

THE DISTRIBUTION OF CORAL, REEFS AND COASTAL HABITATS IN NORTH  
CENTRAL CUBA

by

Aisling Kathleen Brady

A thesis submitted in conformity with the requirements  
for the degree of Masters of Science

Department of Geography  
University of Toronto

© Copyright by Aisling Kathleen Brady, 2008



Library and Archives  
Canada

Published Heritage  
Branch

395 Wellington Street  
Ottawa ON K1A 0N4  
Canada

Bibliothèque et  
Archives Canada

Direction du  
Patrimoine de l'édition

395, rue Wellington  
Ottawa ON K1A 0N4  
Canada

*Your file Votre référence*

ISBN: 978-0-494-58764-5

*Our file Notre référence*

ISBN: 978-0-494-58764-5

#### NOTICE:

The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

---

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

#### AVIS:

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

---

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

■ ■  
Canada

The Distribution of Coral, Reefs and Coastal Habitats in North Central Cuba

Aisling Kathleen Brady

Masters of Science

Department of Geography  
University of Toronto

2008

**ABSTRACT**

Coral communities have begun to form under small inlet-style bridges along the causeway connecting Cayo Coco to Cayo Guillermo. To understand how these bridge-reefs formed and characterize their attributes relative to surrounding communities, a combination of ecological observations and  $^{13}\text{C}$  isotopes were analyzed from the bridges and surrounding reefs, mangrove channels and seagrass patches. Hierarchical Cluster Analysis, Detrended Correspondence Analysis and Canonical Correspondence Analysis were carried out to group which physical attributes contributed to the coral communities in the bridge-reefs and also which habitats they were most similar to, with respect to coral and benthic composition. Bridge reef coral assemblages resembled shallow patch reefs and mangrove channels, while benthic coverage was similar to mangrove channels. Organic matter was from combined seagrass and mangrove sources, with mangrove dominating in some regions more than others. This work demonstrates that habitats within the seascape are inter-related through varying mechanisms and development is multi-dimensional.

## **ACKNOWLEDGMENTS**

I would like to first and foremost thank Sharon Cowling for not only giving me this opportunity to work in Cuba on coral reefs, but also for all her support, encouragement, supervising and overall enjoyment over the past few years. I hope one day to return and make great collaborations with you! You have not only been my supervisor, but also an amazing mentor, a travel companion and a friend. Thank you for everything!

I would like to acknowledge and thank my family for all of their support and guidance during my masters, especially all the career advice and listening ears from Mum, Dad, Siobhan, Liam and Jeremy. Siobhan and Liam – you've both been an inspiration for me to continue in academia, and of course my parents in their encouragement to continue with what I love. And although he hasn't been with me for the entirety, I would like to thank Andre for all his encouragement, being a sounding board for ideas and his interest and support in what I am doing.

My lab mates... where would I be without you? Carlos, thank you so much for all your intelligence, ideas, editing and advice in not only all the statistics of my project, but also inspiring me through our varying conversations on land/seascape ecology, island biogeography, community ecology and other theories; and of course all your help with practicing my Spanish! You have helped me grow intellectually, and I thank you for it. ¡Muchas gracias! Younglan, your encouragement has been never fading since our first class together over 4 years ago. I hope one day to be as dedicated to my work as you are to yours. Melissa, your laughter is always contagious, and I couldn't have asked for anyone better to sit beside me. You made coming in to the lab such a joyful experience. I am sure success will follow you wherever you are. And last but certainly not least, Rebecca. Sharing an office with you has been such an amazing time. Your insight, experience and amazing sense of humour have made my Masters so enjoyable. You have been there for me through the good and the bad, and I am going to miss seeing you on a daily basis. I hope our friendship will continue through the years, and we will maintain our support network for each other as we continue to become incredible female scientists.

