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# Post Disturbance Coral Populations: Patterns in Live Cover and Colony Size Classes from Transect Studies in Two Oceans

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**POST DISTURBANCE CORAL POPULATIONS: PATTERNS IN LIVE  
COVER AND COLONY SIZE CLASSES FROM TRANSECT STUDIES IN  
TWO OCEANS**

By

**Claire A. Dolphin**

Submitted to the Faculty of  
Nova Southeastern University Oceanographic Center  
in partial fulfillment of the requirements for  
the degree of Master of Science with a specialty in:  
Marine Biology

Nova Southeastern University

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**Thesis of**  
**Claire A. Dolphin**

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Nova Southeastern University  
Oceanographic Center

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## **Abstract**

This study analyzes data acquired in French Polynesia in the Pacific and The Bahamas (Atlantic), both oceans affected by recent, well documented and sequential disturbances. For the purposes of this study, a disturbance is defined as a perturbation of environmental, physical or biological conditions that causes a distinct change in the ecosystem. After several decades of coral bleaching events, biological change, and anthropogenic impacts, rapid assessments of the coral community were accomplished by collecting photo-transects across the reefs to extract size structure of the corals, percent live tissue cover and perform a faunal evaluation. Cluster analyses and spatial autocorrelation tests were done to examine the community structure and dynamics at both locations. All multivariate analyses pointed to a disturbed ecosystem and the lack of spatial correlation indicated the impact of a local disturbance over that of a regional event. In assessing the spatial coral community structure, different responses to large versus small scales of disturbance were found. This emphasizes the importance of tailoring management of coral reefs to specific impacts. These two distinct regions were shown to have correlated spatial response patterns to sequential disturbances, supporting the idea of community pattern signatures for different scales of disturbance and the need for an adjustment in management protocols.

**Keywords:** population dynamics, size frequency distributions, coral community patterns, ecological disturbance, spatial correlation

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*This thesis is dedicated in whole to the late David Harder Mitchell for his love of life, nature and the world around him*

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## **1 Introduction**

Previous environmental conditions can significantly influence the outcome of a coral community's response and success (Maina et al. 2008). For the purposes of this study, a disturbance is defined as a perturbation of environmental, physical or biological conditions that causes a distinct change in the make-up of organismic populations.

Different types of disturbance have varying impacts on coral reefs (Vermeji and Bak 2000; Pratchett et al. 2011), can be of natural or of anthropogenic origin, and have region-wide or more localized effects. Investigating these impacts can provide important insight into ecological mechanisms of recovery and their controls (Hughes et al. 2010).

The population structure of corals via their size distribution reflects the intensity and frequency of disturbances through partial or total mortality of coral tissue (Zvuloni et al. 2008). By extension, the community composition is therefore sensitive to frequency and spatial distribution of disturbances and their impacts as well (Riegl and Purkis 2009). Many (Vermeji and Bak 2000; Bak and Meesters 1998; Meesters et al. 2001; Adjerdoud et al. 2007; Penin et al. 2007; Hughes 1984) have studied specific coral genera and their population size structures in response to disturbances and have come to the conclusion that it is necessary to consider population dynamics, not just patterns of abundance, as expressed by measures of living coral cover. Population dynamics encompasses reproduction, recruitment, settlement, growth and mortality (Van Woesik and Jordan-Garza 2011) and is therefore often itself a product of the size structure of coral colonies (Bak and Meesters 1999). Therefore, studies of quantitative variables such as size classes of corals and their distribution over species can help to understand the mechanisms and responses to disturbances which can vary from small scale, such as local



predation or isolated coral disease, to large-scale processes such as bleaching and storms (Van Woesik and Jordan-Garza 2011; Meesters et al. 2001).

In the present study, the analysis of population-level measurements, such as size-structure, is employed to draw inferences about the disturbance history and recovery dynamics of coral populations at several sites with a documented different past. Two regions are surveyed, the Society Islands of French Polynesia in the South Pacific and the Bahamas in the Caribbean of the mid- Atlantic. In the Caribbean, communities that presumably show region-wide or large scale structure decline may lead to a high spatial correlation among coral populations (Hughes 1994; Miller et al. 2000; Nystrom et al. 2000), and in the South Pacific more localized impacts will exhibit a lower spatial correlation among coral populations (Penin et al. 2007; Berumen and Pratchett 2006). It is therefore valuable to assess impacts, or lack thereof, with different metrics based on population structure (size-frequency), community dynamics (cover) and their distribution in reference to space on the reef.

In assessing these populations, it is hypothesized that if a reef were affected by local impacts such as predation or isolated disease, coral cover will be low; size distributions will be skewed towards small corals and also spatially correlated. Region-wide impacts such as storms or bleaching would have varying size distributions and would not exhibit spatial correlation. The aim of this study was to address the questions- Are the signatures of within reef (local) versus between reef (regional) disturbance detectable through examination of colony size classes and their live tissue cover? This aim is assessed at two distinct regions in the Atlantic and the Pacific where both regions differ in coral health and diversity. The motivation for this study is in discovering if the

aforementioned disturbance signatures do exist, for which they can be used as a tool to reconstruct the disturbance history of a coral reef ecosystem allowing us to place current environmental impacts in a historical context.

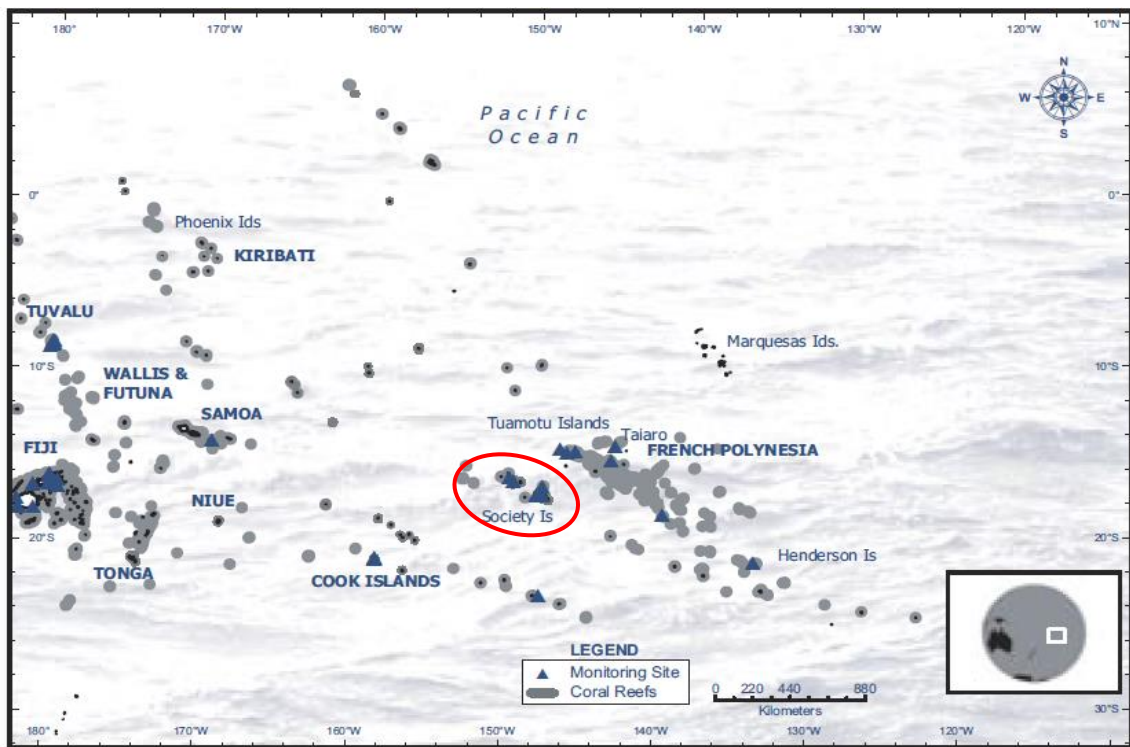
## **2 Study Sites**

### 2.1 FRENCH POLYNESIA

French Polynesia consists of several groups of islands, with the Society Islands being the most populated. Figure 1.1 shows the location of the Society Islands where half of the data to be considered was collected. As part of the Southeastern Pacific, French Polynesia has been subject to extensive predation by *Acanthaster planci* (crown of thorns starfish) and coral bleaching in the past few decades (Salvat 2002). Tourism is a large industry, incorporating the black pearl oyster culture as a major economic contributor. Most damage to the coral reefs is recorded around more the populated islands such as Moorea and Tahiti, often limiting our knowledge (Salvat, 2002).

Over the last three decades there have been seven bleaching events in French Polynesia, all of which largely impacted the Society Islands (Pratchett et al., 2011; Penin et al., 2012; Salvat, 2002). In the South Pacific, the most recent and widespread disturbances recorded have been natural, i.e. *Acanthaster planci* outbreaks and cyclones. *Acanthaster* outbreaks often lead to a shift in community structure, causing disproportionate losses of functional groups such as branching corals (Pratchett et al. 2011). Branching corals are important for habitat complexity which provides the local fish species with habitat, nursing grounds and protection (Graham and Nash 2013). When

considering storm damage, more widespread damage is evident. Instead of a coral assemblage or structure shift, the actual framework and rugosity of the reef is often destroyed and recovery from this type of destruction will take considerably longer (Dollar and Tribble, 1993; Trapon et al., 2011).

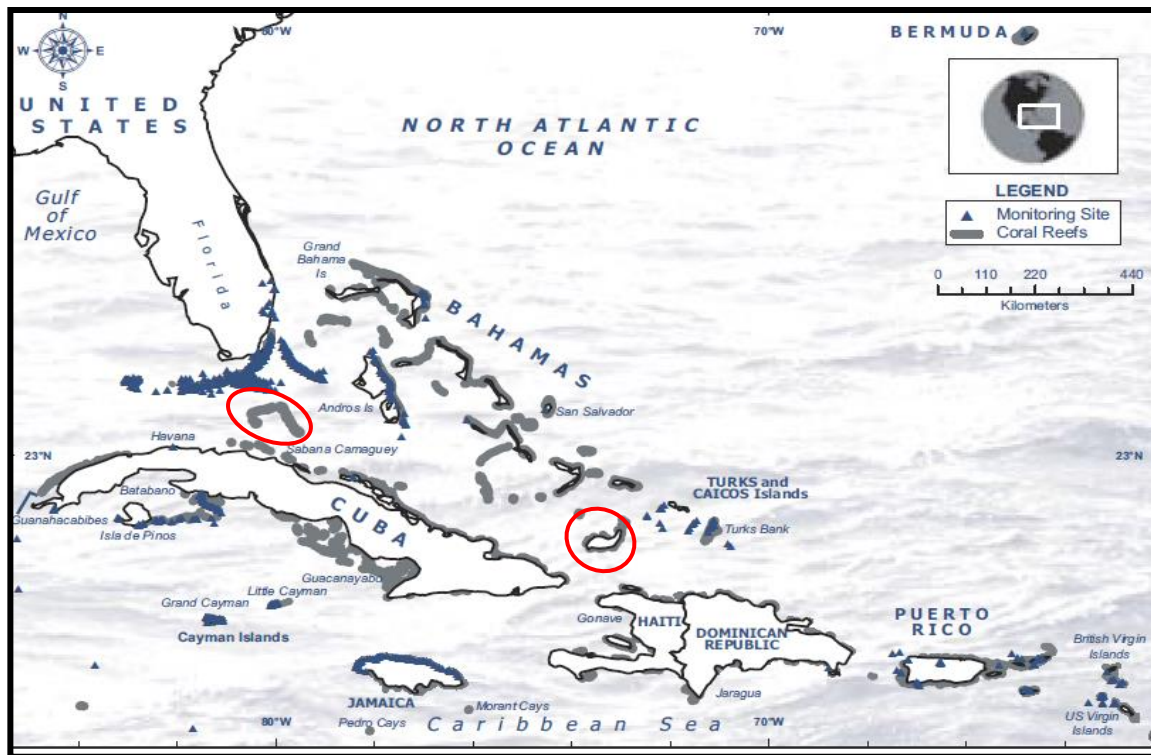


**FIGURE 1.1** Location of the Society Islands within French Polynesia where half of the data for this study was collected; Global Coral Reef Monitoring Network (GCRMN) Status Report of Southeast and Central Pacific Coral Reefs ‘Polynesia Mana Node’ (Salvat, 2002).

## 2.2 CARIBBEAN

Large scale marine disturbances in the Caribbean have steadily increased in the last 30 years (Williams and Bunkley-Williams 2000; Roff and Mumby 2012). The Caribbean region has the greatest number and severity of major marine ecological disturbances than any other region (Zimmerman et al., 1996; Williams and Bunkley-Williams, 2000; Jones et al., 2004). The Bahamas, like other Caribbean countries, face the challenge of losing important ecosystem services such as fisheries, tourism attractions and shoreline protection with the increasing degradation of the coral reef communities (Jones et al., 2004; Williams and Bunkley-Williams, 2000).

In the Caribbean, there are extensive data of overwhelming anthropogenic impacts coupled with natural impacts that have caused major damage to reefs throughout the region (Hughes & Connell, 1999; Bak and Meesters, 1999; Van Woesik and Jordan-Garza, 2011). When extensive disturbances occur with little chance for recovery, coral reef communities can shift to alternative states of complexity of taxonomic composition (Hughes, 1994; Aronson et al., 2004). Alternative states often cannot be reversed and are encouraged by sequential stressors (Hughes et al., 2010; Hughes, 1994; Van Woesik and Jordan-Garza, 2011).



**FIGURE 1.2** Location of the Bahamian Islands within the Caribbean where half of the data for this study was collected; GCRMN Status Report of Coral Reefs in the Northern Caribbean and Western Atlantic Node of the GCRMN (Jones et al., 2004).

### 3. Methodology

#### 3.1 SITE SELECTION

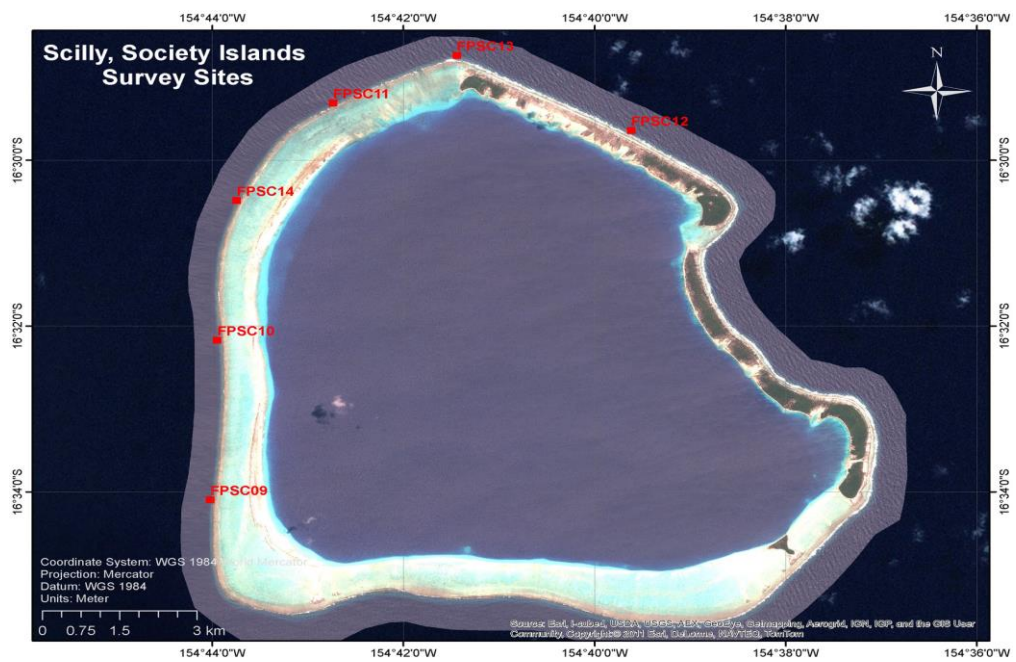
Sites for this study were situated in French Polynesia and the Bahamas. Reef locations and dive sites to be observed during field work were pre-selected by aerial reconnaissance of the islands. The reconnaissance was performed aboard a Cessna seaplane to survey the marine habitats and associated conditions across the islands.



**FIGURE 3.1** Tupai, red dot indicates survey site

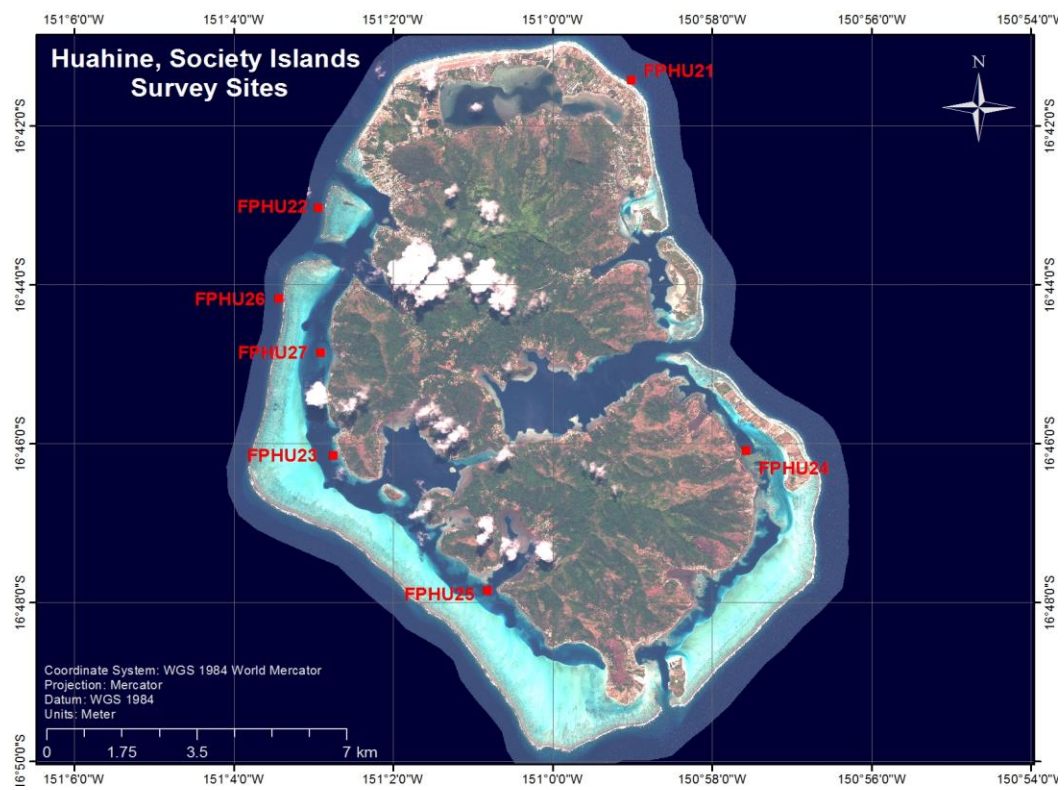


**FIGURE 3.2** Bellingshausen, red dot indicates survey site



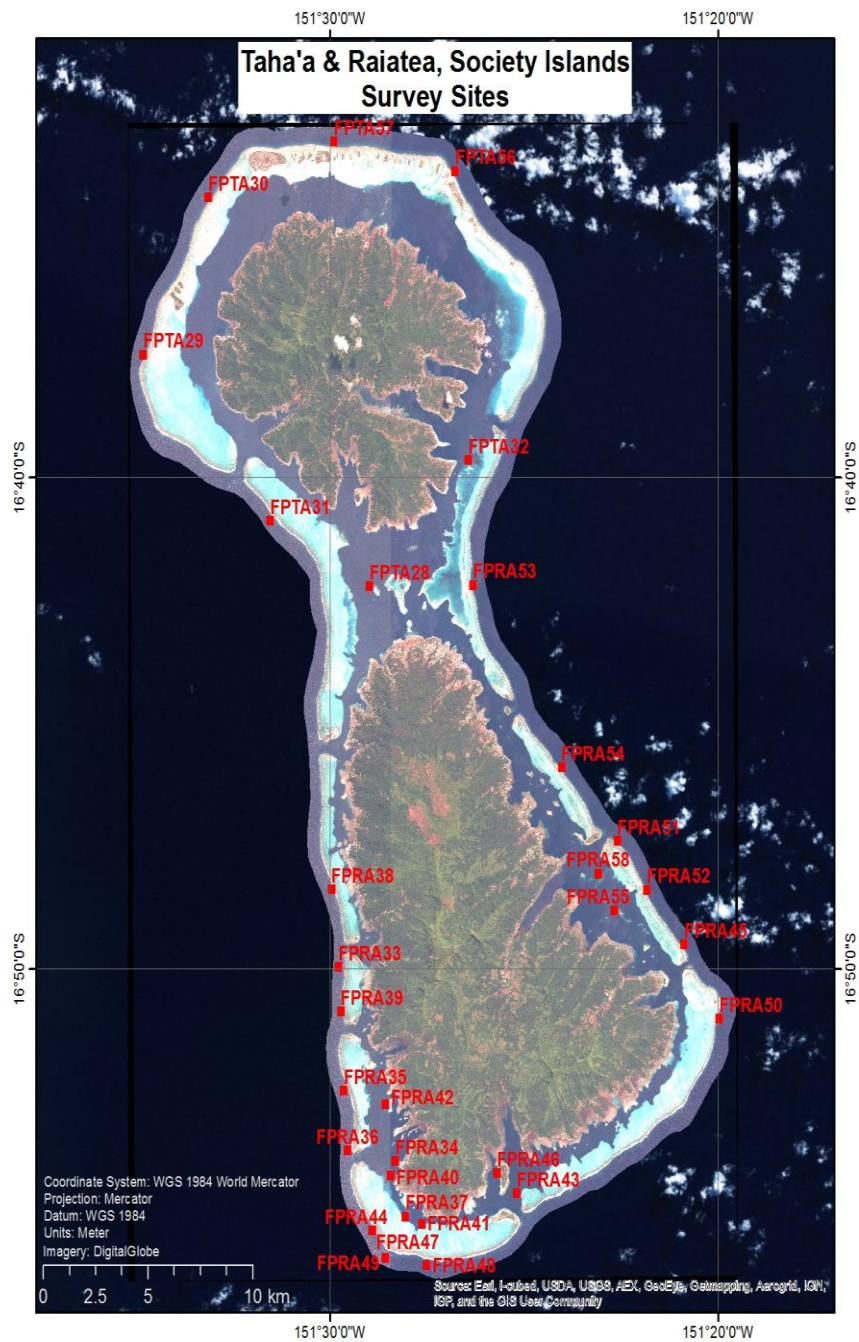
**FIGURE 3.3** Scilly, red dot indicates survey site



