonly consumed corals for *Acanthaster plancii* (Pratchett et al., 2012) possibly indicating a similar link could exist between *C. galea* and Caribbean damselfish populations. Another potential explanation could be that predators for both species are absent resulting in higher numbers for both species. While damselfish populations seem to be a good predictor of *C. galea* density, it is possible damselfish are simply good predictors of coral cover, which is correlated to snail density. Further studies will need to be done to determine if this relationship is direct or purely correlational.

Coral reefs are, without question, affected by a multitude of stressors (Clark & Edwards, 1995; Aronson & Precht, 2001; Becker & Mueller, 2001; Soong & Chen, 2003; Jackson et al., 2014). With a few exceptions (e.g. *Acanthasther planci* in the Indo-Pacific, Birkeland & Lucas, 1990), the effect of corallivores on reefs has often been overlooked. The impact of corallivores like *C. galea* can, however, be very deleterious for coral reefs (Knowlton et al., 1990). The snail prevalence has been a limiting factor for coral colonies, often inhibiting their recovery and growth (Sharp & Delgado, 2015), but not a lot of focus has been placed on them directly. The dynamic between coral and snail remains poorly studied, but discerning what predators may control *C. galea* will add to our understanding of this dynamic. While this research provided some much-needed answers to better understand the relationship of predator-snail-coral dynamics on a coral reef ecosystem, it also opened the door for more questions. The orbicellid relationship with *C. galea* was expected seeing as how frequently the snail was found on both species. It would be interesting to conduct further surveys on coral reefs with more substantial acroporid colonies. While *Acropora* spp. has been documented as suffering high damage from *C. galea* (Miller, 2001; Bruckner et al., 1997; Baums et al., 2003b), Acroporids were only found on few of the reef sites surveyed and in small numbers, thus it is very likely that the data was not sufficient to assess their relationship to *C. galea*. However, even with the low *A. cervicornis* coral cover observed, nearly 14% of the colonies were found with *C. galea* (Appendix 2). This was the third highest representation of coral species found with snails, adding more weight to the relevance of this genus in relation to *C. galea*. The lab studies with *P. argus* represent a start to the understanding of the role of potential predators on *C. galea* and how these may help reduce corallivore numbers and their impact on the reefs. This study confirmed that *P. argus* prey on *C. galea* if given the opportunity, but they do not necessarily have a preference in snail size. This helps clarify the implications of *P. argus'* feeding behaviors. However, further research remains to be done to determine to what extent, if any, fish and invertebrates prey on the gastropod and the effect this predation has upon *C. galea* numbers. Future efforts in coral reef restoration, fishing regulations and management, and ecotourism can only be improved upon with this supplemental research. A better understanding of the top-down control of corallivores and coral reef dynamics, particularly within the ECLSP, are beneficial for not only future research, but also to improve on MPA monitoring and enforcement to ensure continued success for these protected areas. While still insufficient, this study will hopefully contribute to understanding the interactions among corals, corallivores, and their predators, and can be used as a guide to future research.

Appendix

A.2. Side by side comparison of 25 scleractinian coral species found with any *C. galea* from this study (19 species) and Miller, 1981 (14 species). (Note: *Species not observed with *C. galea* during quantitative surveys but were seen with *C. galea* on non-surveyed corals. **Species was classified as *Montastraea annularis* COMPLEX at time of study.)

Coral Species	***Coralliophila galea* Present Y/N**	
	This Study	**Miller, 1981**
Acropora cervicornis	Y	Y
Acropora palmata	Y*	Y
Agaricia agaricites	Y	Y
Colpophyllia natans	Y	N
Dichocoenia stokesii	N	Y
Diploria labyrinthiformis	Y	Y
Favia fragum	N	Y
Helioceris cuculatta	N	Y
Isophyllia sinuosa	Y	N
Madracis decactis	Y	N
Meandrina meandrites	Y*	N
Montastraea cavernosa	Y	N
Mussa angulosa	N	Y
Mycetophyllia spp.	Y	Y
Orbicella annularis	Y	Y
Orbicella faveolata	Y	**
Porites astreoides	Y	Y
Porites porites	Y	N
Pseudodiploria clivosa	*	Y
Pseudodiploria strigosa	Y*	Y
Siderastrea radians	N	Y
Siderastrea siderea	Y*	N
Solenastrea bournoni	Y	N
Scolymia cubensis	Y	N
Stephanocoenia intersepta	Y	N

A.2. Collected survey data from all 20 sites to include 23,937 individual coral colonies and 1,357 *C. galea*. (Note: *Madracis spp*. includes: *M. auretenra*, *M. formosa* and *M. senaria*; *Mycetophyllia* spp. includes: *M. aliciae*, *M. ferox*, and *M. lamarckiana*; *Porites porites* COMPLEX includes: *P. porites*, *P. furcata*, and *P. divaricata*.)