I would like to thank the staff, faculty and grad students at the Department of Geography. I have been a part of this institution for almost 6 years, and it has been a joy. It has been a place where I feel belonging and support, and I am thankful for all the encouragement and success it

has given me. I would especially like to thank Professors Tenley Conway, Tony Davis, Joe Desloges and Sarah Finkelstein. You have each helped me reach the final product of my thesis through varying ways, and I would not have been able to do so without your support.

I have been fortunate to have two amazing field assistants and a co-researcher while completing field work in Cuba. Greg Bunker, you were a pleasure to work and travel with and brought many new ideas to the table. Jeff Blake, spending six weeks with you was so much fun. Your thirst for knowledge was unstoppable, and I was shocked at how much you learned in such a short period of time. I hope one day we can collaborate again, and create a fully restored reef ecosystem. And most importantly, Sarah Caldwell – we started this project together, and I’m sad that we weren’t able to finish together. You have so much experience with fish and tropical systems, and it was such a pleasure to work and live with someone who was as excited about marine biology as I was. You will make an incredible teacher, and your students will be so lucky to have you touch their lives, as you have mine.

Lastly, I would like to acknowledge all the hard work and support given to me from the Centro d’Investigaciones Ecosistemas Costeros (CIEC) in Cayo Coco, Cuba. The scientists and staff working at this research station were such amazing, intelligent people. I have truly been lucky to collaborate with such incredible scientists. The wealth of information gained from this institution will remain with me forever, and I am truly a better scientist for having worked with all of you. I would especially like to thank Vicente for all your hard work coordinating visas, visits, food etc... for myself and all other visiting researchers from the University of Toronto. Fabian, thank you for all your help translating and working with us at the beginning, it was a pleasure sharing our research with you. Roberto, your research skills and depth of knowledge is astounding, and I thank you for all your help in the lab and providing me with new ideas. Mayrene, Gerrardo, Osmani, Omar, Alain, Hector and everyone else who assisted in the collection of data, preparation of samples, technical coordination and identification of species, thank you so much for your help. And last, but certainly not least, I wish to thank Leslie. You are an amazing scientist with an extraordinary wealth of knowledge on coral and invertebrates. I am truly lucky for having had the chance to work with you and have you treat me like family. I hope that one day you will have the opportunity to travel the world and accomplish all that you wish to do. I hope this is the beginning of many more collaborations. Thank you for everything!

## TABLE OF CONTENTS

<b>ABSTRACT .....</b>	ii
<b>ACKNOWLEDGMENTS .....</b>	iii
<b>TABLE OF CONTENTS .....</b>	v
<b>LIST OF TABLES .....</b>	vii
<b>LIST OF FIGURES .....</b>	viii
<b>LIST OF APPENDICES .....</b>	xi
<b>CHAPTER ONE: Introduction .....</b>	1
1.1 Background .....	1
1.2 Bridging Seascape and Landscape Ecology.....	2
1.3 Habitat Development, Succession and Zonation .....	6
1.4 The Discovery .....	10
1.5 Rationale .....	11
1.6 Research Objectives .....	14
1.6.1 Chapter Two .....	14
1.6.2 Chapter Three .....	16
1.7 References .....	17
<b>CHAPTER TWO: Unexpected reef formations under a coastal causeway in Cayo Coco and Cayo Guillermo, Cuba .....</b>	29
1 Introduction .....	29
2 Methods .....	32
2.1 Study Sites .....	32
2.2 Study Systems .....	32
2.2.1 Bridge Reefs .....	32
2.2.2 Mangrove Channels .....	33
2.2.3 Seagrass Beds .....	34
2.2.4 Natural Reefs .....	34
2.3 In-Situ Observations .....	35
2.3.1 Environmental Variability .....	35
2.3.2 Coral Communities .....	37
2.3.3 Benthic Composition .....	38
2.4 Statistical Analysis .....	38
3 Results .....	40
3.1 Inter-Bridge Comparisons .....	40
3.1.1 Environmental Variability .....	40
3.1.2 Coral Communities .....	41
3.1.3 Benthic Composition .....	42
3.2 Inter-Habitat Comparisons .....	43
3.2.1 Environmental Variability .....	43