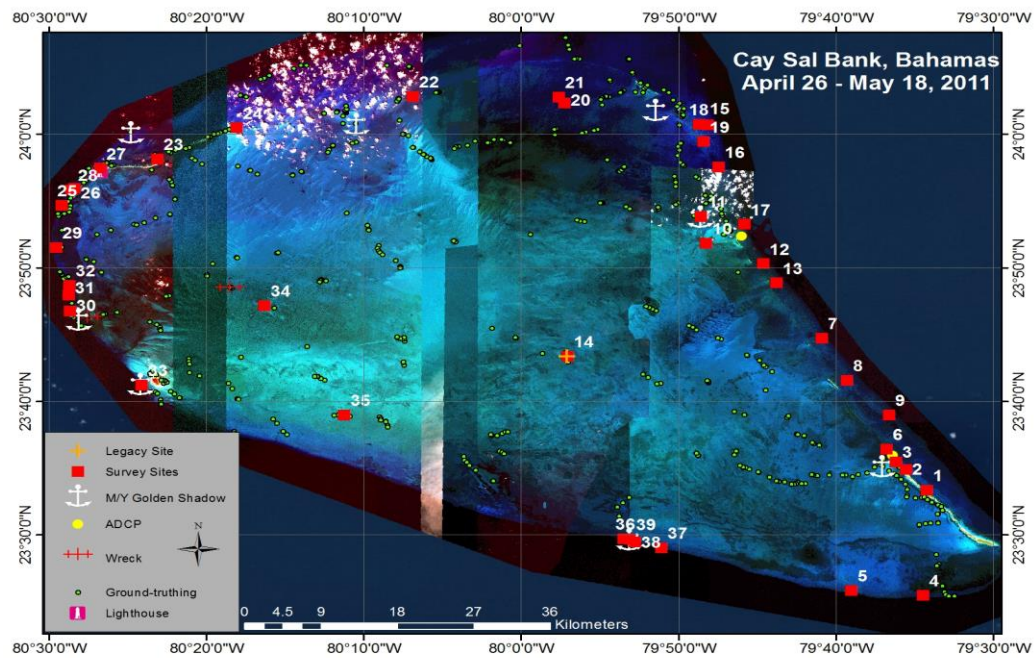


**FIGURE 3.4** Huahine, red dot indicates survey site

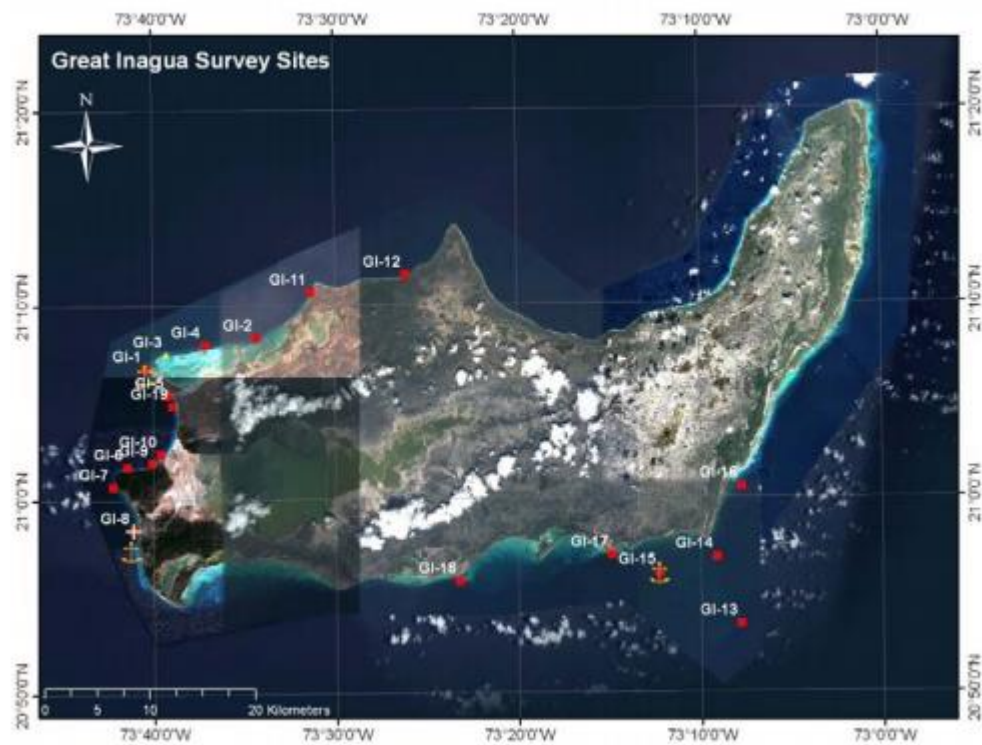




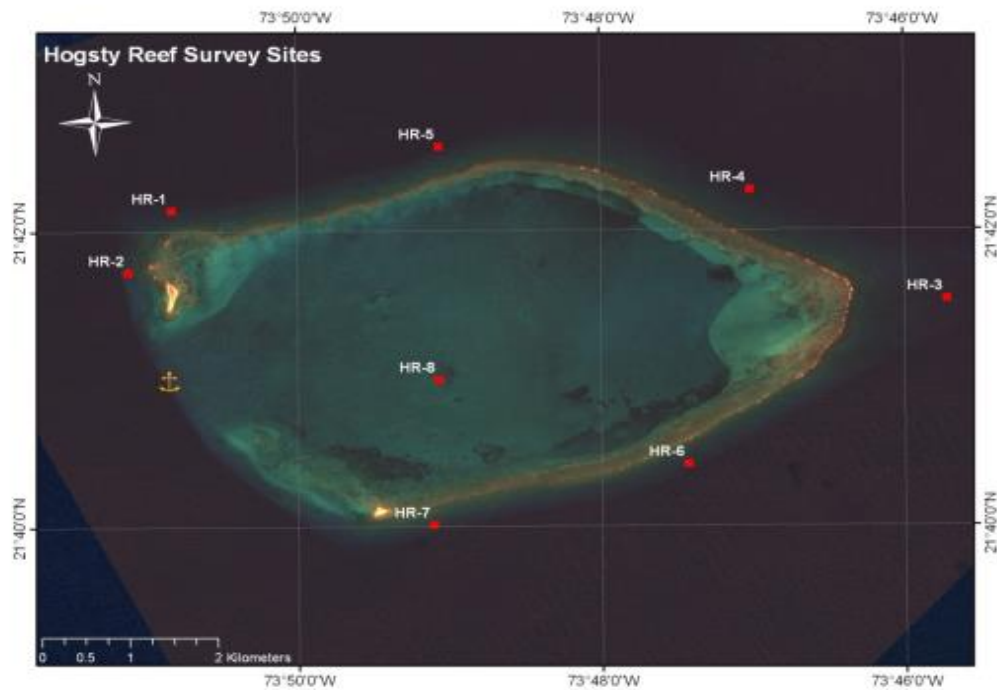
**FIGURE 3.5** Taha'a and Raiatea, red dot indicates survey site



**FIGURE 3.6** Cay Sal Bank, red dot indicates survey site



**FIGURE 3.7** Great Inagua, red dot indicates survey site



**FIGURE 3.8** Hogsty Reef, red dot indicates survey site

### 3.2 MATERIALS USED

For both Pacific and Atlantic field campaigns, the tools used were

- a Canon G11 camera with associated underwater Ikelite housing
- 10 meter weighted transect tape
- Marked meter stick
- SCUBA gear

### 3.3 FIELD CAMPAIGN

Bahamian data was collected at Great Inagua, Little Inagua, Cay Sal Bank and Hogsty Reef. Dive sites and data collection was predetermined by a preliminary aerial survey. French Polynesian data was collected through the Society Island Archipelago. On both campaigns, there were three to four 45-60 minute dives a day where 3 transects were taken per dives. This transect sampling protocol was quantitatively evaluated on previous research cruises by the Living Oceans Foundation in the Red Sea and found to be sufficient sampling size for benthic assessments.

### 3.4 PHOTO-TRANSECTS

#### 3.4.1 USE OF PHOTO-TRANSECTS

Photo-transects have become popular in coral reef monitoring and ecological studies over the past few years. Photo-transects are a method developed to create snapshots in time of benthic communities (Bakand Meesters 1998). These snapshots help to evaluate stages in the dynamic processes of population change on coral reefs. Size results from two processes; individual colony growth and dynamics on a population scale that help determine the number and size of colonies (Bak and Meester 1998). Parameters that describe the shape of the population reflect a general response of the individual corals to the reef condition (Meesters et al. 2001). Population structures, size frequency distributions and species composition all indicate when stress on a reef exists; because disturbances do not affect all species equally, this selectivity is crucial focus to managing impacts (Hughes and Connell 1999).

### 3.4.2 PHOTO-TRANSECT COLLECTION

Several different islands and atolls were visited in the Bahamas and Society Islands of French Polynesia, exhibiting different levels of human habitation and environmental impact (Table 3.1). Photo-transects measuring coral cover and sizes as intercepts on reefs inside lagoons and on ocean-facing reefs were placed in a stratified random pattern at depths of <5m, 10m, 20m, >25m. A weighted 100 meter transect tape was laid out parallel to the reef crest and a photograph was taken at every 1m mark along the transect line using a marked meter stick for calibration. This created 0.5x20m photo-corridors from which the images were merged and coral outlines digitized.

## FRENCH POLYNESIA

<b>Disturbance:</b>	Bleaching Since 1980	Predatory Outbreak:	Fishing pressure	Urbanization/ pollution	Storms	Human population
<b>Island</b>						
Mopelia	7 events, most prevalent on outer reef slope	<i>Acanthaster planci</i>	Intermediate	No record	Cyclones, major El Niño event 1982-1983	Uninhabite d
Scilly	7 events, most prevalent on outer reef slope	<i>Acanthaster planci</i>	Intermediate	No record	Cyclones, major El Niño event 1982-1983	Uninhabite d
Bellingshausen	7 events, most prevalent on outer reef slope	<i>Acanthaster planci</i>	Intermediate	No record	Cyclones, major El Niño event 1982-1983	Uninhabite d
Tupai	7 events, most prevalent on outer reef slope	<i>Acanthaster planci</i>	Intermediate	No record	Cyclones, major El Niño event 1982-1983	Uninhabite d
Huahine	7 events	<i>Acanthaster planci</i>	Pressure increasing, not overfished yet	Runoff damaging reefs, impacts considered low and local	Cyclones, major El Niño event 1982-1983	Population ~ 6,000 people
Raiatea	7 events	<i>Acanthaster planci</i>	Pressure increasing, not overfished yet	Runoff damaging reefs, impacts considered low and local	Cyclones, major El Niño event 1982-1983	Largest, most populated ~12,000 people
Tahaa	7 events	<i>Acanthaster planci</i>	Pressure increasing	Runoff damaging reefs, impacts considered low and local	Cyclones, major El Niño event 1982-1983	Population ~5,000 people

# BAHAMAS

<b>Disturbance:</b>	Bleaching Since 1980	Biological Change	Fishing Pressure	Urbanization/ pollution	Storms	Human population
<b>Island</b>						
Cay Sal Bank	First event in 1998 and increasing occurrence, corals very susceptible from already present disease	<i>Diadema</i> die off, algal overgrowth	Overfished	Air pollution from North America, land based runoff and poorly regulated dredging	Hurricanes	Few inhabitants only on Cay Sal Island
Inagua	First event in 1998 and increasing occurrence, corals very susceptible from already present disease	<i>Diadema</i> die off, algal overgrowth	Overfished	Air pollution from North America, land based runoff and poorly regulated dredging	Hurricanes	Population ~1,000 people
Hogsty Reef	First event in 1998 and increasing occurrence, corals very susceptible from already present disease	<i>Diadema</i> die off, algal overgrowth	Overfished	Air pollution from North America, land based runoff and poorly regulated dredging	Hurricanes	Uninhabited

(B)

**TABLE 3.1** Differing human and environmental impacts between the (A) Society Islands and (B) the Bahamas.

### 3.5 FAUNAL EVALUATION

Work from previous expeditions in the Red Sea, Riegl et al. (2012) has shown that information derived from the photo-transects can be successfully employed to create faunistic catalogs and to provide basic coral demographic information. These catalogs may be archived for all fauna evaluated in the transects as well as the individual sizes, distribution and live coral cover at that time (Bak and Meesters 1998). A list of all identifiable scleractinian corals, their sizes and associated percent cover was formed from the photo-transect archive; completed to the genus level in the Pacific and to the species level in the Atlantic. In the Society Islands, the following corals were identified as the major genera: *Acropora*, *Astreopora*, *Favia*, *Favites*, *Goniastrea*, *Montastrea*, *Montipora*, *Pocillopora* and *Porites*. In the Bahamian regions studied, the following were identified as the major genera/species: *Agaricia*, *Favia fragum*, *Meandrina meandrites*, *Montastrea cavernosa*, *Montastrea annularis*, *Montastrea faveolata*, *Porites astreoides*, *Porites porites*, *Siderastrea radians*, *Siderastrea siderea*, *Eusmilia* and *Copophyllia natans*.

### 3.6 POST PROCESSING ANALYSIS

The following steps were identically replicated for both The Society Islands data and the Bahamas data. In assessing the coral communities of the Society Islands the data set was separated into the two groups; (1) the inner more populated islands which included Huahine, Tahaa, Raiatea and (2) the outer less impacted atolls which included Mopelia, Tupai, Bellingshausen and Scilly. From here on, these two groups will be



referred to as the Inner Islands and the Outer Islands. In assessing the coral populations of several of the Bahamian islands the data set was separated into the three visited regions; (1) Cay Sal Bank of the northern side of the islands, (2) Great and Little Inagua referred to together as just Inagua in the southeastern area of the Bahamas and (3) Hogsty Reef also in the southeastern area and unpopulated.

After image digitization, coding and information extraction, a series of spatial statistics were used to evaluate the data. Two types of data are used: biotic and environmental. The biotic data was extracted from the images and consists of percent live coral cover and coral colony size distributions created by the size classes. The environmental data used is that of the island location for the spatial analysis. GPS coordinates of the islands within the two main regions are used for spatial ordination of the biotic variables within the region and between the two regions as a whole.

#### 3.6.1 IMAGE MERGE AND DIGITIZATION

Every 10 images were merged into a contiguous transect to recreate the underwater reef transect on the computer. This was done using the software Canvas (v10). Overlapping photos were fit by eye to obtain an acceptable level of geometric consistency between images. Merged images were grouped into a contiguous transect and downsized to 300 dpi resolution for efficient storage and archiving.

All corals in the merged transects were individually digitized by outlining with the polygon tool in Canvas. Each individual was then assigned a color with a specific RGB value per genus (or species) from a predetermined color code. Color

coding simplifies the coral populations into functional groups and/or taxonomic assemblages to assign ecological meaning.

### 3.6.2 CODING AND EXTRACTION

A script was written in MATLAB software in order to efficiently extract several forms of information from digitized photo-transect data. All digitized transects were transformed to tiff files with only color coded polygons representative of the corals left on a blank canvas. The code took each transect (10 merged images) and used a binary method to turn all polygons of a genus specified by RGB value to white and index the rest of the picture into black. The rest of the code then calculated the surface area from polygon points and forced every individual into one of five programmed size classes. Finally the percent cover of that genus was calculated per individual measured and output into a matrix. This was repeated for each transect for every genus cataloged in the faunal evaluation.

From the matrices of information extracted from the MATLAB code, the information was organized in excel by genus for each of encountered reef environment. Graphical representation of this data as a summary was created for both the percent cover and size class information. The output matrices of percent cover were put into a bar graph in Excel to identify trends in the change of cover at different reef environments.

The output matrices of the number of individual corals per size class were organized in Excel and graphed per genus. These sets of bar graphs per genus were created for the different reef environments evaluated.

### 3.6.3 MULTIVARIATE STATISTICAL ANALYSIS

#### 3.6.3.1 PRINCIPAL COMPONENTS ANALYSIS

Principal component analysis (PCA) is a type of multivariate ordination where the placement of the samples is an indication of the biological similarity of the samples. A principal component analysis was run on the locational variables (dive sites of data collection) of the Society Islands. Using the PRIMER (v.6) program a two dimensional representation of the data points was created using the axes calculated based on the covariance of the samples. When graphed, the samples were placed on two axes known as principal component one (x-axis) and principal component two (y-axis). Principal component one is the axis which maximizes the variance of points projected perpendicularly onto it. Principal component two maximizes the variance of points as well but is constrained by principal component one. The axes are often referred to by how much of the total variance they explain. When determining the value of the plot and the dimensionality to use, the variance explained by the initial principal components are evaluated. A two dimensional representation was chosen for this study, as the first two principal components explained greater than 95% of the variance in every case.

The PCA is most appropriate to evaluate the variables of the dives sites because the algorithm used converts dissimilarities into Euclidean distance; the method with which it assesses separations in the data (Clarke and Warwicke 2001). In constructing a PCA, the axes are rotated to identify the most meaningful gradients

which is the basis of many abiotic factors (Clarke and Warwicke 2001; Zuur et al. 2007).

A PCA was run first on the French Polynesian data with the environmental variable specified as the sites surveyed or the island groups- inner versus outer islands. In the first analysis, the ordination plots were further analyzed by overlaying the size classes on the island groups which created four different PCA's. A second analysis was performed on all of the islands based on the four size classes measured at each site. After the ordination was constructed, the plot symbols were specified to show which sites were in the outer islands and which were in the inner islands. The validity of each PCA was determined by the percent variation described by the first two principal components.