Coral Species	**No. Observed Corals**	**No. *C. galea***	**Percentage of Coral Species Observed**	**Percentage of Colonies Observed w/ *C. galea***	**Percentage of Total *C. galea* found per Coral Species**
Acropora cervicornis	22	4	0.1%	13.6%	0.3%
Acropora palmata	8	0	0.0%	0.0%	0.0%
Acropora prolifera	1	0	0.0%	0.0%	0.0%
Agaricia agaricites	3480	126	14.5%	2.6%	9.3%
Agaricia fragilis	5	0	0.0%	0.0%	0.0%
Agaricia humilis	2	0	0.0%	0.0%	0.0%
Agaricia lamarcki	57	0	0.2%	0.0%	0.0%
Colpophyllia natans	73	30	0.3%	9.6%	2.2%
Dendrogyra cylindrus	5	0	0.0%	0.0%	0.0%
Dichocoenia stokesii	213	0	0.9%	0.0%	0.0%
Diploria labyrinthiformis	359	58	1.5%	3.3%	4.3%
Eusmilia fastigiata	506	0	2.1%	0.0%	0.0%
Favia fragum	7	0	0.0%	0.0%	0.0%
Helioceris cucullata	84	0	0.4%	0.0%	0.0%
Isophyllastrea rigida	12	0	0.1%	0.0%	0.0%
Isophyllia sinuosa	7	2	0.0%	14.3%	0.1%
Madracis spp.	288	0	1.2%	0.0%	0.0%
Madracis decactus	262	1	1.1%	0.4%	0.1%
Manicina areolata	119	0	0.5%	0.0%	0.0%
Meandrina jacksoni	29	0	0.1%	0.0%	0.0%
Meandrina meandrites	360	0	1.5%	0.0%	0.0%
Montastraea cavernosa	1301	19	5.4%	0.4%	1.4%
Mycetophyllia spp.	189	9	0.8%	0.0%	0.7%
Mussa angulosa	33	0	0.1%	0.0%	0.0%
Orbicella annularis	412	260	1.7%	18.4%	19.2%
Orbicella faveolata	3130	839	13.1%	8.7%	61.8%
Porites astreoides	7097	3	29.7%	0.1%	0.2%
Porites porites COMPLEX	1821	3	7.6%	0.0%	0.0%
Pseudodiploria strigosa	50	0	0.2%	0.0%	0.0%
Scolymia cubensis	16	1	0.1%	6.3%	0.1%
Siderastrea siderea	3217	1	13.4%	0.0%	0.1%
Solenastrea bournoni	418	2	1.7%	0.2%	0.1%
Stephanocoenia intersepta	354	1	1.5%	0.3%	0.1%

Project Funding

The work of this thesis was provided by a private grant through Bruce Purdy and All Star Liveaboards and The Perry Institute of Marine Science as part of the “Reversing the Decline of Bahamian Coral Reefs” program.

Acknowledgments

First, I would like to thank my committee members: Dr. Joana Figueiredo, Dr. Craig Dahlgren, and Dr. David Gilliam for all of their guidance, support and extreme patience. I am also very thankful for the endless time and resources provided to me by the Perry Institute for Marine Science, Bruce Purdy and the All-Star Liveaboard crew, as well as Atlantis, Paradise Island staff in The Bahamas. In particular, I am very appreciative of Captains Des Greyling, Carlis Harrell, and Ron McCaslin for the extra effort they went through to get me to the sites I needed amongst a dive boat full of vacationing divers; and my lab mate and friend, Abby Evans, for joining me on two trips to help collect extra data. Lastly, I would like to thank my parents. Without their support I would not have had the time and endurance to complete this research. I can never repay you for everything you have done and continue to do for me.