3.2.2 Coral Communities .....	45
3.2.3 Benthic Composition .....	46
4 Discussion .....	49
4.1 Bridge Reef Structure and Function .....	49
4.1.1 Coral Community Connectivity .....	49
4.1.2 Physical Environmental Constraints and Controls .....	50
4.1.3 Benthic Community Structure and Form .....	52
4.2 Terrestrial-Marine Continuum: Integrated Seascapes Studies .....	53
4.2.1 Connecting the Bridge Reefs to the Seascapes .....	53
4.2.2 Coral in Marginal Habitats .....	53
4.2.3 The Natural Reefs of the Cayo Coco – Cayo Guillermo Reef Tract .....	55
5. Conclusions .....	57
6. References .....	59
<b>CHAPTER THREE: Using <math>\delta^{13}\text{C}</math> and C/N ratios as tracers in unusual reef habitats and their surrounding seascapes .....</b>	<b>98</b>
1 Introduction .....	98
2 Methods .....	101
2.1 Study Sites .....	101
2.2 Study Systems .....	101
2.3 Primary Productivity .....	101
2.3.1 Seagrass Biomass and Coverage .....	101
2.3.2 Mangrove Forest Characterization .....	102
2.4 Isotope Sampling and Analysis .....	102
2.4.1 Isotope Sampling and Preparation .....	102
2.4.2 Isotope Analysis .....	103
3 Results and Discussion .....	105
3.1 Abiotic and Biochemical Factors Affecting Seagrass Productivity .....	105
3.2 Mangrove “Productivity” .....	106
3.3 Influence of Mangrove Detritus on Organic Carbon Sampled along a Cuban Seascapes .....	107
4 Conclusions .....	110
5 References .....	111
<b>CHAPTER FOUR: Conclusion .....</b>	<b>125</b>
1 Connectivity within the Tropical Seascapes .....	125
2 Future Directions .....	127
3 References .....	130

## LIST OF TABLES

### CHAPTER TWO

<b>Table 2.1.</b> Site locations and habitat types .....	65
<b>Table 2.2.</b> Abbreviations of environmental variables measured and benthic coverage types used in ordination plots .....	66
<b>Table 2.3.</b> Scleractinian and Milliporinian coral colony abundances, based on 0.5x0.5m quadrats at each site (n=25) .....	67

### CHAPTER THREE

<b>Table 3.1.</b> Mean ( $\pm$ standard error) seagrass characteristics for sites supporting <i>Thalassia testudinum</i> meadows: Shoot density, canopy height, percent coverage and seagrass biomass (above and below ground) estimates for those sites supporting seagrass meadows .....	117
<b>Table 3.2.</b> Physical and Environmental Means ( $\pm$ standard error) for each variable measured at all sites .....	118
<b>Table 3.3.</b> C/N Ratios (% weight) for all sites measured, with mean % compositions of Carbon and Nitrogen included .....	119
<b>Table 3.4.</b> Perimeter (km) and area (km <sup>2</sup> ) of mangrove forest ( <i>Rhizophora mangle</i> ) surrounding bridge reefs and mangrove channels in Zones 2 and 3, based on satellite imagery from Landsat-7 ETM+, 2001 .....	120

## LIST OF FIGURES

### CHAPTER ONE

**Figure 1.1.** The traditional view of landscape ecology, and how it has developed into seascape ecology. Stemming from seascape ecology are the main components driving this new field.... 28

### CHAPTER TWO

**Figure 2.1.** Location of study sites in Jardines del Rey, Ciego d'Avila province, Cuba. See Table 2.1 for co-ordinates of sites and site descriptions ..... 68

**Figure 2.2.** Distribution of mixed-species mangrove forests surrounding the bridge reef sites, and the delineation of zones, based on the presence of bridge sites, used in analysis ..... 69