The next set of Principal Component Analyses was conducted on the Caribbean data of the three regions in the Bahamas. The first analysis used all sites in the three regions of the Bahamian Islands as the environmental variables to construct the ordination. They were further analyzed by overlaying the four size classes for a spatial ordination based on the number of individuals measured per size class. The second analysis was again performed on all sites as a whole and grouped by island based on the four size classes measured per site. The last analysis consisted of all sites ordinated again by the number of individuals in each of four size classes, overlaid with a trajectory representing the percent live coral cover per island. The validity of each Principal Component Analysis was determined by the

percent variation described by the first two principal components which was greater than 95% for each analysis.

#### 3.6.3.2 NON METRIC MULTI-DIMENSIONAL SCALING

Non metric multi-dimensional scaling (MDS) is an ordination technique based on a resemblance matrix; most often based on the Bray Curtis resemblance. Of all multivariate spatial analyses, MDS is the most effective in preserving rank order relations when ordinating the samples and is thus commonly used with biomass data (Clarke & Ainsworth 1993, Clarke & Warwick 2001). Preserving rank order relations is important in evaluating size classes because for the purposes of this study rank order relations are the focal point of coral size structuring. The MDS was used to analyze the size distributions of all size class data.

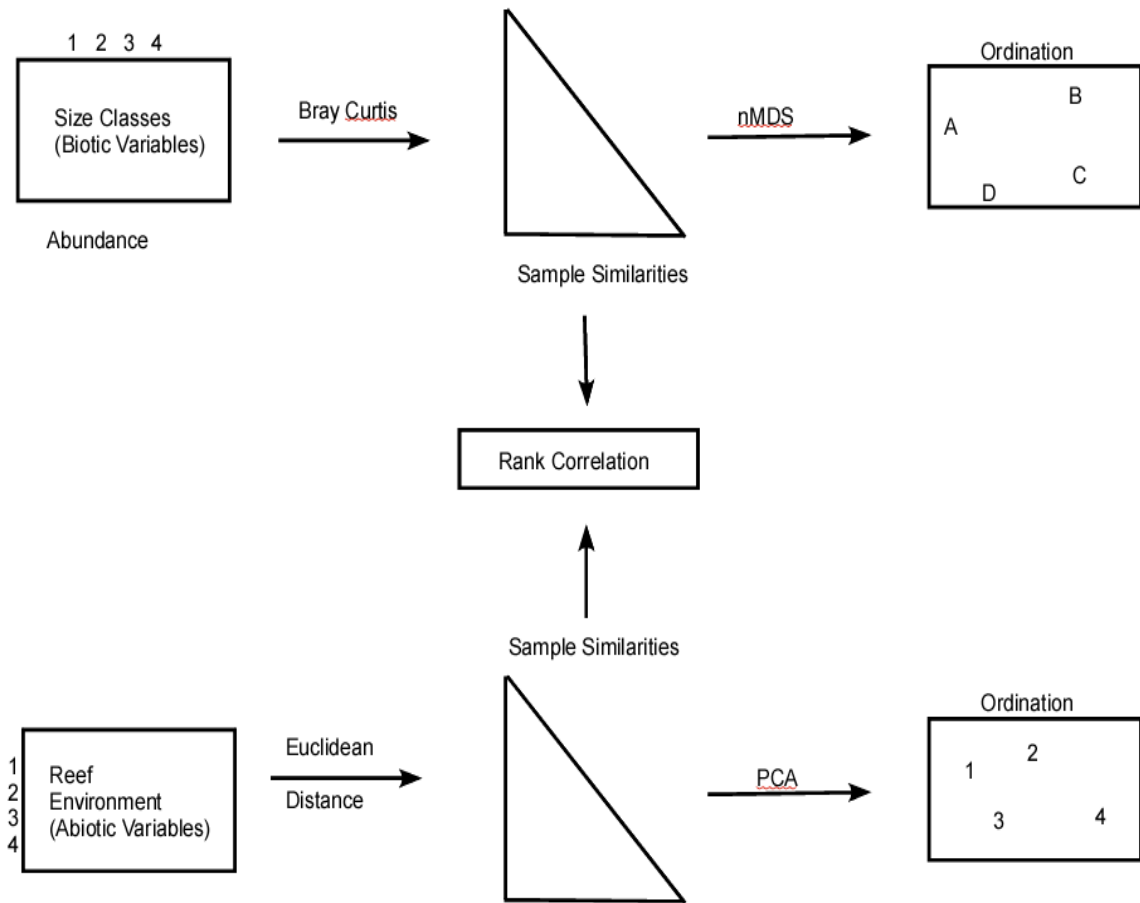
Multi-dimensional scaling (MDS) is often used as an explanatory method to identify underlying dimensions in similarities of community structure. In MDS, the similarities among samples as calculated by a similarity (Bray Curtis) matrix are represented as a spatial map. In the MDS algorithm, a similarity (or dissimilarity) matrix is created to visualize the community data in a lower dimensional (i.e. two-dimensional as a triangular matrix) form. The algorithm is iterated ten times to rearrange  $m$  dimensions for the best ordination (Clarke & Warwick 2001). The relationship between geometric distance and the  $m$  dimensional configuration by fitting a non-parametric regression curve is known

as stress; a value which must be lower than 0.1 for an accurate representation (Zuur et al. 2007).

Several different MDS ordinations were run on the Society Island data to examine the biotic variables of size class and percent cover. The Society Islands Archipelago was split into the inner and outer islands as aforementioned. The first MDS ordinated all islands surveyed in the Society Islands based on the size classes. They were then grouped by similarity values based on a cluster analysis. The second MDS ordination was constructed based on size class but used only the inner island group and the third MDS ordination was constructed based on size classes as well but used only the outer island group. A last set of multi-dimensional scaling ordinations was performed per major genus, based on the size classes across all islands and grouped by similarity values.

In the Bahamian dataset, the first MDS is constructed from all regions studied in the Bahamian Islands and ordinated by size class with similarity groupings based on a cluster analysis for the number of individuals per size class. The second set of MDS ordinations used the same method as the first but data were broken down per island studied with similarity groupings by cluster analysis. An MDS per major genus/species was not done for the Caribbean as it was for the Pacific. The reasoning behind that spatial analysis was to observe functional group differences; but only one of the twenty major species was branching.

## Multivariate Analysis Progression



**FIGURE 3.9** Visual diagram of the multivariate statistical analysis progression; demonstrates how the highest rank correlation is obtained from the biotic similarity matrix and the matching distance matrix of the optimal subset of environmental variables (Clarke et al. 2008).

#### 3.6.3.3 CORAL COVER MAPPING

To consider spatial clustering of live coral cover among sample sites, several maps were created using Arc GIS software. Shape files were created in Arc using the percent live coral cover values assigned to a color gradient. These shape files were layered on top of Arc database base-maps of the areas surveyed.

#### 3.6.3.4 (SEMI) VARIOGRAM

Spatial relationships exist on all scales of an ecosystem because real world conditions are characterized by a more systematic distribution as opposed to stochasticity (Griffith 2009). Spatial autocorrelation occurs when an observation at one point affects the observation at a neighboring point, an event that very often observed in ecological data (Legendre and Legendre 1998; Zuur et al., 2007). Similarities between neighboring units previously disturbed are examined using percent live coral cover. A (semi)variogram (often referred to as just a variogram but also known as an experimental variogram) is a structure function testing for spatial autocorrelation (Legendre & Fortin 1989). Through geostatistical analysis the idea is to illustrate how spatial variance increases with an increasing spatial scale, more simply put how correlation  $[\gamma(h)]$  between neighbors disappears as distance increases (i.e. first law of geography). The variogram is a fundamental tool of spatial statistics and used in evaluating spatial correlations among geographic distances by kriging, or linear interpolation through space (Legendre & Fortin 1989; Crawley 2007). Multiple variograms



were created for this study in looking for spatial correlation of the live coral cover after multiple disturbances in the areas studied. The objective in looking for spatial correlation was to look for a disturbance signature with respect to live coral cover specific to a type of disturbance and how a local versus region-wide scale of disturbance affected the community.

The formula for the variogram computation is:

$$\gamma(h) = \frac{1}{2} \frac{\sum_{i,j \in N(h)} (z_i - z_j)^2}{|N(h)|}$$

where  $\gamma(h)$  is the autocorrelation variable,  $|N(h)|$  is the number of distinct pairs,  $N(h)$  is the Euclidean distance between each pair and  $z_i - z_j$  is the value of the response variable at spatial locations  $i$  and  $j$  (Crawley 2007). The variograms were programmed and created in R using data input as the longitude, latitude and percent live coral cover. These variables were input as a text file for the values of the axes, and the above variogram formula from the spatial library in the R program.

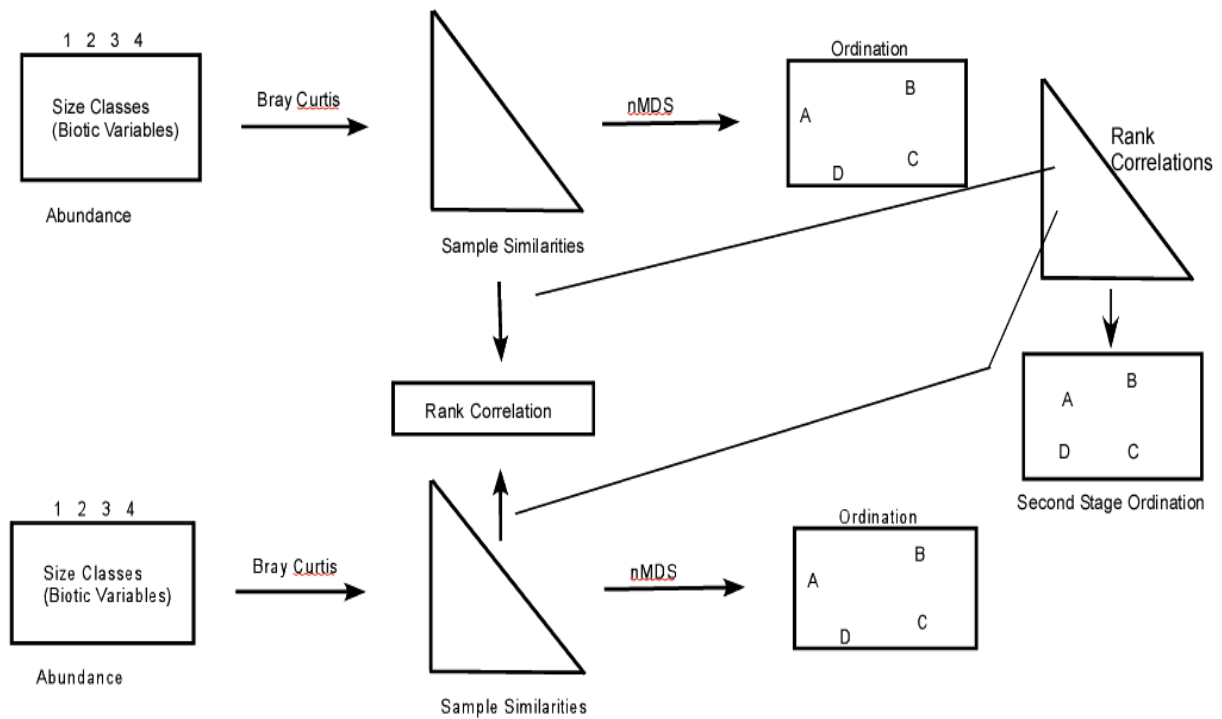
For the Society Island data set, two variograms were created; one for the Inner Islands and one for the Outer Islands. For the Caribbean data set, one variogram of the Bahamian region was created encompassing the three areas surveyed.

#### 3.6.3.5 SECOND STAGE MULTI-DIMENSIONAL SCALING

Subsets of the data showing strong (correlation) relationships can be used in smaller groups to observe important patterns. In a method called a second stage MDS by PRIMER; a triangular resemblance matrix of correlation coefficients between two MDS spatial patterns is constructed. This correlation assessment was run between the spatial ordination pattern of the Society Islands and the spatial ordination pattern of the Bahamas to give a summary of the relationship between the specified multivariate sample patterns.

For the purposes of this study, multi-dimensional scaling plots have been used extensively to examine the community structure of two island groups. But many MDS plots can cloud the patterns arising or provide too much information in a lower dimension. The goal of this final ordination was to give correlation values. These values were used in evaluating the relationship of the spatial patterns formed by the coral community given in the first stage MDS. A second stage MDS was run on the resulting resemblance matrices of the following data; the biotic variables of the inner versus the outer Society Islands, biotic variables from the Society Islands versus the Bahamian Islands surveyed and environmental variables of the Society Islands versus the Bahamian Islands

## Second Stage Analysis



**FIGURE 3.10** Schematic Diagram the progression to a second stage MDS using previously calculated resemblance matrices and rank correlations (Clarke & Warwick 2001).

## **4. RESULTS**

In order to assess the coral communities of the Society Islands, the data set was separated into the two groups; of the inner versus outer islands. To assess the coral communities of the Bahamian islands, that data set was separated into three regions; (1) Cay Sal Bank of the more northern side of the islands closer to populated Florida and Cuba, (2) Great and Little Inagua referred to as just Inagua in the southeastern area of the Bahamas and (3) Hogsty Reef also in the southeastern region of the Bahamas.

### 4.1 CORAL POPULATION ASSESSMENT

#### 4.1.1 DIGITIZING

In the French Polynesian data set, a total of 20 genera were distinguished (by RGB color coding)\; in the final analyses only 15 of those 20 were used. The five genera that were excluded had two or fewer individuals across the whole archipelago and were therefore considered outliers (Table 4.1).

<b>SOCIETY ISLANDS</b>	<u>Reef Environment</u>		
Genera	<u>Leeward Fore Slope</u>	<u>Windward Fore Slope</u>	<u>Lagoon</u>
<i>Acropora</i>	X	X	X
<i>Astreopora</i>	X	X	X
<i>Cycloseris</i>			
<i>Cyphastrea</i>	X	X	
<i>Echinophyllia</i>			
<i>Favia</i>	X	X	X
<i>Favites</i>	X	X	X
<i>Fungia</i>	X		X
<i>Gardineroseris</i>			X
<i>Goniastrea</i>	X		X
<i>Herpolitha</i>			
<i>Leptoseris</i>	X		
<i>Lobophyllia</i>	X	X	X
<i>Montastrea</i>	X	X	X
<i>Monitpora</i>	X	X	X
<i>Pachyseris</i>			
<i>Pavona</i>	X	X	
<i>Pocillopora</i>	X	X	X
<i>Porites</i>	X	X	X
<i>Psammocora</i>			

**TABLE 4.1** List of all genera known in the Society Islands, those found and included in the study are marked with an ‘x’.

In the Caribbean data set, a total of 20 genera/species were distinguished (by RGB color coding) across the regions of Hogsty Reef, Great and Little Inagua and Cay Sal Bank. In the final analysis only 12 of these genera or species were used. Those excluded were left out because they were present at only one island or had less than three individuals included in all of the photo-transects (Table 4.2).

BAHAMAS	Region Surveyed		
Species	<u>Cay Sal Bank</u>	<u>Inagua</u>	<u>Hogsty Reef</u>
<i>Acropora cervicornis</i>			
<i>Agaricia</i>	X	X	X
<i>Favia fragum</i>	X	X	X
<i>Diploria strigosa</i>			
<i>Diploria labyrinthiformis</i>			
<i>Manicina areolata</i>			
<i>Meandrina meandrites</i>	X		X
<i>Montastrea annularis</i>	X	X	X
<i>Montastrea cavernosa</i>	X	X	X
<i>Montastrea faveolata</i>	X	X	X
<i>Mycetophyllia lamarckiana</i>			
<i>Porites astreoides</i>	X	X	X
<i>Porites porites</i>	X	X	X
<i>Siderastrea radians</i>	X	X	X
<i>Siderastrea siderea</i>	X	X	X
<i>Eusmilia</i>	X	X	X
<i>Stephanocoenia intersepta</i>			
<i>Copophyllia natans</i>	X	X	X
<i>Solenastrea bournoni</i>			
<i>Isophyllia sinuosa</i>			

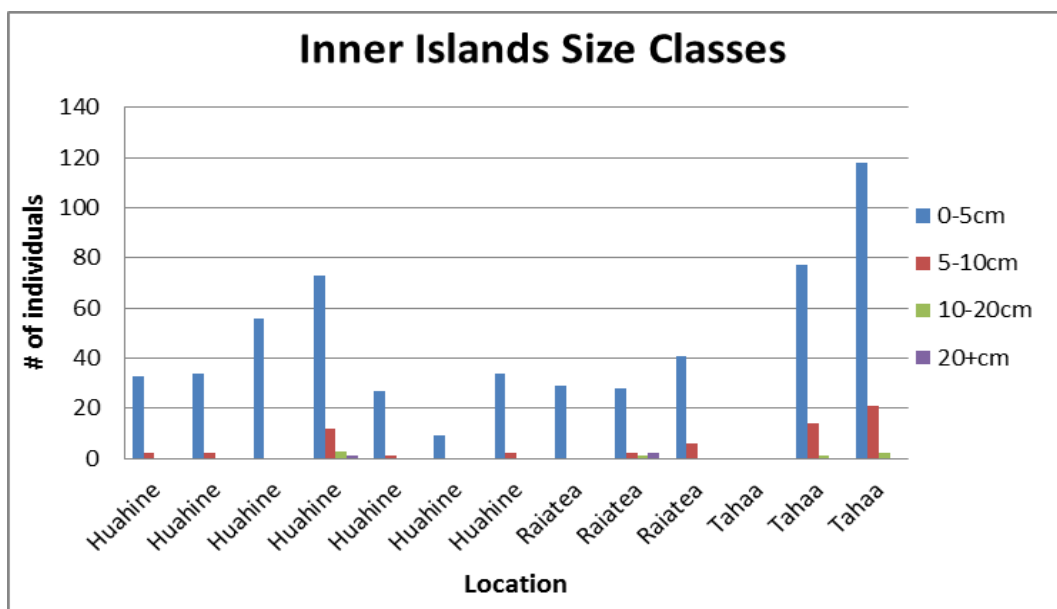
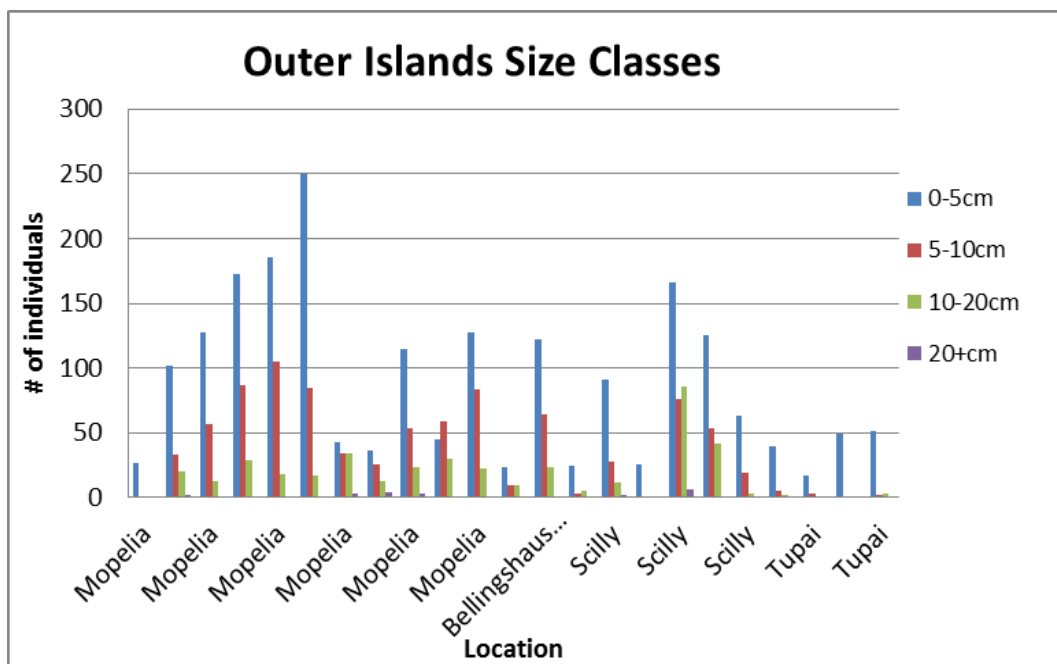
**TABLE 4.2** List of all genera known in the Bahamian region, those found and included in the study are marked with an ‘x’.