References

Armstrong, Shannon. "The Status of the Coral Predator *Drupella cornus* at Ningaloo Marine Park." *Department of Environment and Conservation, The Government of Western Australia. p* 18 (2009).

Aronson, Richard B., and William F. Precht. "White-Band Disease and the Changing Face of Caribbean Coral Reefs." *The Ecology and Etiology of Newly Emerging Marine Diseases* (2001): 25-38.

Barnes, Margaret. "The Acanthaster Phenomenon." *Oceanography And Marine Biology* (1986): 379.

Baums, Iliana B., Margaret W. Miller, and Alina M. Szmant. "Ecology of a Corallivorous Gastropod, *Coralliophila abbreviata*, on Two Scleractinian Hosts. I: Population Structure of Snails and Corals." *Marine Biology* 142 (2003a): 1083-1091.

Baums, I. B., M. W. Miller, and A. M. Szmant. "Ecology of a Corallivorous Gastropod, *Coralliophila abbreviata*, on Two Scleractinian Hosts. II. Feeding, Respiration and Growth." *Marine Biology* 142 (2003b): 1093-1101.

Becker, Lillian C., and Erich Mueller. "The Culture, Transplantation and Storage of *Montastraea faveolata*, *Acropora cervicornis* and *Acropora palmata*: What We Have Learned So Far." *Bulletin of Marine Science* 69, no. 2 (2001): 881-896.

Birkeland, Charles, and John Lucas. *Acanthaster planci: Major Management Problem of Coral Reefs*. CRC press, 1990.

Bright, Allan J., Caitlin M. Cameron, and Margaret W. Miller. "Enhanced Susceptibility to Predation in Corals of Compromised Condition." *PeerJ* 3 (2015): e1239.

Bruckner, R. J., A. W. Bruckner, and E. H. Williams Jr. "Life History Strategies of *Coralliophila abbreviata* Lamarck (Gastropoda: Coralliophilidae) on the Southwest Coast of Puerto Rico." In *Proc 8th Int Coral Reef Symp*, vol. 1, pp. 627-632. 1997.

Bouchet, Philippe, Jiří Frýda, B. Hausdorf, W. Ponder, A. Valdés, and A. Warén. "Classification and Nomenclator of Gastropod Families." (2005): 85-397.

Carpenter, Robert C. "Invertebrate Predators and Grazers." *Life and Death of Coral Reefs. Chapman and Hall, New York* (1997): 198-229.

Clark, S., and A. J. Edwards. "Coral Transplantation as An Aid to Reef Rehabilitation: Evaluation of a Case Study in the Maldive Islands." *Coral reefs* 14 (1995): 201-213.

Cox, Carrollyn, John H. Hunt, William G. Lyons, and Gary E. Davis. “Nocturnal Foraging of the Caribbean Spiny Lobster (*Panulirus argus*) on Offshore Reefs of Florida, USA.” *Marine and Freshwater Research* 48, no. 8 (1997): 671-680.

Ghiold, Joe, and Paul Enos. "Carbonate Production of the Coral *Diploria labyrinthiformis* in South Florida Patch Reefs." *Marine Geology* 45, no. 3-4 (1982): 281-296.

Gibson, R. N., Margaret Barnes, and R. J. Atkinson. "Territorial Damselfishes as Determinants of the Structure of Benthic Communities on Coral Reefs." *Oceanography and Marine Biology: An Annual Review* 39 (2001): 355-89.

Gignoux-Wolfsohn, S. A., Christopher J. Marks, and Steven V. Vollmer. "White Band Disease Transmission in the Threatened Coral, *Acropora cervicornis*." *Scientific reports* 2, no. 1 (2012): 1-3.

Goldberg, Walter M. "A Note on the Feeding Behavior of the Snapping Shrimp *Synalpheus fritzmuelleri* Coutière (Decapoda, Alpheidae)." *Crustaceana* 21, no. 3 (1971): 318-320.

Hata, Hiroki, Katsutoshi Watanabe, and Makoto Kato. "Geographic Variation in the Damselfish-Red Alga Cultivation Mutualism in the Indo-West Pacific." *BMC Evolutionary Biology* 10, no. 1 (2010): 1-10.