**Figure 2.3.** Characteristic view of Bridge Reef Zone 1: a) entrance area of inlet; b) scouring of pools (facing south) ..... 70

**Figure 2.4.** Water flow entering inlets on the north side of Bridge Reef Zone 2 ..... 71

**Figure 2.5.** Water flow entering inlets on the south side of Bridge Reef Zone 3 ..... 71

**Figure 2.6.** Mangrove channel reef areas: a) interior portion approaching Bridge Reef Zone 3; b) dense mangrove forest along edges of channels; and c) initial channel looking seaward (north) ..... 72

**Figure 2.7.** Cumulative number of coral species vs. number of quadrats sampled for reefs at (a) Zone 1, (b) Zone 2 and (c) Zone 3 ..... 73

**Figure 2.8.** Physical-Environmental variables measured at each bridge reef site during high tide measurements: a) Conductivity ( $\text{mS cm}^{-1}$ ); b) Salinity (ppt); c) Total Dissolved Solids ( $\text{g L}^{-1}$ ); d) Dissolved Oxygen ( $\text{mg L}^{-1}$ ); e) Current speed ( $\text{cm s}^{-1}$ ); f) Complexity ratio ( $\text{m m}^{-1}$ ); g) Depth (m); h) Temperature ( $^{\circ}\text{C}$ ); i) Water turbidity (NTU). The upper and lower boundaries of the box plot indicate the 75<sup>th</sup> and 25<sup>th</sup> percentile, respectively. The thin solid line within the box is the median, and the thick solid line is the mean ..... 74-75

**Figure 2.9.** Hierarchical Cluster Analysis dendrogram of bridge reef sites, based on physical variables measured at each bridge reef, using relative Euclidean distance measurements ..... 76

**Figure 2.10.** Detrended Correspondence Analysis of the Bridge Reef Sites, with physical variables used to determine site scores (eigenvalue scores: axis 1 = 0.0369; axis 2 = 0.0034) ..... 77

**Figure 2.11.** Detrended Correspondence Analysis of the Bridge Reef Sites, with replicated coral quadrats used to determine species scores, based on coral species abundances (eigenvalue scores: axis 1 = 0.6354; axis 2 = 0.1129) ..... 78

<b>Figure 2.12.</b> Coral colony size and number of colonies counted for entire transect (n = 25 quadrats) at each site. Box plots represent colony size, and line plots represent the number of colonies present at the individual site. The upper and lower boundaries of the box plot indicate the 75 <sup>th</sup> and 25 <sup>th</sup> percentile, respectively. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5 <sup>th</sup> and 95 <sup>th</sup> percentiles. Outliers (circles) and low number of colonies (<3) (squares) are plotted as individual points .....	79-81
<b>Figure 2.13.</b> Benthic coverage for a) Zone 1, b) Zone 2, c) Zone 3. Box plots represent percent coverage variation for each coverage type, with the lower boundary of the box indicating the 25 <sup>th</sup> percentile and the upper boundary of the box the 75 <sup>th</sup> percentile. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5 <sup>th</sup> and 95 <sup>th</sup> percentiles. Outliers (circles) are plotted as individual points .....	82-83
<b>Figure 2.14.</b> Hierarchical Cluster Analysis dendrogram, using relative Euclidean distance measurements, of bridge reef sites, based on percent benthic coverage quadrats measured at each bridge reef .....	84
<b>Figure 2.15.</b> Detrended Correspondence Analysis of the Bridge Reef Sites, with replicated percent benthic coverage quadrats used to determine site scores (eigenvalue scores: axis 1 = 0.4734; axis 2 = 0.3593). Outlying benthic coverage ordination points were removed to better demonstrate trends, with the exception of Coral and Other coverage categories, due to their more scattered occurrences .....	85
<b>Figure 2.16.</b> Physical-Environmental variables measured at all sites: a) Conductivity (mS cm <sup>-1</sup> ); b) Salinity (ppt); c) Total Dissolved Solids (g L <sup>-1</sup> ); d) Dissolved Oxygen (mg L <sup>-1</sup> ); e) Current speed (cm s <sup>-1</sup> ); f) Complexity ratio (m m <sup>-1</sup> ); g) Depth (m); h) Temperature (°C); i) Water turbidity (NTU). The upper and lower boundaries of the box plot indicate the 75 <sup>th</sup> and 25 <sup>th</sup> percentile, respectively. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5 <sup>th</sup> and 95 <sup>th</sup> percentiles. Outliers are plotted as individual points .....	86-87
<b>Figure 2.17.</b> Hierarchical Cluster Analysis dendrogram of all sites, based on physical variables measured at each site, using relative Euclidean distance measurements .....	88
<b>Figure 2.18.</b> Detrended Correspondence Analysis of all sites, based on physical and environmental variables to determine site scores (eigenvalue scores: axis 1 = 0.0462; axis 2 = 0.0074) .....	89
<b>Figure 2.19.</b> Hierarchical Cluster Analysis dendrogram of all sites, based on coral species diversity and abundances, using relative Euclidean distance measurements .....	90
<b>Figure 2.20.</b> Detrended Correspondence Analysis of all sites and coral species, based on coral quadrats to determine species scores (eigenvalue scores: axis 1 = 0.5419; axis 2 = 0.2591) .....	91