#### 4.1.2 EXTRACTION: SIZE CLASS AND LIVE COVER INFORMATION

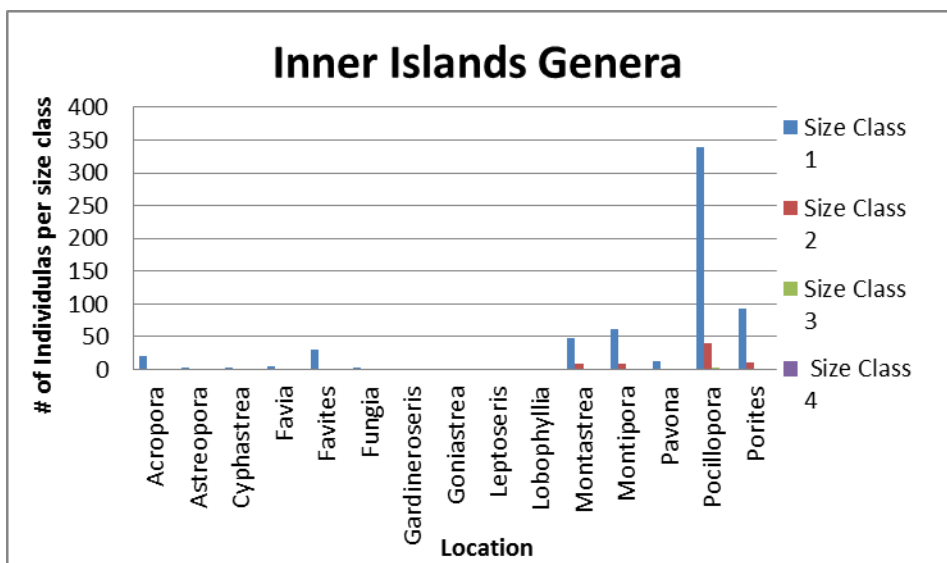
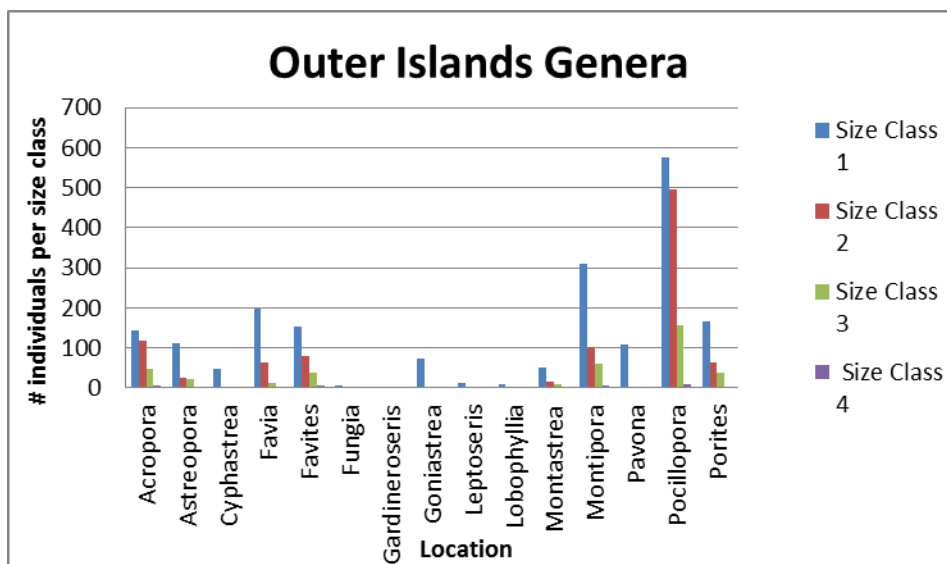
Using the code created in MATLAB, the number of individuals per genera per island was binned into size class as well and percent live tissue cover values were calculated. The four size classes were: Size Class 1= 0-5centimeters, Size Class 2= 5.1-10 centimeters, Size Class 3= 10.1-20 centimeters and Size Class 4= 20.1-50 centimeters. Size class 5 (50 + cm) was eliminated because only values of 0 were calculated across all genera or species in all environments.

In extracting the size class information from Society Island Reefs, the two island groups in the Society Islands were compared (Figure 4.1). The outer islands exhibited a wide array of size classes although dominated by the lowest size class of 0-5 centimeters. More branching genera were seen as compared to the inner islands and a higher diversity of genera was observed as well (Figure 4.2). The inner islands had a lower number of individuals in all size classes. Size class 1 (0-5 cm) dominated, followed by size class 2 (5.1-10 cm). There were less than 20 individuals in size class 3 (10.1-20 cm) and no larger individuals (Figure 4.1).



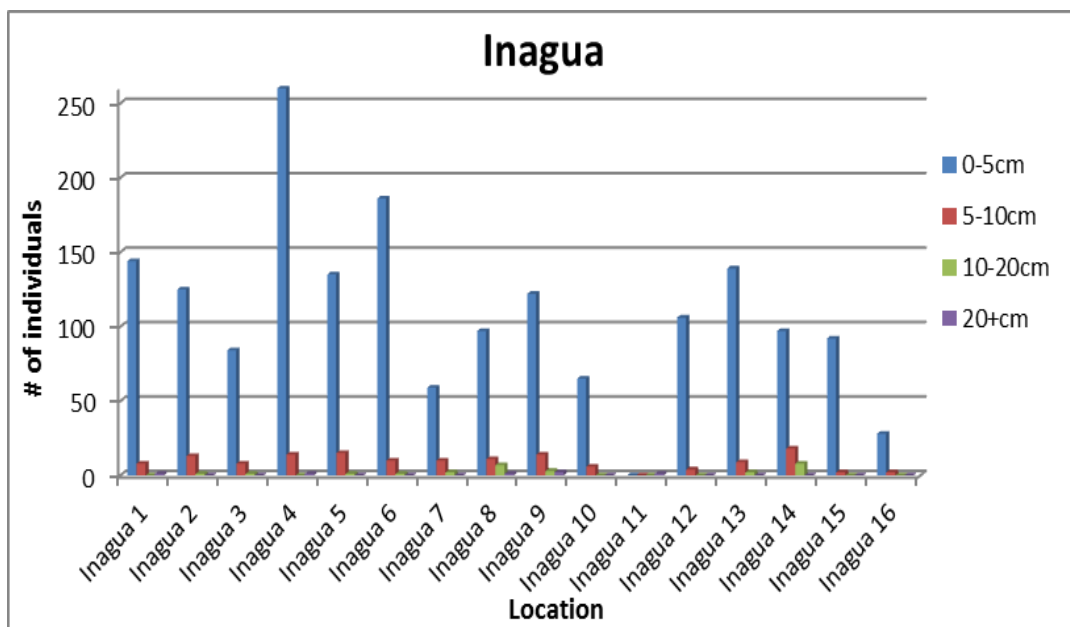
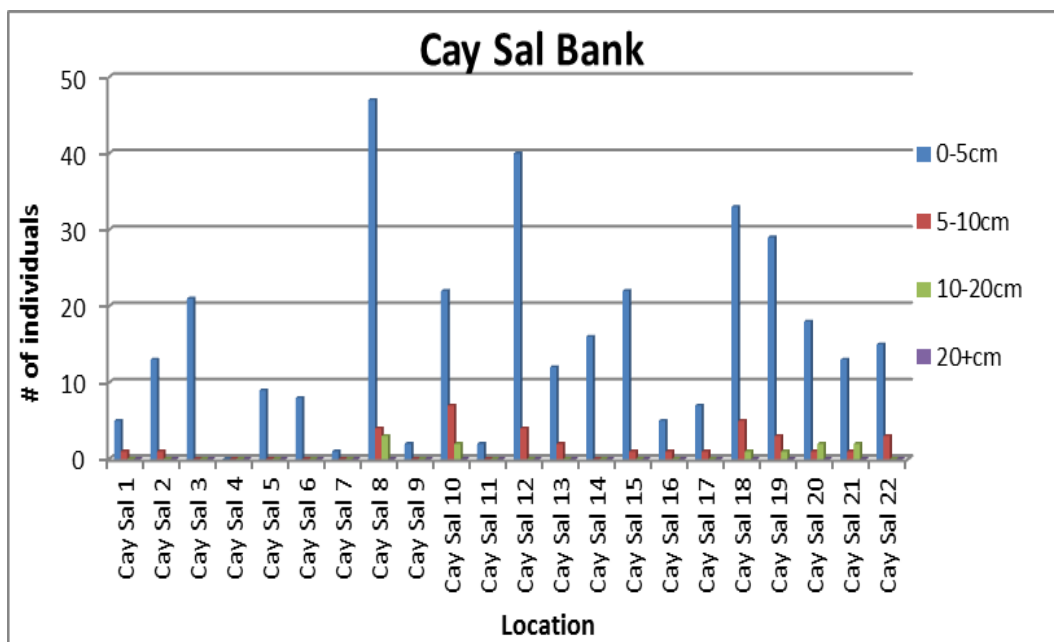


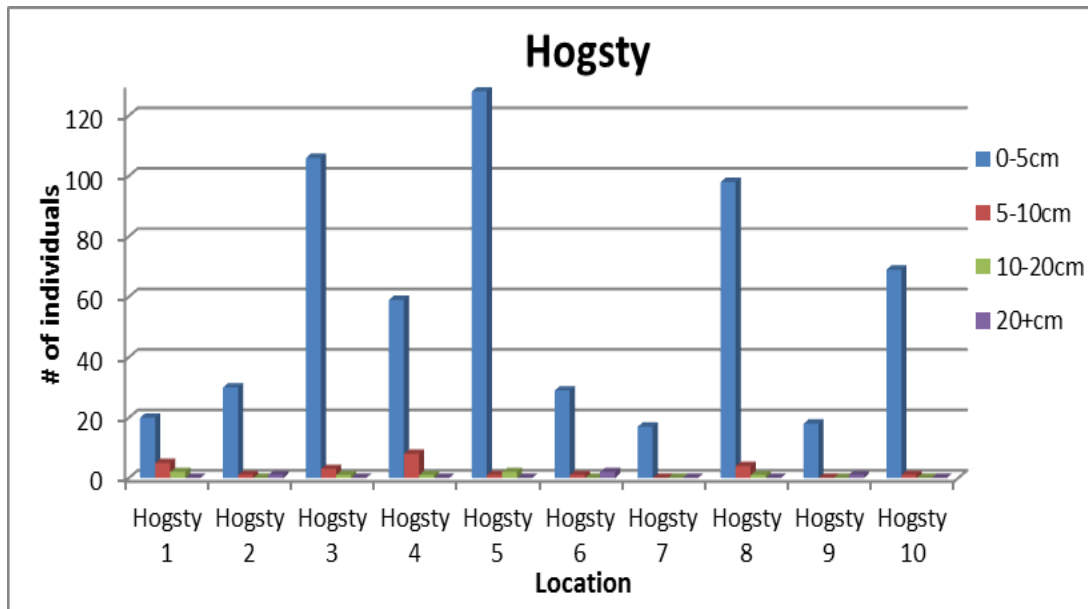
**FIGURE 4.1** Graphical output of size classes of live corals per island in the Society Islands, split into the Inner and Outer Islands.



**FIGURE 4.2** Graphical representation of the diversity in genera between the Outer and the Inner Islands of the Society Islands.

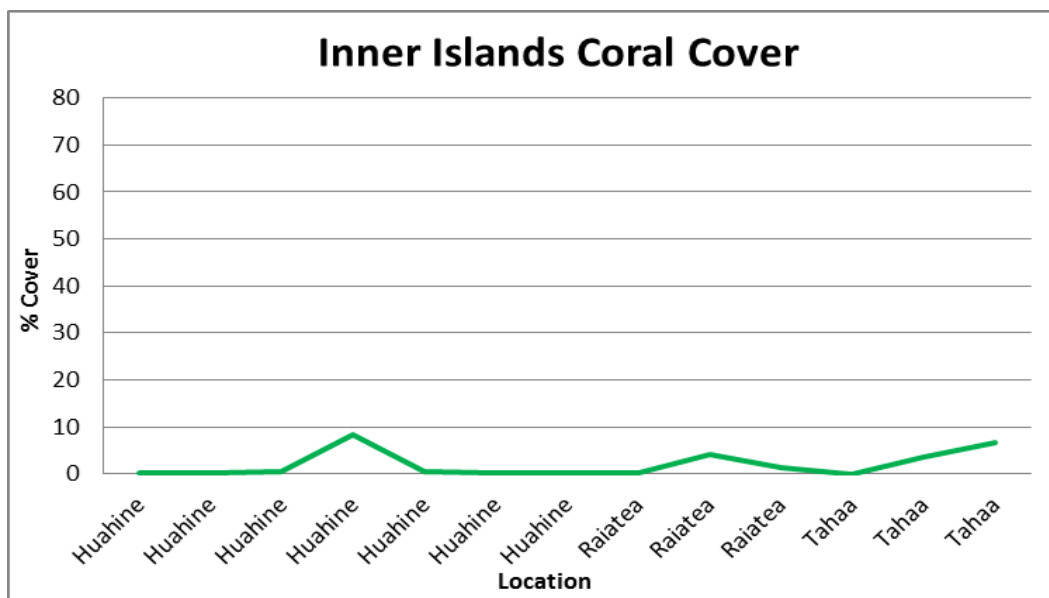
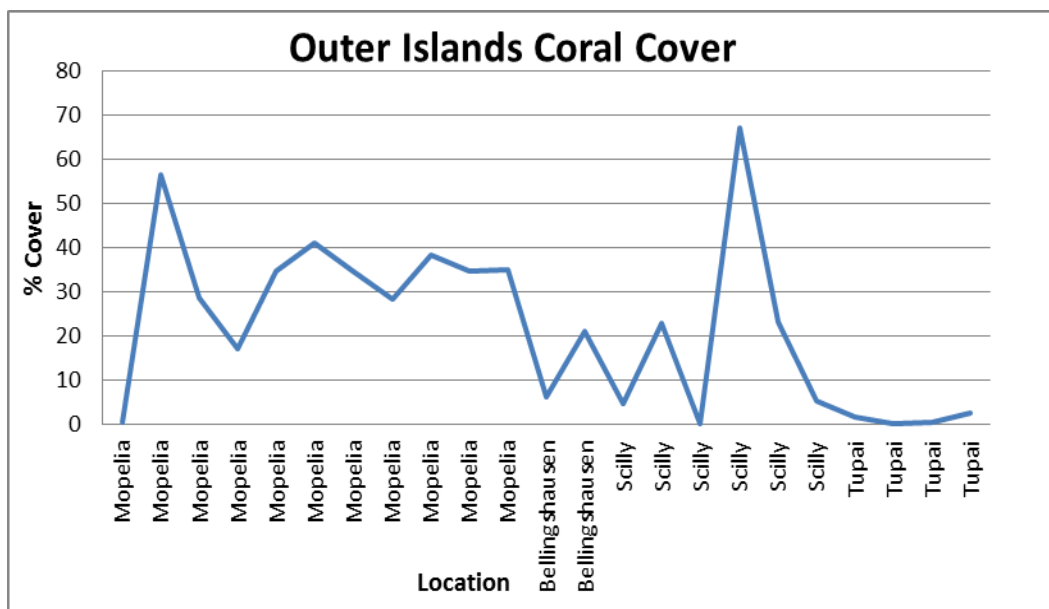
Three separate regions in the Bahamas were evaluated: Great and Little Inagua, Hogsty Reef and Cay Sal Bank (Figure 4.2). Cay Sal had the largest array of size classes as compared to the other two Bahamian regions, but was dominated by size class 1 (0-5cm). Cay Sal Bank was most heavily sampled which in theory may have a bearing on the array of size classes. However, since the distribution of size classes was considered in the study not abundance of individuals in each class, several additional sites at one location is not enough to create a significant margin of error. Size classes 2 and 3 were observed but not both at every site and always with less than 10 individuals. Great and Little Inagua were grouped into what will be called 'Inagua', a region which was dominated by size class 1 (0-5 cm) with a high number of individual corals surveyed. Size class two (5.1-10cm) was present at almost every site but did not exceed ten percent of the individuals. Only 5 survey sites hosted individuals of size class 3 (10.1-20 cm) with less than 10 individuals each. Hogsty Reef had the least dynamic population in terms of size classes observed. Hogsty exhibited size class 1 at every site with an exponential increase in individuals from any other size class. Size class 2 was exhibited at several sites with less than 10 individuals each time; no other size classes were recorded at the survey sites (Figure 4.2).





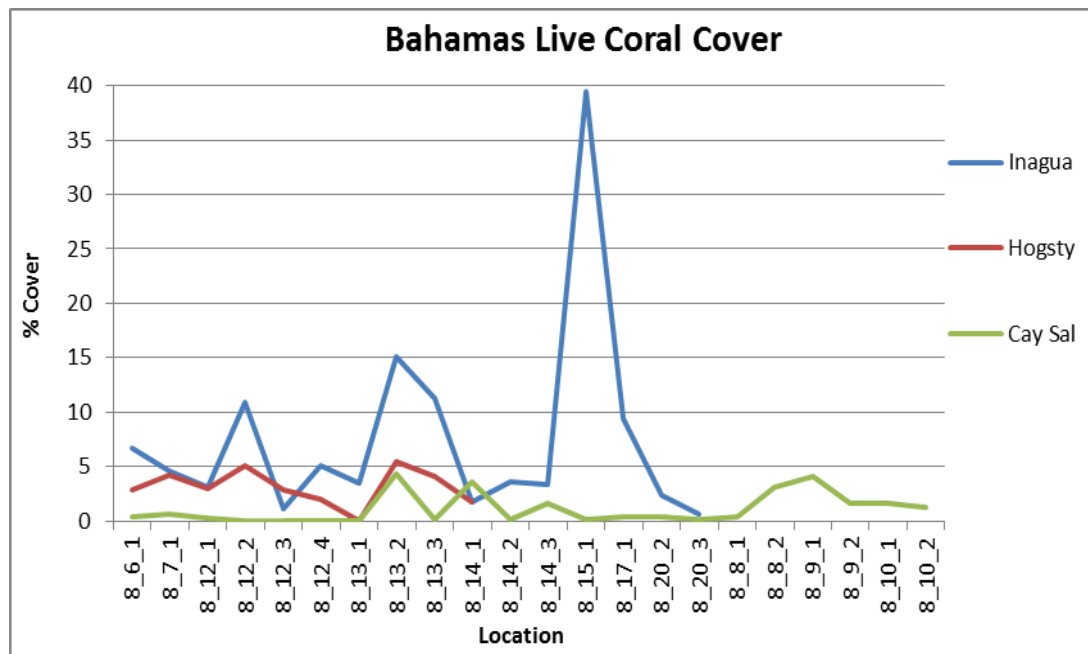
**FIGURE 4.3** Graphical output of size classes of live corals per island in the Caribbean.

Percent cover was analyzed at each site separately. In the Society Islands, the outer islands had a significantly higher percent live tissue cover (Excel paired t-test,  $p=0.008$ ) (Figure 4.4). At the inner islands, percent cover is about tenfold lower and overall less dynamic. A distinct increase in cover is seen at the lagoon sites; although still lower than ten percent total cover (Figure 4.4).



**FIGURE 4.4** Graphical representations of the percent live coral cover among the inner versus outer Society Islands.

In the Bahamian data set, percent cover was calculated in the same way. Figure 4.4 shows all three regions on one graph. Inagua had the highest cover of the regions surveyed in the Bahamas, with a substantial spike at the last few survey sites located on the more protected side of the island. Hogsty Reef had low cover across all sampling sites, not exceeding 5%. Although Cay Sal Bank had more sampling sites, it was consistently low; all survey sites had less than 5% cover.



**FIGURE 4.5** A graphical representation of the percent live coral cover at the islands studied in the Bahamas.

## 4.2 MULTIVARIATE STATISTICS

### 4.2.1 NON METRIC MULTI-DIMENSIONAL SCALING

A non-metric multidimensional scaling (nMDS) ordination was constructed on the resemblance matrices formed of all size class (abundance) data of the individual corals. The data set was separated into the inner more populated islands and the outer less populated atolls.