Hayes, Joshua Austin. *The Biology and Ecology of Coralliophila abbreviata Lamarck (Gastropoda: Coralliophilidae): The Importance of Corallivores in the Ecology of Coral Reefs*. The University of Texas at Austin, 1989.

Hayes, Joshua A. "Distribution, Movement and Impact of the Corallivorous Gastropod *Coralliophila abbreviata* (Lamarck) on a Panamanian Patch Reef." *Journal of Experimental Marine Biology and Ecology* 142, no. 1-2 (1990): 25-42.

Jackson, Jeremy, Mary Donovan, Katie Cramer, and Vivian Lam. *Status and Trends of Caribbean Coral Reefs: 1970-2012*. Gland, Switzerland: Global Coral Reef Monitoring Network; International Union for the Conservation of Nature (IUCN), 2014.

Johnston, Lyza, and Margaret W. Miller. "Variation in Life-History Traits of the Corallivorous Gastropod *Coralliophila abbreviata* on Three Coral Hosts." *Marine Biology* 150 (2007): 1215-1225.

Johnston, Lyza, Margaret W. Miller, and Iliana B. Baums. "Assessment of Host-Associated Genetic Differentiation Among Phenotypically Divergent Populations of a Coral-Eating Gastropod Across the Caribbean." *PLoS One* 7, no. 11 (2012): e47630.

Kamerman, T.Y. Personal observations. October 2014.

Knowlton, Nancy, Judith C. Lang, and Brian D. Keller. "Case Study of Natural Population Collapse: Post-Hurricane Predation on Jamaican Staghorn Corals." (1990).

Knowlton, Nancy, Judith C. Lang, M. Christine Rooney, and Patricia Clifford. "Evidence for Delayed Mortality in Hurricane-Damaged Jamaican Staghorn Corals." *Nature* 294, no. 5838 (1981): 251-252.

Lang, J.C., K.W. Marks, P.A. Kramer, P.R. Kramer, and R.N. Ginsburg. 2010rev. AGRRA PROTOCOLS VERSION 5.4

Lipcius, Romuald N., William T. Stockhausen, and David B. Eggleston. "Marine Reserves for Caribbean Spiny Lobster: Empirical Evaluation and Theoretical Metapopulation Recruitment Dynamics." *Marine and Freshwater Research* 52, no. 8 (2001): 1589-1598.

MacArthur, Robert H., and Eric R. Pianka. "On Optimal Use of a Patchy Environment." *The American Naturalist* 100, no. 916 (1966): 603-609.

McClanahan, T. R. "Coral-Eating Snail *Drupella cornus* Population Increases in Kenyan Coral Reef Lagoons." *Marine Ecology Progress Series* (1994): 131-137.

Mendonça, Vanda Mariyam, Musallam Mubarak Al Jabri, Ibrahim Al Ajmi, Mohamed Al Muharrami, Mohamed Al Areimi, and Hussain Ali Al Aghbari. "Persistent and Expanding Population Outbreaks of the Corallivorous Starfish *Acanthaster planci* in the Northwestern Indian Ocean: Are They Really a Consequence of Unsustainable Starfish Predator Removal Through Overfishing in Coral Reefs, or a Response to a Changing Environment." *Zool Stud* 49, no. 1 (2010): 108-123.

Miller, Alan C. "Cnidarian Prey of the Snails *Coralliophila abbreviata* and *C. caribaea* (Gastropoda: Muricidae) in Discovery Bay, Jamaica." *Bulletin of Marine Science* 31, no. 4 (1981): 932-934.

Miller, M. W. "Corallivorous Snail Removal: Evaluation of Impact on *Acropora palmata*." *Coral Reefs* 19 (2001): 293-295.

Miller, Margaret Wohlenberg, Iliana Baums, Dana Elizabeth Williams, and Alina Szmant-Froelich. "Status of Candidate Coral, *Acropora palmata*, and Its Snail Predator in the Upper Florida Keys National Marine Sanctuary, 1998-2001." (2002).

Morton, Brian, Graham Blackmore, and C. T. Kwok. "Corallivory and Prey Choice by *Drupella rugosa* (Gastropoda: Muricidae) in Hong Kong." *Journal of Molluscan Studies* 68, no. 3 (2002): 217-223.