<b>Figure 2.21.</b> Canonical Correspondence Analysis of coral species and sites corresponding to environmental and physical variables (eigenvalue scores of axis 1 = 0.542 and axis 2 = 0.37)	92
<b>Figure 2.22.</b> Benthic coverage for a) MC2, b) MC3, c) NR1PR, d) NR1RC, e) NR2SG, f) NR3RS. Box plots represent percent coverage variation for each coverage type, with the lower boundary of the box indicating the 25 <sup>th</sup> percentile and the upper boundary of the box the 75 <sup>th</sup> percentile. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5 <sup>th</sup> and 95 <sup>th</sup> percentiles. Outliers (circles) are plotted as individual points	93-94
<b>Figure 2.23.</b> Hierarchical Cluster Analysis dendrogram of all sites based on replicated percent benthic coverage quadrats, using relative Euclidean distance measurements	95
<b>Figure 2.24.</b> Detrended Correspondence Analysis of all sites and benthic coverage percentages, based on percent coverage quadrats to determine site scores (eigenvalue scores: axis 1 = 0.4129; axis 2 = 0.2897). Outlying benthic coverage ordination points were removed to better demonstrate trends, with the exception of Other coverage category, due to its more scattered occurrence	96
<b>Figure 2.25.</b> Canonical Correspondence Analysis of coral species and sites corresponding to benthic coverage types (eigenvalue scores of axis 1 = 0.419 and axis 2 = 0.323)	97

## CHAPTER THREE

<b>Figure 3.1.</b> Typical setup used to collect <i>T. testudinum</i> biomass cores <i>in-situ</i> . Small x's radiating out from the centre (delineated by a circle with X inside) were the sites of cores collected. Each radiating line measured approximately 5 m, and was taken at random angles from the centre	121
<b>Figure 3.2.</b> $\delta^{13}\text{C}$ isotope values for varying sediments and leaves of three different zones and types of habitats within the seascape: a) bridge reefs; b) mangrove channels; c) seagrass beds; and d) natural reefs	122-123
<b>Figure 3.3.</b> Cayo Coco-Guillermo seascape transect in seaward direction, indicating habitat types, typical species and route of juvenile reef fish. Size of reef fish indicates typical age of fish found in that particular habitat (i.e. small = juveniles, medium = intermediates, large = adults) ...	124

## LIST OF APPENDICES

<b>APPENDIX A:</b> Gonzalez-de Zayas, R. 2005. <i>Dynamics of salt, nutrients and organic matter in three bridges of Cayo Guillermo causeway</i> . Unpublished Report. CIEC, Cayo Coco.....	134
<b>APPENDIX B:</b> Fish presence/absence throughout the bridge reefs, based on fish surveys conducted in February 2005 .....	141