An MDS was constructed with respect to the size classes and shows groups overlaid of similarity values based on a cluster analysis. Cluster analysis and the MDS plot suggest that there are several distinct groupings in the data. On the MDS plot, the relative distances between points represent rank order. Points that are closer together are more similar in community composition with respect to size classes. The outer atolls show the presence of size classes one, two and three as being somewhat similar with a resemblance level of 40% while size class two and three are most similar with a resemblance value of 60%. Size class four is shows no relation to the other size classes. At the inner islands, size classes three and four are most similar with a similarity value of 40% while the other size classes have no relationship. Since the similarity value is based on spatial distribution of size classes, the value is referring to the assessment of size frequency distributions of individual corals. Because size class two and three show a 60% similarity grouping, this means they contribute the most similar distribution of the number of individual coral colonies to the community composition (Table 4.3).



	Island	# Genera	# Colonies	# Size Class 1	# Size Class2	#Size Class 3	# Size Class4
Outer Islands	Mopelia	14	2088	1231	624	219	14
	Scilly	12	734	397	180	148	9
	Bellingshausen	7	253	145	73	33	2
	Tupai	10	117	106	9	2	0
Inner Islands	Huahine	2	286	266	16	3	1
	Raiatea	9	109	98	8	1	2
	Tahaa	6	233	195	35	3	0

**TABLE 4. 3** Community composition of the Society Islands based on species, and total number of colonies broken down by size class.

A similar non-metric multidimensional scaling ordination was conducted with the resemblance matrices of the Caribbean data. On the MDS plot, the relative distances between points represent rank order. Size classes on the plot that are closer together are more similar in community composition. Size class one and four are isolated, showing the lowest rank in similarity, while size class two and three are much more similar in abundance and distribution among the three regions (Table 4.4).

	Island	# Species	# Colonies	# Size Class 1	# Size Class2	#Size Class 3	# Size Class4
Bahamas	Cay Sal Bank	14	386	340	35	11	0
	Inagua	14	1921	1745	144	26	6
	Hogsty Reef	13	609	574	24	7	4

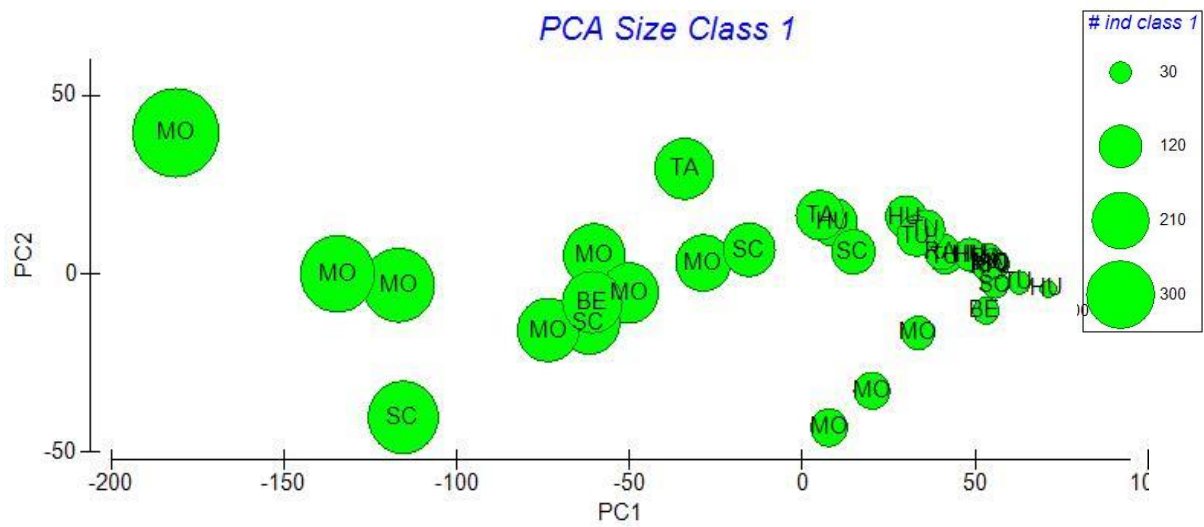
**TABLE 4.4** Community composition of the Bahamas based on species, and total number of colonies broken down by size class.

An MDS ordination was done on the biotic data of the individual size classes separated per genera as well. No clear patterns arose giving no functional group or physiological distinctions. The patterns among abundance and size class distribution are most informative.

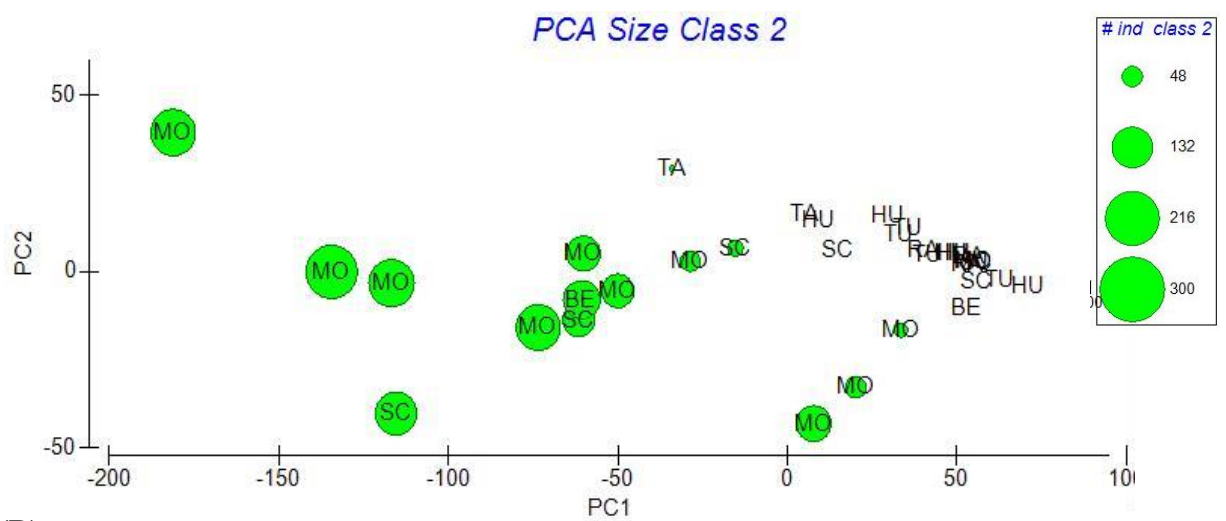
#### 4.2.2 PRINCIPAL COMPONENTS ANALYSIS

Principal component analyses were run on the locational variables of the Society Islands. The environmental variables here are defined as the island, whose environment changes by location in the archipelago. A first principal component analysis (PCA) was constructed based on the island location or sites surveyed with each of the four size classes overlaid in a two-dimensional bubble plot (Figure 4.8). This analysis shows size class 1 as being the most abundant and widespread of the four size classes with size class 2 being close in abundance but

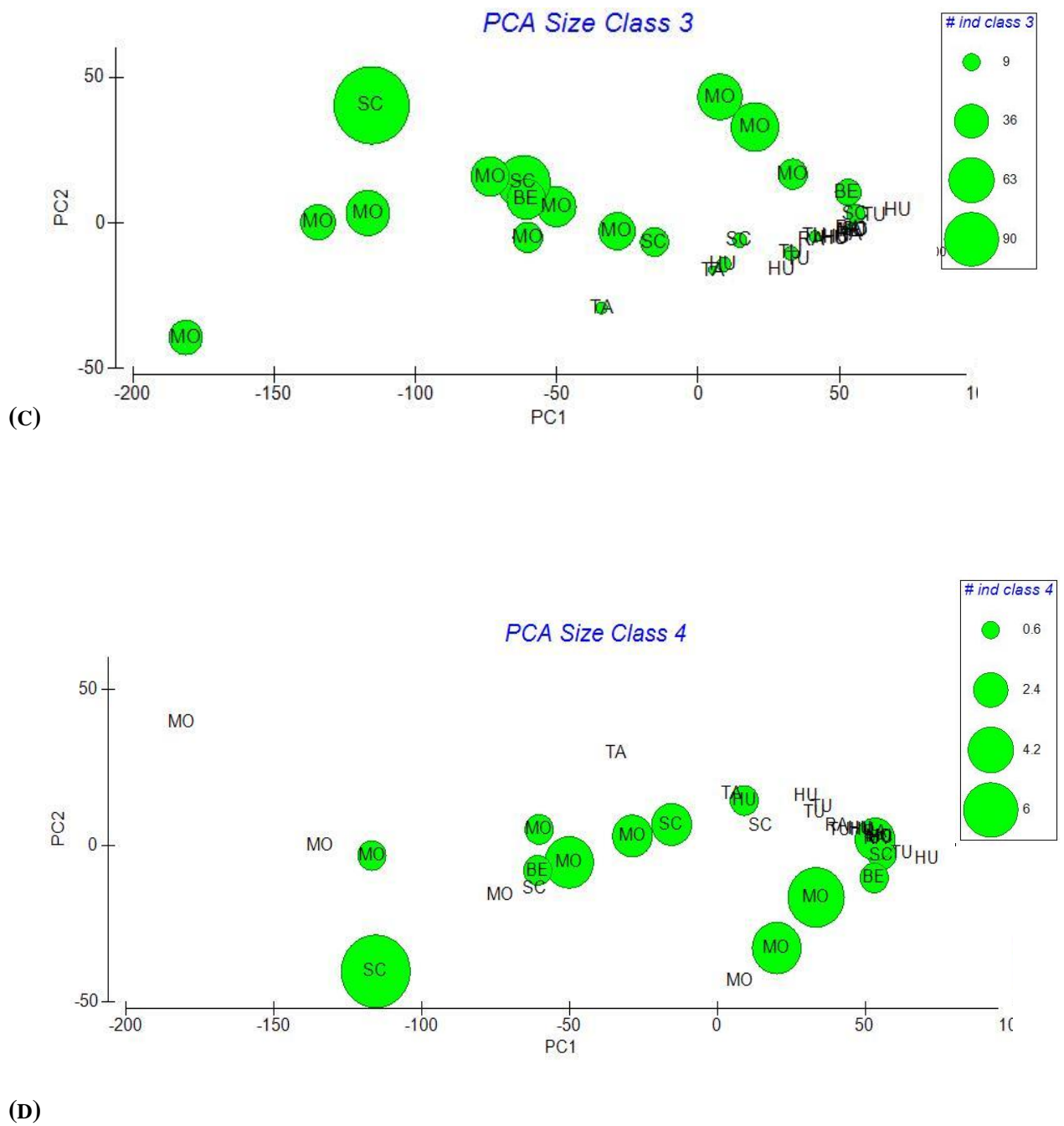
with a lower distribution. Size class 2 is more concentrated in the outer islands. Interestingly, size class 3 has a distribution similar to that of size class 1 but much lower in abundance of individual corals. Size class 4 has both a low abundance and distribution with the highest numbers at the outer islands. A third and final PCA was constructed using the same ordination of islands but now labeled as part of either the inner or outer islands group (Figure 4.9).



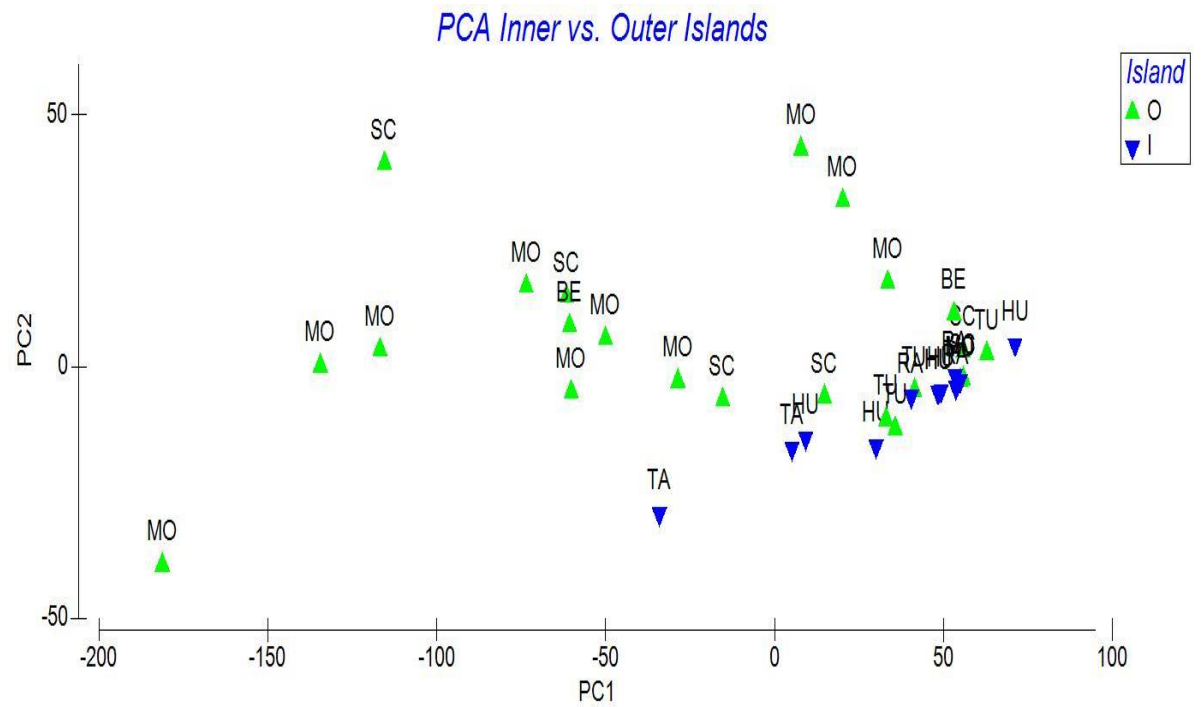
(A)



(B)

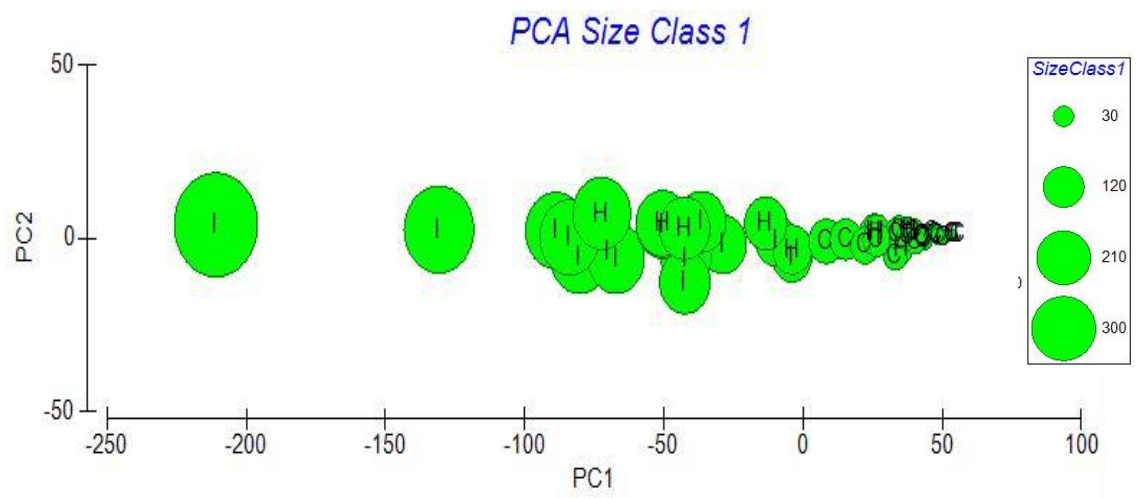


**FIGURE 4.6** Principal component analysis ordination using environmental variables (a) Size class one values overlaid by bubble values (b) Size class two overlaid by bubble values (c) Size class three overlaid by bubble values (d) Size class four overlaid by bubble values

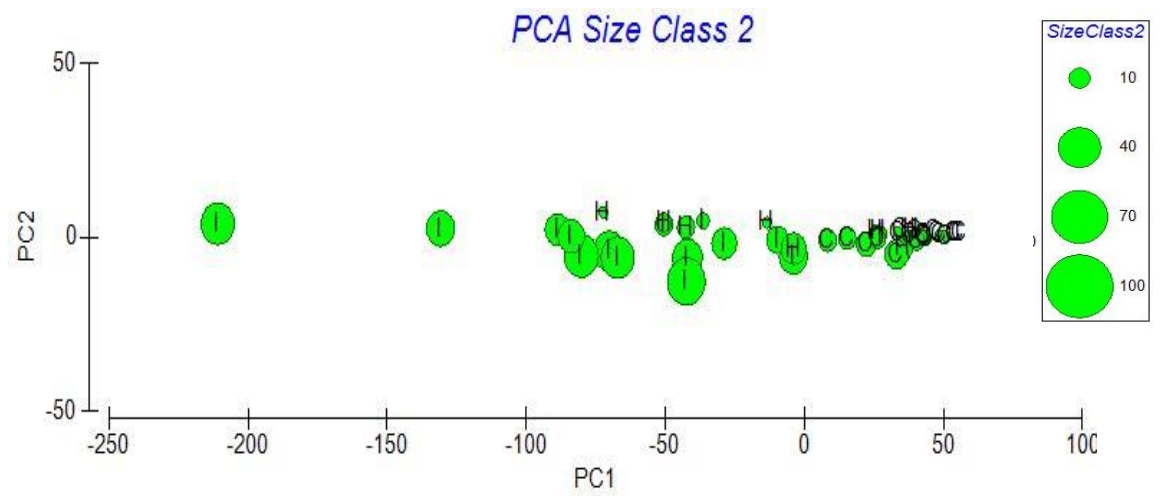


**FIGURE 4.7** Principal component analysis ordinations by locational variables and further grouped into the inner versus the outer islands based on size class distribution. Separation by the island surveyed shows distinct groupings in the data; the legend depicts the two island groups as Outer (O) and Inner (I).

The same principal component analyses were constructed for the Bahamian region data set. The first analysis was made up of four ordinations based on the island location or sites surveyed with each of the four size classes overlaid in a two-dimensional bubble plot. Size class 1 exhibited the highest abundance and widespread frequency distribution. Size class 2 and 3 exhibited the similar abundances but size class 2 was more widespread across the surveyed regions whereas size class 3 was more concentrated at Hogsty Reef and Cay Sal Bank. Size Class 4 had the lowest abundance and was distributed evenly throughout albeit sparsely.