Mumby, Peter J., Craig P. Dahlgren, Alastair R. Harborne, Carrie V. Kappel, Fiorenza Micheli, Daniel R. Brumbaugh, and Katherine E. Holmes. "Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs." *Science* 311, no. 5757 (2006): 98-101.

Mumby, Peter J., Alastair R. Harborne, Jodene Williams, Carrie V. Kappel, Daniel R. Brumbaugh, Fiorenza Micheli, Katherine E. Holmes, Craig P. Dahlgren, Claire B. Paris, and Paul G. Blackwell. "Trophic Cascade Facilitates Coral Recruitment in a Marine Reserve." *Proceedings of the National Academy of Sciences* 104, no. 20 (2007): 8362-8367.

Pratchett, Morgan S., Darren J. Coker, Geoffrey P. Jones, and Philip L. Munday. "Specialization in Habitat Use by Coral Reef Damselfishes and Their Susceptibility to Habitat Loss." *Ecology and Evolution* 2, no. 9 (2012): 2168-2180.

Sharp, William C., and Gabriel A. Delgado. "Predator-Prey Interactions Between the Corallivorous Snail *Coralliophila abbreviata* and the Carnivorous Deltoid Rock Snail *Thais deltoidea*." *The Biological Bulletin* 229, no. 2 (2015): 129-133.

Shaver, Elizabeth C., Julianna J. Renzi, Maite G. Bucher, and Brian R. Silliman. "Relationships Between a Common Caribbean Corallivorous Snail and Protected Area Status, Coral Cover, and Predator Abundance." *Scientific Reports* 10, no. 1 (2020): 16463.

Shears, Nick T., and Russell C. Babcock. "Marine Reserves Demonstrate Top-Down Control of Community Structure on Temperate Reefs." *Oecologia* 132 (2002): 131-142.

Smith, S. R. "Patterns of Coral Recruitment and Post-Settlement Mortality on Bermuda's Reefs: Comparisons to Caribbean and Pacific Reefs." *American Zoologist* 32, no. 6 (1992): 663-673.

Soong, Keryea, and Tai-an Chen. "Coral Transplantation: Regeneration and Growth of *Acropora* Fragments in a Nursery." *Restoration Ecology* 11, no. 1 (2003): 62-71.

Stella, Jessica, Morgan Pratchett, Pat Hutchings, and Geoffrey Jones. "Coral-Associated Invertebrates." *Oceanography and Marine Biology* (2011).

Sutherland, Kathryn Patterson, James W. Porter, Jeffrey W. Turner, Brian J. Thomas, Erin E. Looney, Trevor P. Luna, Meredith K. Meyers, J. Carrie Futch, and Erin K. Lipp. "Human Sewage Identified as Likely Source of White Pox Disease of the Threatened Caribbean Elkhorn Coral, *Acropora palmata*." *Environmental Microbiology* 12, no. 5 (2010): 1122-1131.

Sweatman, Hugh. "No-Take Reserves Protect Coral Reefs From Predatory Starfish." *Current Biology* 18, no. 14 (2008): R598-R599.

Turner, Stephanie J. "The Biology and Population Outbreaks of the Corallivorous Gastropod *Drupella* on Indo-Pacific Reefs." *Oceanography and Marine Biology: An Annual Review* (1994).

Ward, Jonet. "The Digestive Tract and Its Relation to Feeding Habits in the Stenoglossan Prosobranch *Coralliophila abbreviata* (Lamark)." *Canadian Journal of Zoology* 43, no. 3 (1965): 447-464.

Williams, Dana E., and Margaret W. Miller. "Coral Disease Outbreak: Pattern, Prevalence and Transmission in *Acropora cervicornis*." *Marine Ecology Progress Series* 301 (2005): 119-128.

Williams, Dana E., Cait Cameron, and Margaret W. Miller. *Interim Report on Effectiveness of Corallivorous Snail Removal*. PRBD--2011--11. US National Marine Fisheries Service 10, 2011.

Wolf, Alexander T., and Maggy M. Nugues. "Synergistic Effects of Algal Overgrowth and Corallivory on Caribbean Reef-Building Corals." *Ecology* 94, no. 8 (2013): 1667-1674.

Worm, Boris, and Ransom A. Myers. "Meta-Analysis of Cod–Shrimp Interactions Reveals Top-Down Control in Oceanic Food Webs." *Ecology* 84, no. 1 (2003): 162-173.