## **CHAPTER ONE: Introduction**

### **1.1 BACKGROUND**

Tropical coastal regions globally are experiencing rapid development due to tourism, agriculture and urbanization, often resulting in adverse effects on marine ecosystems and processes (Schaffelke et al. 2005). As population growth expands in the Caribbean and Latin America, land-use change becomes more prevalent, with shifts from rural to urban settings. As a result of this land-use shift, all surrounding ecosystems, including marine, have experienced dramatic resource exploitation efforts to meet population demands.

Containing the highest population and landmass in the Caribbean, Cuba has experienced significant land-use change over the past century, causing several environmental concerns. Due to the political uniqueness of this country, Cuba became dependent on agriculture during a time of recession and isolation in the 1990s, with over a third of persons in the labour force working in agriculture (Perez 1995). Some of the major environmental concerns following the ‘Special Period’ (1990-2000) have included terrestrial degradation, especially deforestation for wood and farming, dam construction, mining and clearing of land for tourism and military operations (Maal-Bared 2006). Marine degradation has also occurred, with increased levels of eutrophication from runoff, over-fishing of commercial fish and lobster species and sedimentation from land-use changes (Alcolado 1991, Claro and Lindeman 2003, González-Díaz et al. 2003). Recently, tourism has become one of Cuba’s main sources of income, with tourists arriving from mainly Canada and Europe. To encourage and continue this success, many coastal areas previously undisturbed have become havens for resort development. North-Central Cuba was particularly an ideal choice due to

the crystal white sands and aqua blue waters characteristic of the Jardines del Rey region. Development however, comes with inherent environmental risks and can cause coastal ecosystems to transform in both positive and negative manners.

The overall purpose of this chapter is to explain some of the key underlying theories of the thesis, including seascape ecology and habitat development in the tropical marine environment. A detailed description of the sites will then be made, followed by the specific goals addressed in each chapter. The overlying objective of this thesis however, is to demonstrate the connectivity of a seascape through a unique intermediate habitat found accidentally in north central Cuba. By using coral community structure, physio-chemical variables, benthic structure and primary productivity with sources of organic matter, we will show the importance of the tropical seascape.

## **1.2 BRIDGING SEASCAPE AND LANDSCAPE ECOLOGY**

The use of the term ‘seascape’ has become more commonplace when discussing the interaction between coral reefs, seagrasses and mangroves (Ogden 1997, Kendall et al. 2004, Galindo et al. 2006, Grober-Dunsmore et al. 2007, Pittman et al. 2007), however seascape ecology is a term not clearly defined. Landscape ecology can have several definitions but most commonly refers to the ecological effects resulting from spatial patterns across a heterogeneous landscape (Robbins and Bell 1994, Turner et al. 2001). Seascape ecology stems from terrestrial dominated landscape ecology theory. Although the definition of landscape ecology does not explicitly state terrestrial ecosystems, the actual title indicates overt association to land rather than encompassing land, marine and aquatic habitats. Some inter-tidal communities have been used to discuss elements within landscape ecology, such

as disturbance regimes and species distributions relating from biotic interactions of mussels and starfish (Paine and Levin 1981), yet completely submerged environments are generally ignored. Although seascape ecology is discussed in several articles, it is generally mentioned in terms of applications, rather than an underlying theoretical framework (see January 2008 issue in *Landscape Ecology* and Robbins and Bell (1994)).

Seascape ecology follows several of the same principles of landscape ecology and has been derived from the same concepts which formed landscape ecology (Figure 1.1) yet inherent differences exist once environments are submerged. There are a variety of factors that contribute to patterns seen both in the land- and seascape, although the interactions of these factors can differ. Of most importance to the seascape are abiotic factors, biotic interactions, human land-use patterns, disturbance and succession (Turner et al. 2001).