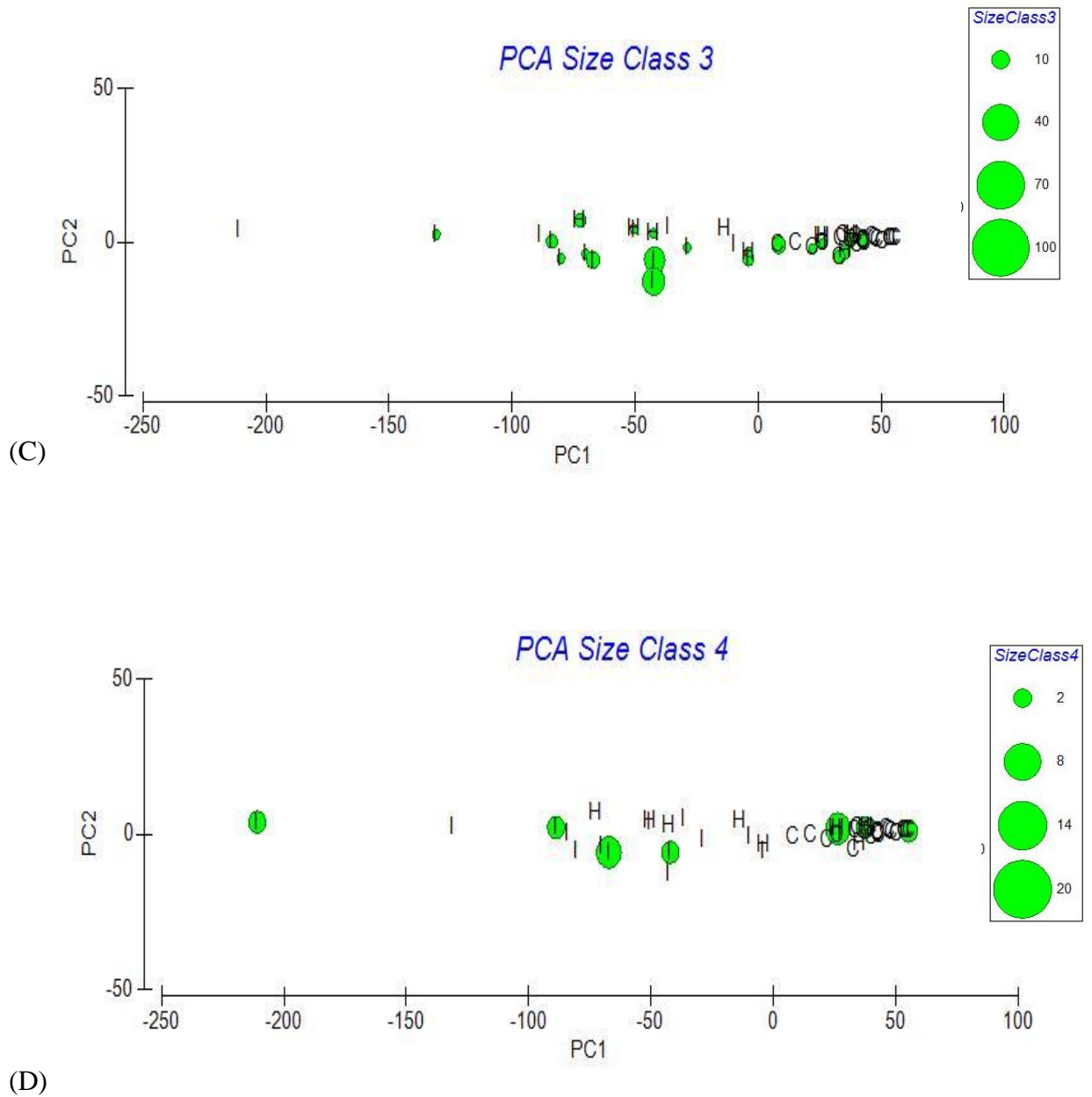


(A)

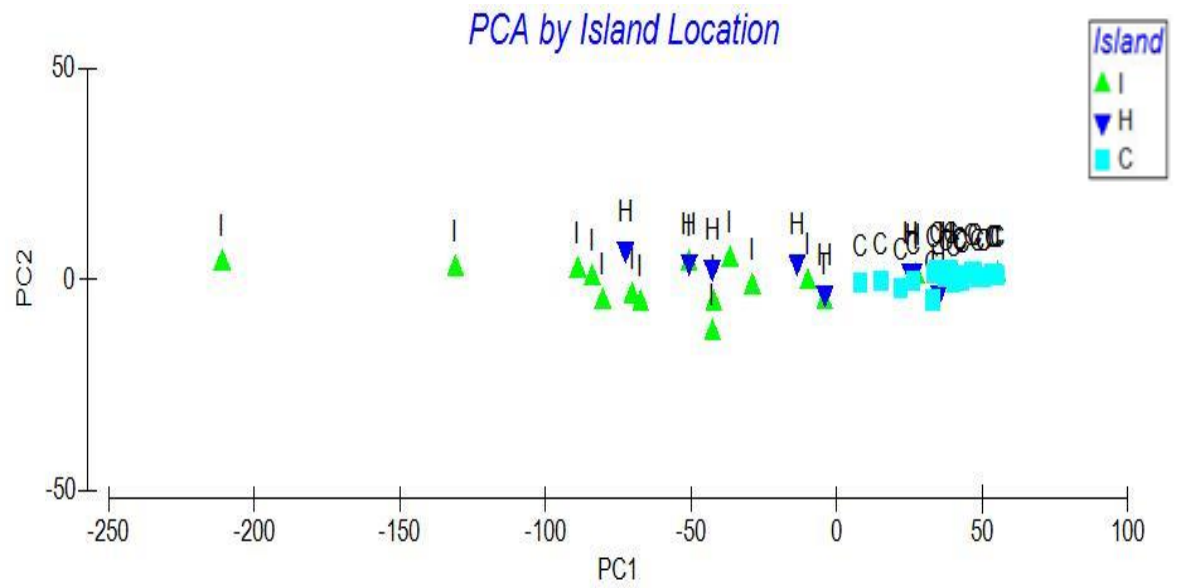


(B)





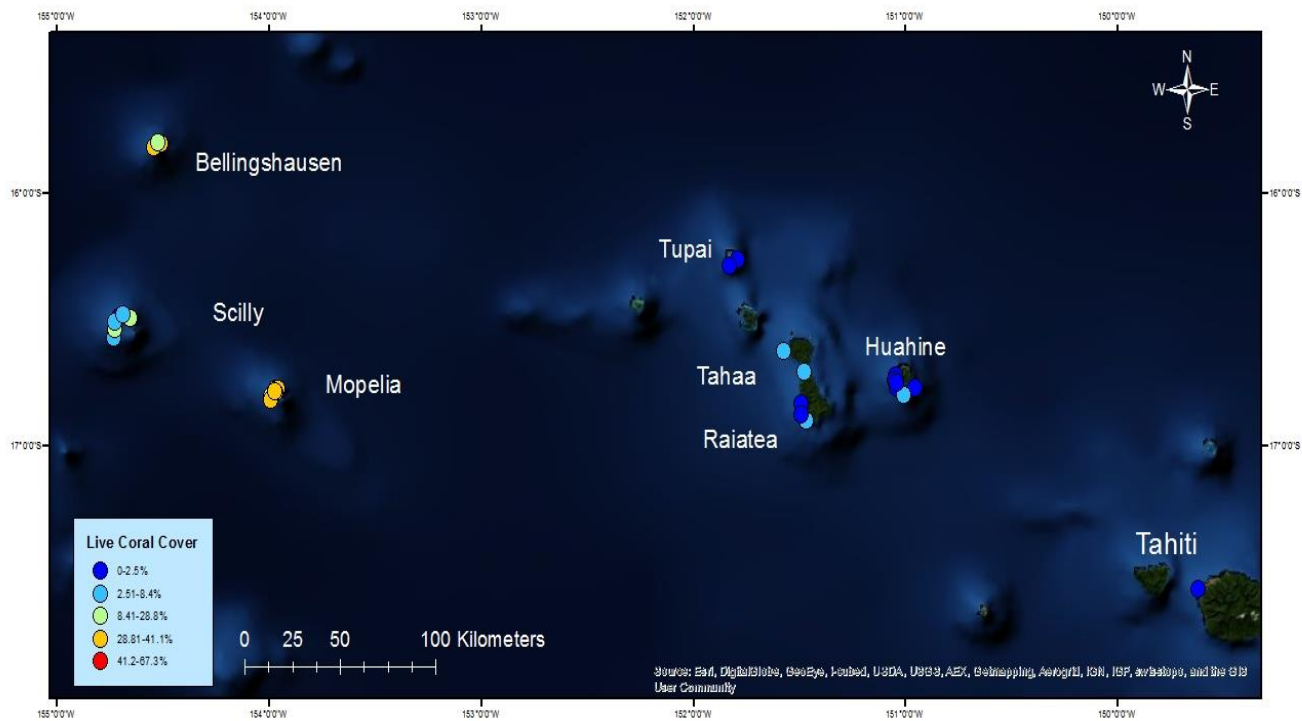
**FIGURE 4.8** Principal component analysis ordination using environmental variables of the Bahamian regions surveyed (a) Size class one values overlaid by bubble values (b) Size class two overlaid by bubble values (c) Size class three overlaid by bubble values (d) Size class four overlaid by bubble values



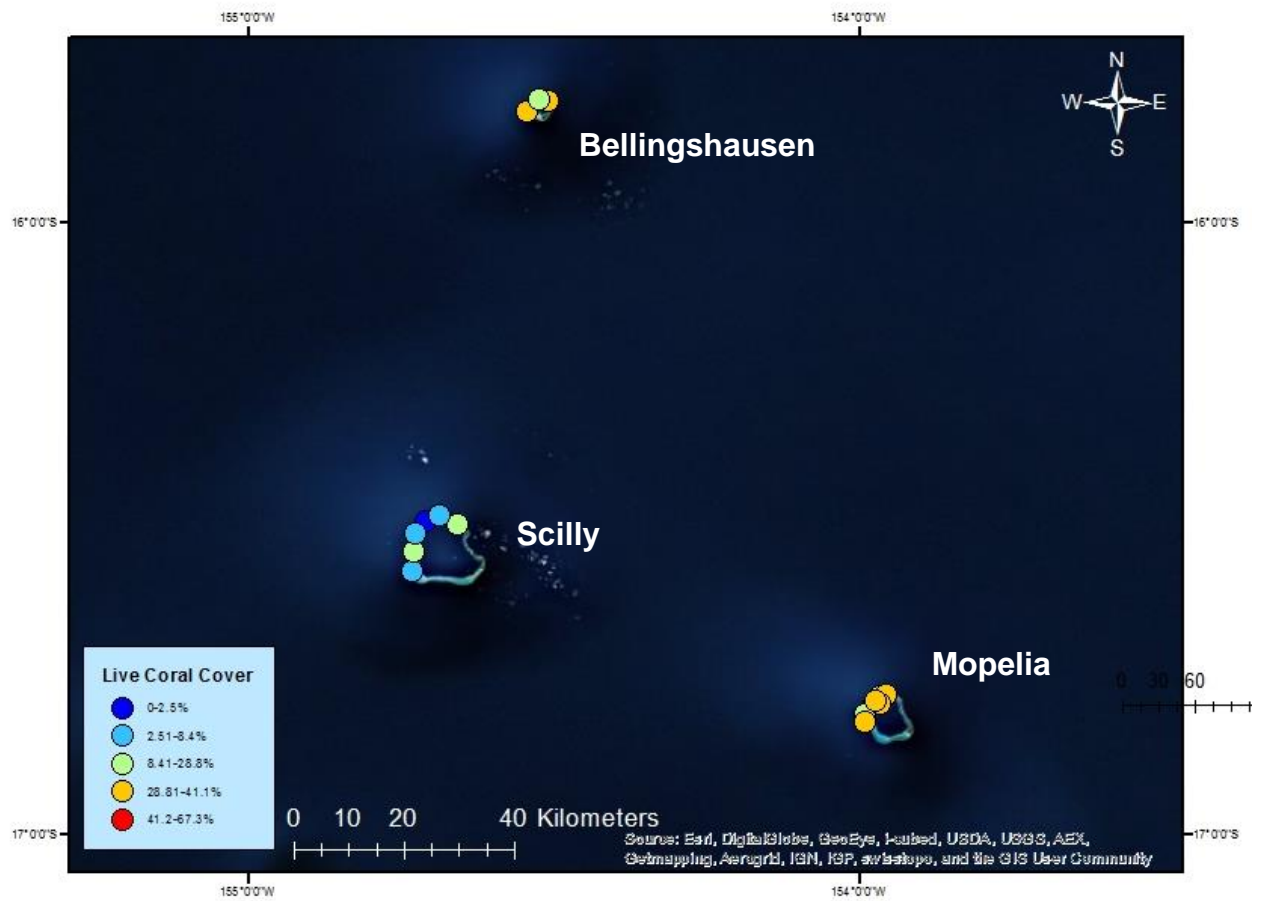
**FIGURE 4.9** Principal component analysis ordinations by study site; separation by the island surveyed shows groupings in the data. The legend depicts the islands as Inagua (I), Hogsty Reef (H) and Cay Sal Bank (C).

#### 4.2.3 CORAL COVER MAPPING

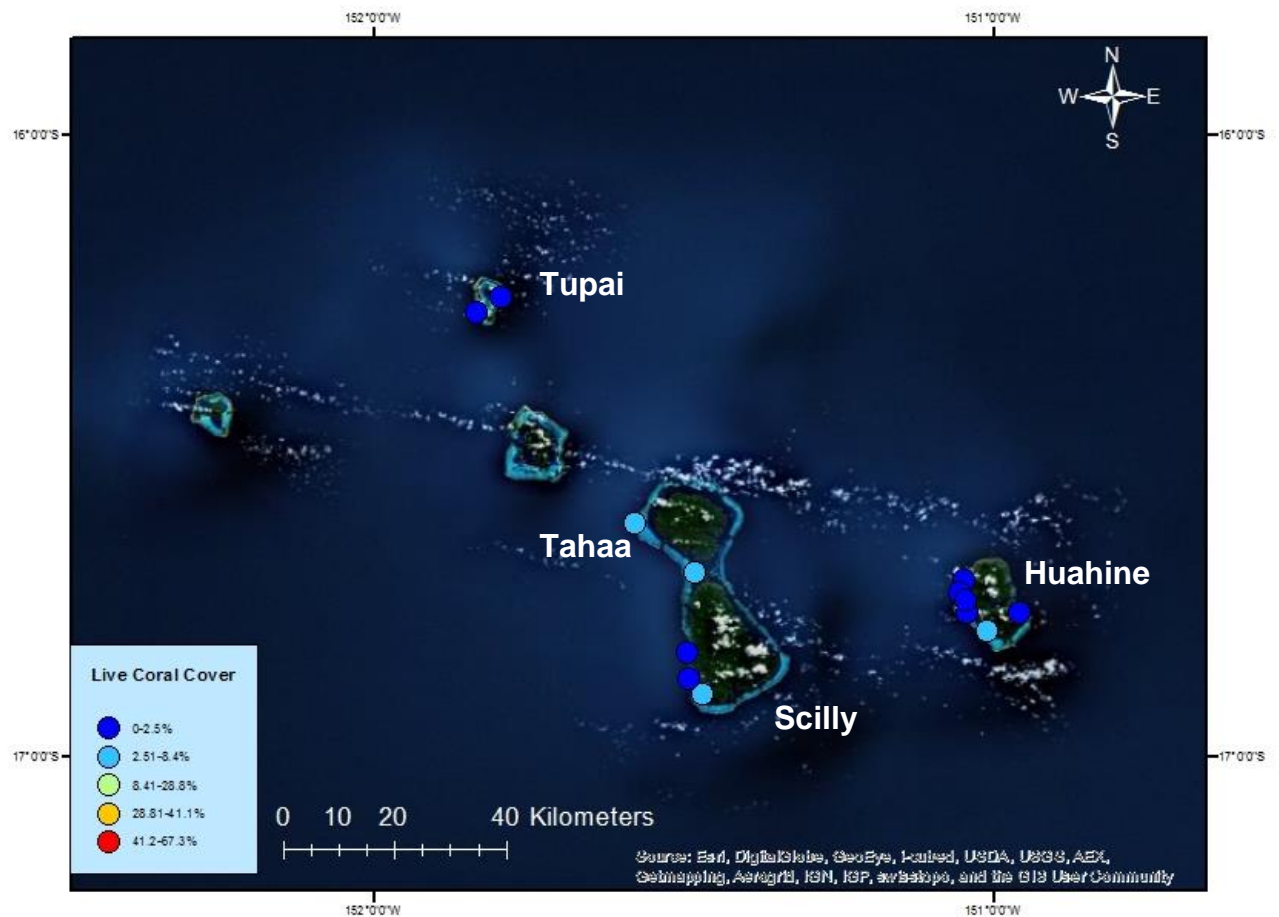
Several maps were created using Arc GIS to consider the presence of spatial clustering. The first set of maps has an overall view of all 7 islands in the Society Islands studied (Fig. 4.10) and the next two are zoomed in on the Outer Islands (Fig. 4.11) and the Inner Islands (Fig. 4.12). The color scale is based on the Jenks' natural classification of the percent live coral cover and layered on top of a base map to show the coral cover at the exact location measured. The second set of maps has an overall view of the Bahamas to note the areas surveyed (Fig. 4.13), the next map is a close up of the live coral cover at Cay Sal Bank (Fig. 4.14) and the last map is a close up of the live cover at Inagua and Hogsty reef (Fig. 4.15).



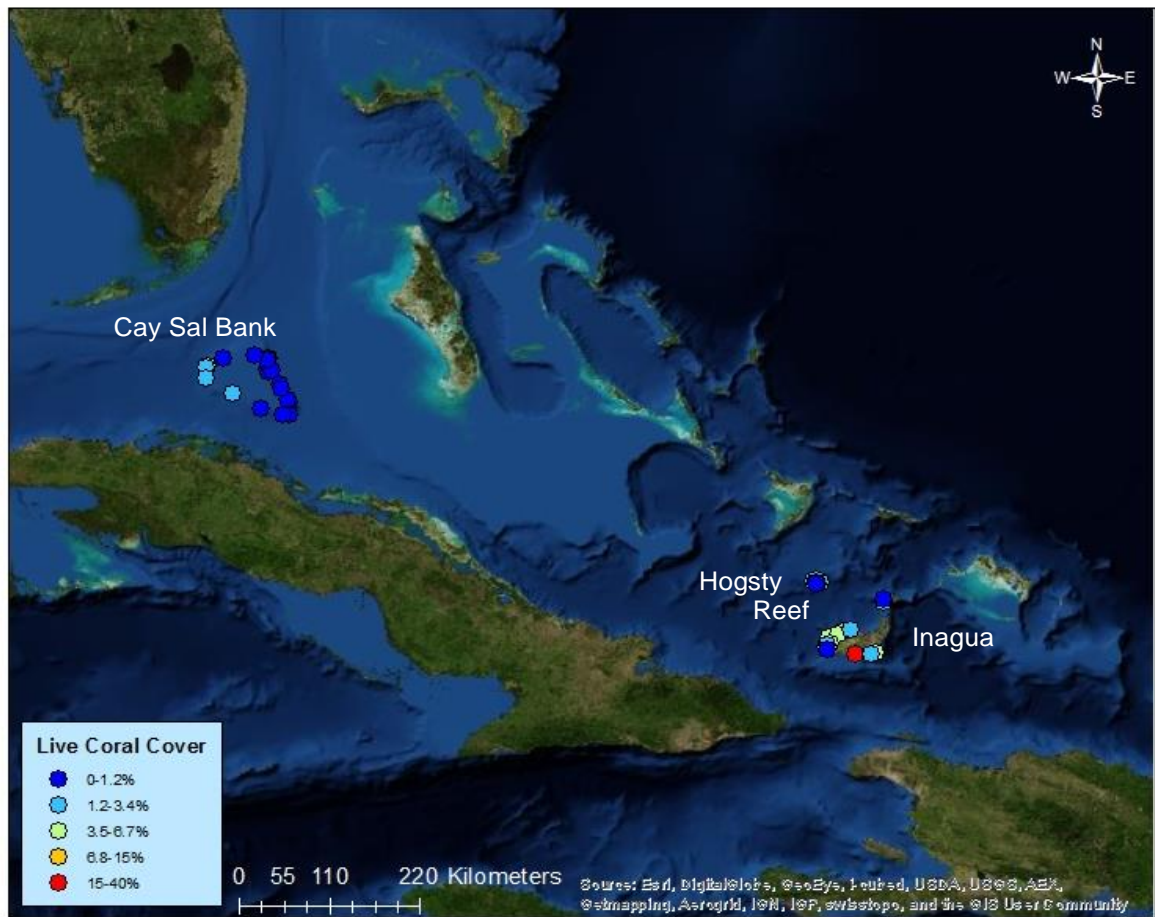
**FIGURE 4.10** Arc GIS map of the Society Islands in French Polynesia. The color coded dots display the percent live coral cover at each location surveyed; see legend for values associated values.



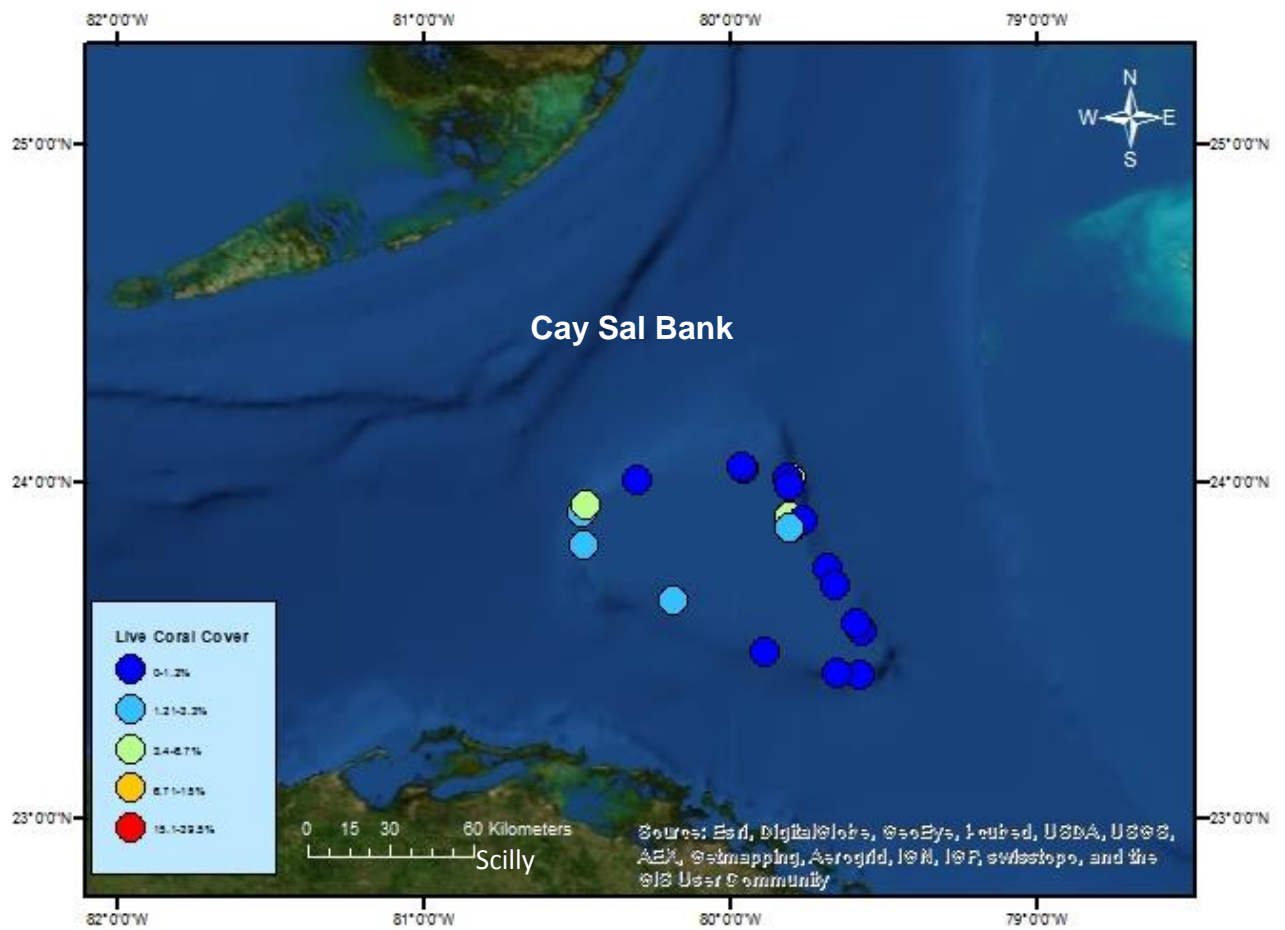
**FIGURE 4.11** Arc GIS close up map of the outer islands at the Society Islands. The color coded dots display the percent live coral cover at each location surveyed; see legend for associated values.



**FIGURE 4.12** Arc GIS close up map of the inner islands at the Society Islands. The color coded dots display the percent live coral cover at each location surveyed; see legend for associated values.

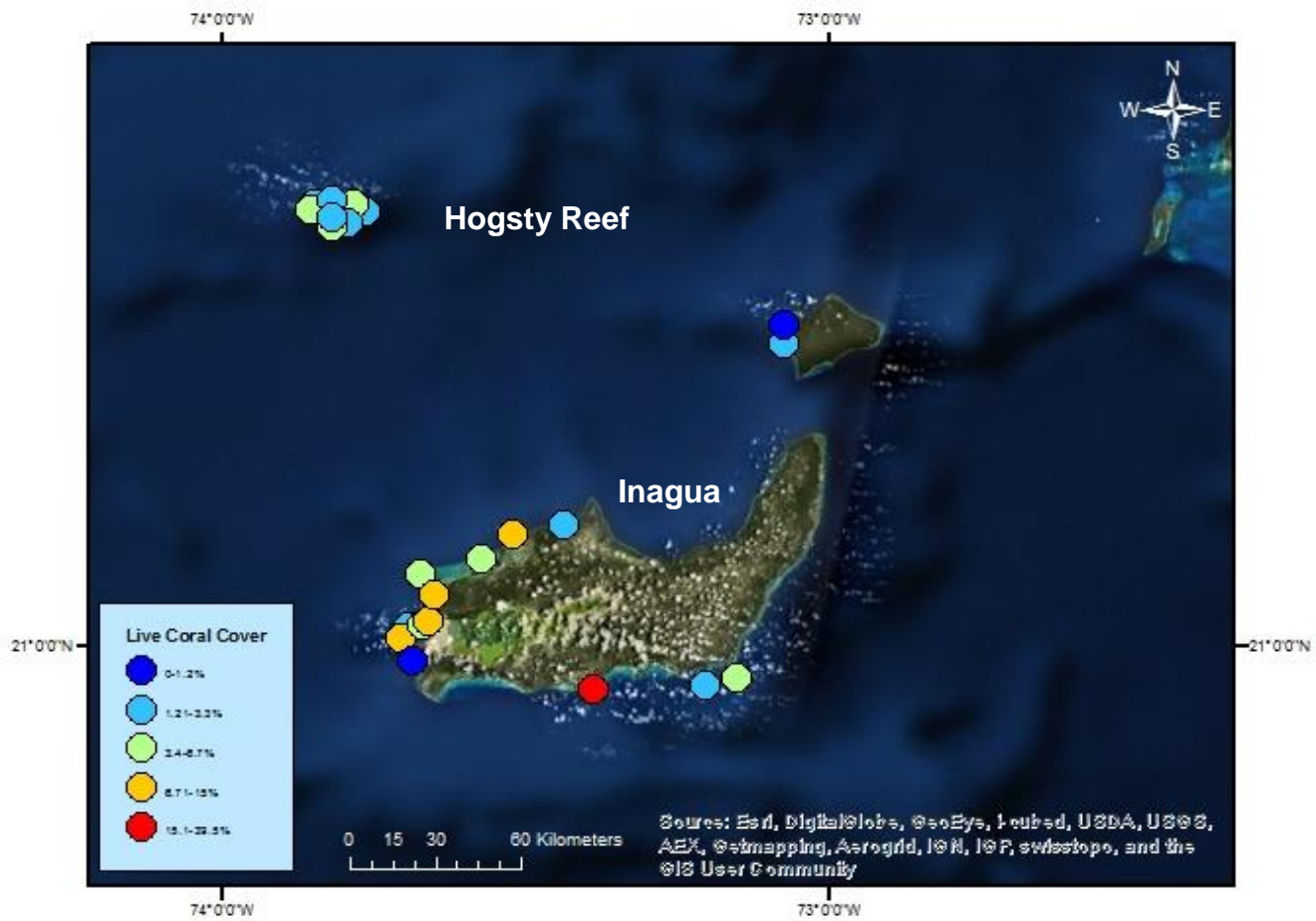


**FIGURE 4.13** Arc map of the Bahamas highlighting the three areas surveyed. The color coded dots display the percent live coral cover at each location surveyed; see legend for associated values.



**FIGURE 4.14** Arc GIS close up map of Cay Sal Bank. The color coded dots display the percent live coral cover at each location surveyed; see legend for associated values.

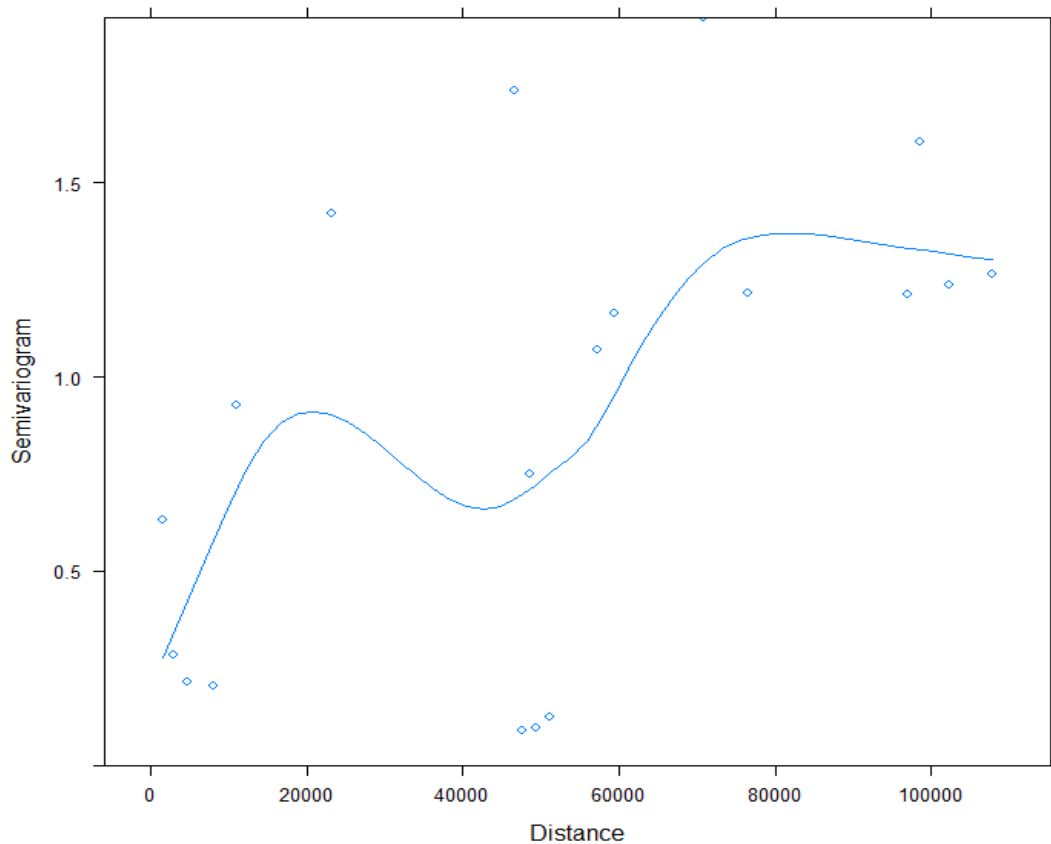




**FIGURE 4.15** Arc GIS close up map Inagua and Hogsty Reef. The color coded dots display the percent live coral cover at each location surveyed; see legend for associated values.

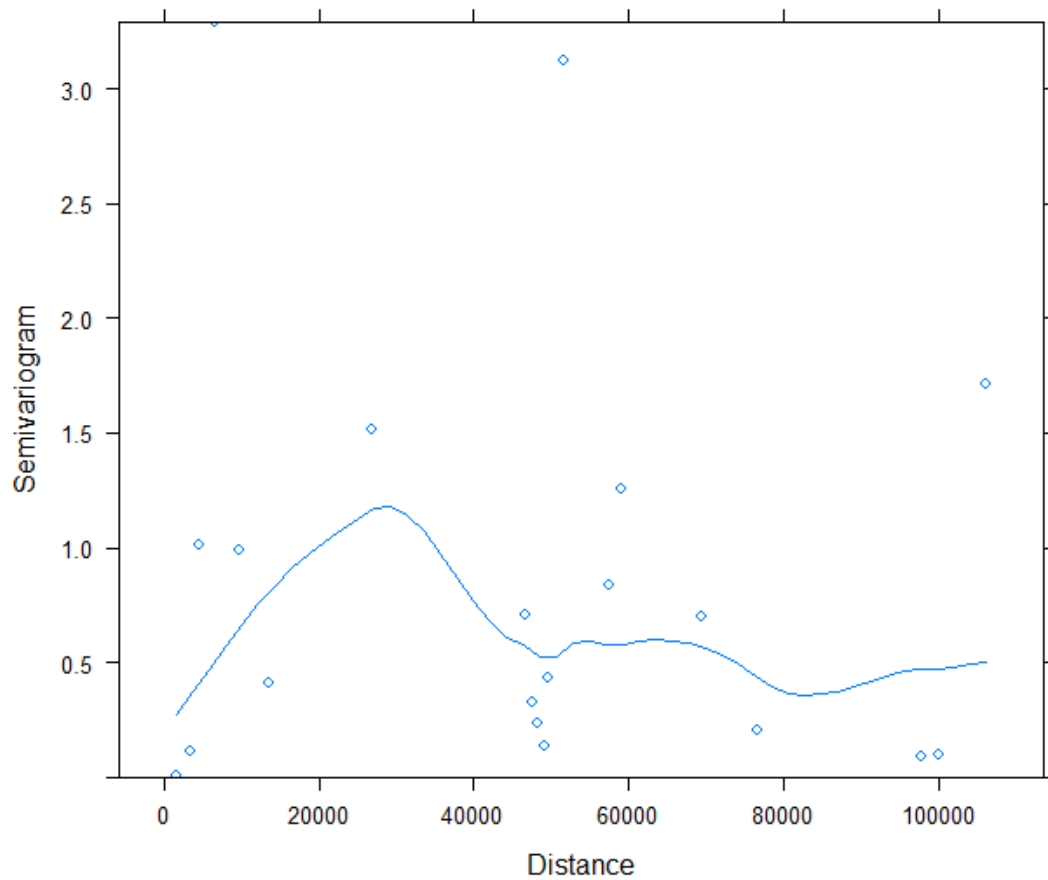
#### 4.2.4 SPATIAL AUTOCORRELATION

A variogram shows how spatial variance increases with spatial scale (Crawley 2007). To illustrate the presence or absence of spatial structure and correlation among the live coral cover data, variograms were constructed for each region surveyed. To help demonstrate this concept, synthetic data was created and used to show an ideal variogram that would occur from correlated live coral tissue cover (Fig. 4.16).

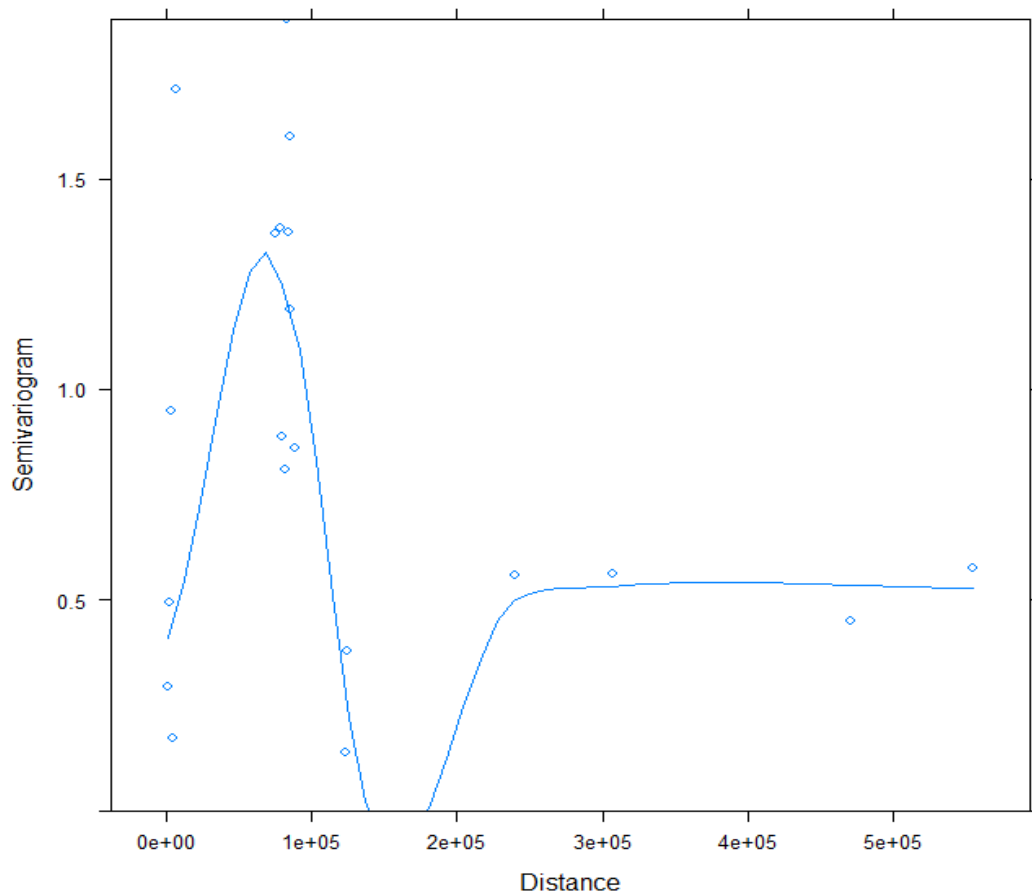


**FIGURE 4.16** Example variogram showing autocorrelation constructed from synthetic data of latitude and longitude coordinates of Universal Transverse Mercator units (kilometers) on the x-axis and semi-variance values  $\gamma(h)$  on the y-axis.

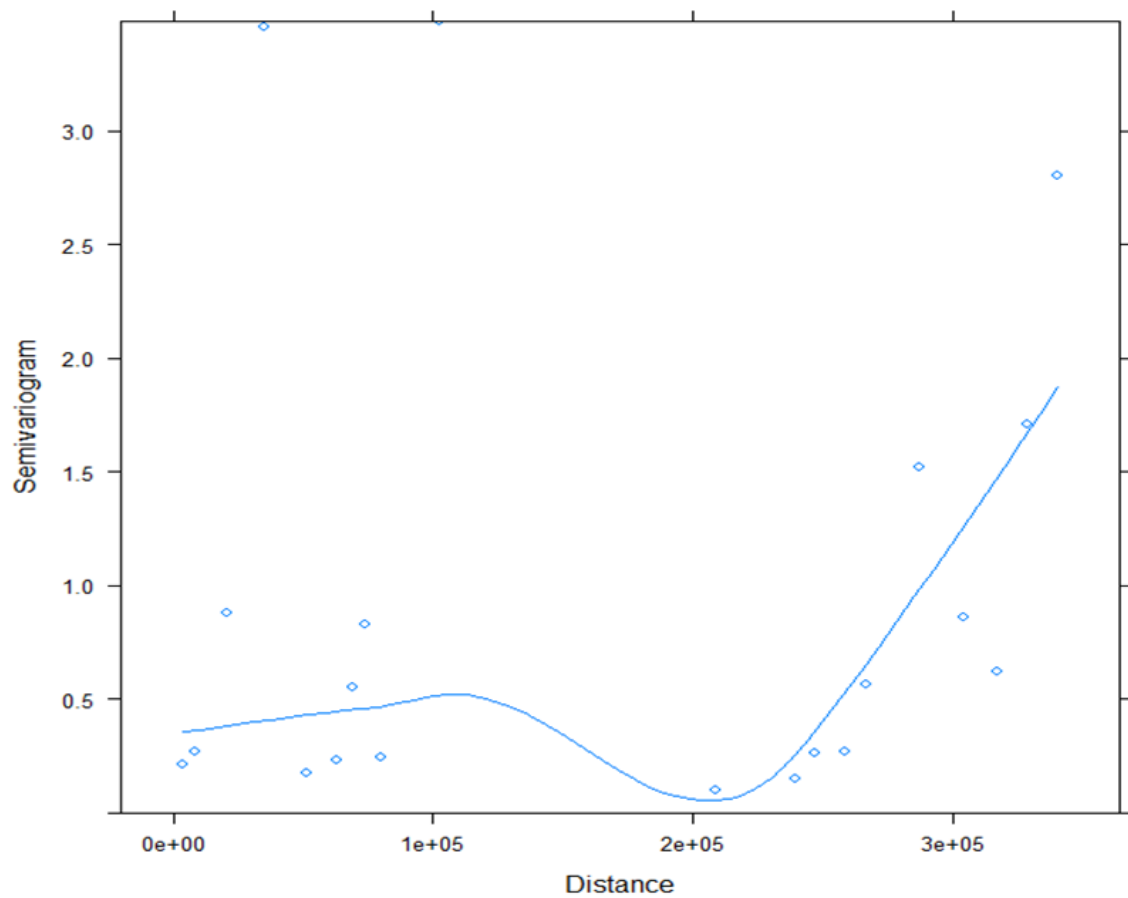
The variograms for this study use latitude and longitude translated into Universal Transverse Mercator (UTM) units of kilometers to observe the presence or absence of correlation between live tissue cover and geographic distance of each study site. Both positive and negative correlations have implications for management of the reefs post-disturbance (Legendre 1993). The variogram for the inner islands of Polynesia (Fig. 4.17) shows very little spatial correlation yet no clear asymptote to display the relationship between semi-variance and distance. The variogram from the outer islands size class data (Fig. 4.18) shows no clear correlation as there is a sinusoidal type curve followed by a drop in semi-variance and then an asymptote. This suggests a possible correlation between the more closely situated of the inner islands (Raiatea and Tahaa) but not all three. In the variogram of the Bahamian islands (Figure 4.19), there is also a lack of spatial correlation in the data shown by an extreme drop in semi-variance with relation to distance lag in kilometers and the value then rapidly increases. This shows no correlation among the three islands of the Bahamas. In assessing the variograms, caution should be taken, for a variogram must have an ample amount of data points and is used to describe the overall spatial structure but is not a test of spatial patterning nor is it useful in making comparisons of spatial variables (Fortin et al. 2002).



**FIGURE 4.17** Variogram representing the low level of spatial autocorrelation from the Inner Islands of the Society Islands in French Polynesia. The y-axis shows the semi-variance value  $\gamma(h)$  and the x-axis represents the distance lag between the study sites in kilometers by Universal Transverse Mercator units.



**FIGURE 4.18** Variogram representing the low level of spatial autocorrelation from the outer islands of the Society Islands in French Polynesia. The y-axis shows the semi-variance value  $\gamma(h)$  and the x-axis represents the distance lag between the study sites in kilometers by Universal Transverse Mercator units.



**FIGURE 4.19** Variogram representing the lack of spatial autocorrelation from Cay Sal Bank, Hogsty Bank and Inagua in the Bahamian Islands. The y-axis shows the semi-variance value  $y(h)$  and the x-axis represents the distance lag between the study sites in kilometers by Universal Transverse Mercator units.

#### 4.2.5 SECOND STAGE MULTI-DIMENSIONAL SCALING

The second stage analysis was done with size class data from the Society Islands and the size class data from the Bahamas. This analysis was performed to compared the spatial patterns of the Society Islands as a whole to the Bahamian Islands as a whole citing a strong relationship between the spatial ordinations of size classes in both regions,  $\rho = 0.829$  (Table 4.5). This analysis represented the comparison of strictly spatial patterns in assessing the trajectory of disturbance has occurred between two geographically distinct regions.

	Society Islands Size Classes	Bahamas Size Classes
Society Islands Size Classes		
Bahamas Size Classes	0.829	

**TABLE 4.5** Correlation matrix produced from second stage MDS of biotic variables

## **5. DISCUSSION**

### **5.1 FRENCH POLYNESIA**

The Society Islands of French Polynesia are impacted by multiple stressors. They have been subject to predatory outbreaks of *Acanthaster planci*, increasing coastal development and seven bleaching events over the past three decades (Pratchett et al. 2011; Salvat 2002). Multivariate statistics and spatial analyses are combined to observe the effect of compounding stressors on population structure of the coral colonies in this coral reef ecosystem.

#### **5.1.1 POPULATION STRUCTURE AND SPATIAL ASSESSMENT**

The distinct groupings in the Inner versus the Outer islands of the Society Islands provided an initial distinct division in the data set. Throughout the multivariate analysis, this division was used for further examination of the data. The composition of genera at the Outer Islands was more diverse with a larger number of branching corals. Branching corals are important for habitat complexity (Connell and Jones 1981; Pulliam et al. 1992) and the presence of branching corals is indicative of the health of the community as a whole (Soong 1992). The size classes measured showed high variation with individuals across all four size classes. The Inner Islands exhibited a lower diversity of coral genera with mainly massive corals and few branching genera. Only size class one (0-5cm) and two (5.1-10cm) were found, with no older aged corals of the larger size classes.

This assessment of coral diversity and sizes shows the Outer Islands have a better chance at recovery, mainly from less stress on the coral colonies (Penin et al. 2007; Nystrom et al. 2000). The greater diversity of corals and range of size classes (all ages of corals) is a sign of a healthier ecosystem (Hughes et al. 2010; Bruckner 2011). The Inner



Islands have a lower diversity of coral genera that consist mainly of smaller corals (younger aged corals). This suggests that this structure of diversity and sizes is due to delayed recovery after a major disturbance, most likely from the synergistic effect of multiple stressors (Golbuu et al. 2007; Vermeji and Bak 2000; Hughes 1984). The Inner Islands have a higher level of human habitation with resultant increased pollution (i.e. runoff and coastal development). Once a disturbance occurs; the coral populations have a lower chance of regrowth and further development at this location. Damaged corals cannot easily regrow and reefs subject to continual runoff, fishing and tourism have fewer resources for these coral to recover (Golbuu et al. 2007; Van Woesik and Jordan-Garza 2011; Done 1988).

Percent live cover was observed in the photo-transects and assessed from basic graphs and a bubble plot using GPS coordinates. The graphs showed a tenfold increase in percent live coral cover at the Outer Islands with high cover at the most isolated atolls of Scilly and Bellingshausen. The Inner Islands had low percent live cover, with the highest cover measured at the lagoonal sites. Lagoonal sites are not as often perturbed by storms as outer reef sites (Riegl et al. 2012) and therefore can maintain a higher live coral cover. The bubble plots showed the same results as the live cover bar graphs in terms of live cover at the islands. The high level of cover at the outer islands is probably characteristic of a low impact ecosystem. Without compounding natural and anthropogenic stresses, the corals have a much better chance at recovery when hit by bleaching, disease, or predators (Golbuu et al 2007).

The MDS ordinations give insight as to the community composition at the Inner and Outer Islands in terms of the different size classes (Clarke and Gorley 2006; Moyer

et al. 2003; Clarke and Warwicke 2001). At the Outer Islands, size class one was the most abundant, far ahead of classes two and three and size class four had a very low abundance. In terms of population structure this demonstrates support for the ability of coral populations at the Outer Islands to recover quicker or presumably less disturbance in the first place. Since it takes a long time to grow into size class four, few large individual corals are found, (Van Woesik and Jordan-Garza 2011, Graham and Nash 2013). This may also suggest continual disturbances that are not allowing corals to reach that large size (Penin et al. 2012; Golbuu et al 2007; Vermeji and Bak 2000; Graham and Nash 2013). The literature largely suggests the low level of larger corals at the Outer Islands is because of the slow growth rate of the corals. Recovery is evident from their presence, and with low sequential disturbances the corals simply take longer to reach the larger sizes (Hughes 1994; Vermeji and Bak 2000). At the Inner Islands, size classes three and four had the most similar contribution to community composition because of their rarity. The Inner Islands are made up entirely of size classes one and two (Table 4.3), i.e. by small corals only. The overall conclusions of the MDS plots are that the Outer Islands have a size frequency distribution showing a healthier coral community (Clarke and Warwicke 2001) than that of the Inner Islands. The MDS of the Outer Islands is highlighting the important transitional stages of the life history of the individual corals.

The principal component analyses exhibits two important conclusions ;( 1) the locational distribution of the size classes and (2) distinct grouping of the data between the islands groups. Size class one, the smallest corals, is most widely distributed across the islands with the greatest number of individuals. Size classes two and three were clearly more abundant at the outer islands and size class four was overall rare.

Most spatial structures found in nature are due to large-scale gradients (Legendre and Fortin 1989) making observations at neighboring points dependent. The ecological phenomenon of similarity among neighboring points is referred to as spatial autocorrelation. Experimental variograms were used to investigate spatial autocorrelation among the live cover at the islands. Constructing two variograms, one for the Outer Islands and one for the Inner Islands led to the conclusion of no spatial autocorrelation among either set of islands, suggesting that the structure of the communities/populations is not influenced by a large-scale trend. Since coral communities typically are indeed influenced by such trends, their demonstrated absence here hints at a disturbance having occurred and the live coral cover not yet having recovered (Zuur 2007; Griffith and Layne 1999).

Spatial correlation was very low and no large scale spatial structure based on size classes or live tissue cover was observed at the Inner or Outer islands; an interesting note since coral communities tend to show strong spatial auto-correlation, i.e. form distinctly similar spatial clusters on a between reef scale of neighboring islands (Pratchett et al. 2011; Adjeroud et al. 2007). The apparent lack of widespread spatial structure should be seen as evidence of effectively local disturbance. Furthermore, it is most likely attributed to localized disturbances with prominent impact (Legendre and Fortin 1989; Griffith and Layne 2007). In assessing the variogram, one must be cautious in that a variogram must have an ample amount of data points and is used to describe the overall spatial structure but is not a test of the spatial pattern and is not useful in making comparisons of spatial variables (Fortin et al. 2002).

### 5.1.2 CORAL COMMUNITY

The overall picture seen in the Society Islands is foremost a distinction between the Outer and the Inner Islands. The clear distinction between the locations supports the severity of increasing anthropogenic effects is a driving factor. The Society Archipelago has bleached seven times in the past three decades and spatial patterns among bleaching have been shown to be consistent among several different bleaching episodes (Penin et al 2012; Berumen and Pratchett 2006). The increasing number of bleaching events is accompanied by a rising number of storms that can displace many of the corals and cover others in sediment. If a regional event such as a storm or bleaching were responsible for the initial demise of the coral community, a widespread spatial structure would be evident, as opposed to the small scale structures currently seen across the reefs (Berumen and Pratchett, 2006; Adjeroud et al., 2007; Penin et al., 2007).

Coral populations are highly dynamic, and interference with the early successional stages of a coral community can negatively affect the development success of that community (Penin et al. 2007). The low diversity of coral genera, narrow range of coral size classes and lack of spatial autocorrelation at the Inner Islands suggests that the community structure was shaped by several localized disturbances, potentially followed by a continual disturbance that have not allowed the coral community as a whole to recover. The higher diversity of coral genera, increasing range of size classes yet lack of spatial autocorrelation at the Outer Islands suggests localized disturbances there as well, but an ecosystem without the compounding anthropogenic stresses that is allowing the corals to recover (Pratchett et al. 2011; Berumen and Pratchett 2006, Salvat 2002).

## 5.2 THE BAHAMAS

Most Caribbean studies are focused on populated areas. The regions of the Bahamas used in this study are largely unpopulated and of low direct human impact. The reefs present however are still in very poor condition. Multivariate statistics and spatial analyses are combined to observe the effect of compounding stressors on population structure of the coral reef ecosystem.

### 5.2.1 POPULATION STRUCTURE AND SPATIAL ASSESSMENT

The species composition observed across the Bahamas was very similar. Only one species of branching corals were seen (*Porites porites*) and one genera of plating (*Agaricia spp.*), leading to a low habitat complexity at almost all sites. Low habitat complexity can be detrimental to the community surrounding the corals (Connell and Jones 1981; Pulliam et al. 1992) by failing to provide habitat and protection for associated fish species (Hughes 1994; Hughes and Connell 1999). At all regions, size class one (0-5cm diameter) was the most dominant, while the sites varied with transitional size classes. At Cay Sal Bank, there was an increase in the presence of size class two (5.1-10cm) and three (10.1-20cm) on the North East section of the bank. Inagua's size class distribution was similar with mostly size class one and several individuals of size class two on the north west side of the island. On Hogsty reef a similar distribution was found of mostly all size class one but the presence of size class two on the North side of the reef. From this assessment of coral diversity and sizes, there were no significant differences found across the islands. The results show the Bahamas as whole is an extensively disturbed reef ecosystem. This is demonstrated by the dominance of the

small size class coinciding with low coral cover. The small size class refers to recruits or partial mortality (Meesters et al. 2001; Bak and Meesters 1998; Bruckner 2011). Compounding disturbances such as large storms degrade reefs in addition to more localized disturbances such as coral disease (Bruckner 2011; Berumen and Pratchett 2006; Jones et al. 2004). The results of the coral diversity support the small size class dominance as the majority of corals are massives; mostly slow growing species (Veron 2000). Differences in size class distributions can be caused by multiple factors on a reef. Most often noted is the random variation in coral settlement. This is due to chemical cues and physical factors such as currents that influence the settlement of coral recruits (Richard and Hunter, 1990; Maina et al., 2008). However, the focus of this study was on the effects of disturbance

The MDS ordination of the Bahamian region identifies size classes two and three as the most similar in their contribution to the composition of the coral community. Although size class one is dominant, size class four is almost nonexistent; this explains the isolation on the MDS plot. The presence and similarity of size classes two and three show the presence of transitional life history stages although there are very few corals of that age. The PCA confirms distinct clustering in the data set, specifically Inagua and Hogsty as one group and Cay Sal Bank as another; a clustering that makes sense due to the geographic separation. Both locations show the same coral species present, size class distributions and percent coral cover. Being separated by a 620km ground distance, the similarities in biotic characteristics of these islands supports the idea of local disturbances being the most influential stressor (Pratchett et al 2011; Bruckner 2011).

An experimental variogram was used to look for spatial autocorrelation among the live coral cover across the three Bahamian regions. The variogram constructed showed no spatial correlation, discounting region-wide perturbations as the influential factor on the population dynamics of the coral community. The size class distribution and low coral cover supports continuous disturbance while the lack of spatial correlation again suggests that a localized disturbance was the initial source of destruction (Legendre and Legendre 2012; Legendre and Fortin 1989).

### 5.2.2 CORAL COMMUNITY

Population dynamics must be taken into consideration when studying ecological processes and their effects on coral populations. Patterns of abundance are affected by settlement, growth, mortality and disturbances on any of those processes (Adjeroud et al. 2007). Size structure can vary enormously over small scales, and when variation exists only between small sizes and is accompanied by low cover, it is often due to a recent perturbation (Penin et al. 2007; Hughes 1994; Van Woesik and Jordan-Garza 2011). The combined effect of multiple disturbances can lead to permanent shifts in the community (Berumen and Pratchett 2006; Adjeroud et al. 2007).

Interestingly, in the Caribbean region, smaller size classes observed were often from partial mortality in the coral communities instead of recruits. This can often imply disease as the vector of local disturbance (Bruckner 2011; Bruckner 2002). A second likely vector of localized disturbance is algal overgrowth (Hughes et al. 2005; Mumby et al. 2007). After the die off of *Diadema antillarum*, macro algae growth in the Caribbean greatly increased, covering up much of the hard substrate that coral recruits would use to settle on (Nystrom et al. 2000; Hughes 1994; Miller et al. 2000).

### 5.3 FRENCH POLYNESIA AND THE BAHAMAS

As hypothesized, a distinct spatial structure exists as a result of synergistic disturbances. In accordance with Legendre and Fortin (1989), the spatial structure present shows no autocorrelation, but an underlying structure in the form of variation in size classes in coral populations. This is likely due to varying disturbances sources. A second stage MDS was used to compare (spatial) patterns of the size frequency distributions (Clarke and Gorley 2006) from the Society Islands and the Bahamas. By comparing only the patterns shown across both regions, a spearman rank correlation test was run with a result of  $\rho = 0.829$ . This value is close to 1, showing a strong relationship in the spatial patterns of both the Bahamas and French Polynesia. The two regions are very different in location, reef composition and oceanographic characteristics and cannot be compared numerically. However, a rank correlation evaluating the spatial pattern will produce a valid assessment of how disturbance in general has affected both regions (Clarke and Warwicke 2001). The strong relationship displayed shows that in both areas, the disturbances that are actually killing the corals are local, not regional. Although hurricanes/cyclones and bleaching are discussed most often, these disturbances can cause extensive damage to the reef but do not seem to be the source of death for the corals. Local disturbances such as *Acanthaster* in the Pacific or coral diseases in the Caribbean are presumably responsible for the majority death of the corals (Pratchett et al. 2011; Berumen and Pratchett 2006; Bruckner 2011). Since death occurs at different times it results in unique regeneration patterns that negate autocorrelation (Pratchett et al. 2011). Regional widespread disturbances seem to secondarily destroy the structure of the already dead coral community.



The overall spatial assessment at both locations is clear evidence of disturbed reefs. When using the coral size structure data to assess the origin of disturbance the spatial correlation results are important. One of two major conclusions can be drawn from this data; either an overprint of local events on region-wide events in disturbance or local regeneration dynamics are overprinting region-wide disturbance. Both conclusions highlight the importance of observing localized impacts and being able to manage the affected reefs according to the scale of the impact.

#### **5.4 MANAGEMENT IMPLICATIONS**

Size frequency distributions provide a sensitive means of discerning change in coral communities in response to disturbances. Size distribution studies help identify differences between populations exposed to differing degrees of environmental stressors (Bruckner 2011). The spatial and sometimes temporal consistency in bleaching patterns is important for conservation planning. This consistency shows how some areas can acclimatize and cope with bleaching while others are not able to (Penin et al. 2007; Adjeroud et al 2007).

As an objective of this study, an overall picture of disturbance has been created at two distinct regions with the effects of local versus regional scale perturbations defined. It has been noted that both coral cover and size classes together are necessary to provide a meaningful data set that considers the health of the coral community as a whole. In observing the different responses to scaling of disturbances, the importance of tailoring management of coral reefs to specific disturbance (Elmqvist et al. 2003; Bellwood et al. 2004; Dale et al. 1994) is apparent.

Structural complexity is integral to coral reef ecosystems (Graham and Nash 2013). It is a component that should be adapted into monitoring protocols and management objectives. Management actions should foster survival of the residuals and the spatial heterogeneity that supports the desired pattern of recovery (Dale et al. 1994). The lack of spatial autocorrelation implicates localized disturbances as the main source of destruction. Therefore, recovery plans should focus on critical stages of the successional processes at disturbed reefs of these characteristics. With continued large scale disturbances occurring after the small scale perturbations, it is crucial to identify the need for action as quickly as possible. There is now ongoing research of coral reef communities with focus on synergistic effects of combined or sequential disturbances (Berumen and Pratchett 2006).

Severe disturbance or synergistic disturbances may lead to permanent shift in dominance and or community structure (Berumen and Pratchett 2006; Dale et al. 1994). Permanent shifts are associated with environmental degradation a loss of functional groups. Certain functional groups are crucial for a certain level of ecosystem services, making this a vital focal point of conservation on coral reefs (Dale et al. 1994; Elmqvist et al. 2003).

## **6. SUMMARY AND CONCLUSIONS**

Disturbances have an important influence on coral reef ecosystems. Although region-wide disturbances are thought to be the most severe, it appears these impacts are not to blame for initial demise of the coral communities surveyed for this study. Although the reef exhibit key signs of continual disturbance, the lack of spatial correlation in

population patterns suggests that localized disturbances are most influential. In French Polynesia, *Acanthaster planci* outbreaks are presumably the culprit of initial coral death. Bleaching, cyclones, and or coastal development then occur and further degrade the remainder of the coral community. As slow growing organisms, corals require a long time between impacts to maintain a healthy community - apparently more time than has been available. The Polynesia Outer Islands of the Society Archipelago experienced regeneration. This is shown by a wide array of size classes and higher live cover. The Outer Islands differ in that they are uninhabited and suffer very low direct human impact. The Inner Islands however experience continual impacts from direct human impact of coastal development on top of natural disturbances.

In the Caribbean, frequent and severe disturbances are characteristic of the region. For this study, the reefs surveyed were farther from direct human impact and away from inhabited areas. Interestingly the coral communities were still in poor condition and disturbed. Low diversity and live cover as well as mainly small corals were observed. No spatial correlation was calculated showing again small scale disturbance was to blame for the demise of the community. Most likely coral disease and algal overgrowth are the reasons. Region-wide disturbances such as bleaching or hurricanes are recorded for the area, but must be the secondary factor and are responsible for sequential perturbations.

From a management perspective, the identification of a disturbance origin is important for effective monitoring protocols. Management actions must promote survival of recruits, residuals and spatial heterogeneity for a desired recovery pattern. Tailoring protocols to focus on early successional stages of the corals is a suitable place to start. Specific functional groups are crucial to maintain many ecosystem services. Identifying

the services most important to the region and the functional groups responsible is a best management practice for regions such as Polynesia where livelihood of the local people thrives on many services from the reefs. Ecosystem responses can vary regionally due to differences in population dynamics, but it is vital that our methods of management change to cope with more localized disturbance.

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