The physical environment controls habitat structure within the seascape and biological interactions between ecosystems. For example, clear water conditions are essential for coral reef growth, yet without mangrove forests and seagrass beds, less turbid conditions would not be possible. Sediment from land runoff is captured within prop roots of mangrove trees, while dense leaves of seagrass patches cause particulate matter to settle and stay trapped within the vegetation providing clear water to reef environments (Scoffin 1970). The water flow between these three main tropical habitats allows successful habitat connectivity, quite different to wind or other terrestrial dispersal mechanisms. Coral reefs are primarily developed through the import of fish, coral and other invertebrate larvae along oceanic currents and tides (Roberts 1997), while mangrove and seagrasses import and export considerable amounts of bulk organic matter between habitats (Hemminga et al. 1994, Kitheka 1997). In addition to organic matter, mangroves and seagrasses also play an

important role in the migration of juvenile fish to coral reefs, as juvenile reef fish develop in these habitats free from predators until they are safely able to migrate to the reef (de la Moriniere et al. 2004, Dorenbosch et al. 2004, Mumby et al. 2004).

Biotic interactions are the most obvious exchanges influencing the ecology of the seascape, and could be discussed at large between the three main tropical ecosystems: coral reefs, seagrasses and mangroves. In addition to the ever important concept of mangroves acting as nurseries for juvenile coral reef fish, other interactions throughout the seascape also occur, including competition between species for development, space, light and nutrients, as well as the terrestrially-coined term ‘edge-effects’. Defined habitat patch edges in the seascape, created either naturally or by humans, demonstrate similar terrestrial edge effect characteristics, such as changed microclimates and species compositions (Saunders et al. 1991). Surrounding coral reef patches, distinct “halos” or ecotones can form, separating seagrass beds from coral reefs. While radiation fluxes and wind changes are not experienced in the submerged environment, wave action can be increased in this boundary region, causing seagrass uprooting, leaving coarse sand separating the reef from the seagrass (Ogden and Zieman 1977). Species composition is not necessarily changed along reef edges and in the halos, but species found near to reef edges (or are mobile) can aid in habitat edge halo formation. For example, diurnal and nocturnal feeding forays of reef fish and the sea urchin *Diadema antillarum* have created halo effects from grazing large quantities of seagrass surrounding the reefs (Randall 1965, Ogden et al. 1973).

Traditional landscape ecology discusses the effects of habitat fragmentation from human disturbances, especially deforestation and clearing of land for agriculture, urban sprawl and development. Human influences in the seascape are also prevalent, with

fragmentation occurring in all parts of the seascape, including actions such as seagrass dredging for commercial fish and crustaceans, deforestation of mangrove forests, removal of reef materials for construction and tourism and reef blasting for harbour creation. All acts of human disturbance severely affect not only the habitat, but also create smaller habitat patches which can leave unsuitable matrices of sediment and sparse algae that many organisms cannot migrate through (Hovel and Regan 2008). Human disturbances are not limited to those mentioned above, yet the consequences of most are usually detrimental for species survival, with the exception of prescribed disturbances intended for ecosystem rehabilitation.

Similar to terrestrial environments, natural endogenous disturbances are an important part of habitat development and succession within marine ecosystems. Hurricanes are the most common natural disturbance that affects tropical seascapes on a fairly regular basis (up to several times a decade, depending on the region). Although stressful on marine environments, hurricanes also encourage development of new habitat patches through dispersal. For example, some branching coral species found in shallower depths will break into smaller pieces after being disturbed by storm surge and wave action, and clonally begin new coral colonies after resettling on another hard substrate (Bruno 1998, Foster et al. 2007). Seagrasses also regenerate new patches following hurricanes by redistributing seed banks from the mechanical removal of seeds and roots during storms (Bell et al. 2008). Other types of endogenous disturbances also occur throughout the seascape, including the migration at dusk of large schools of grunts and snappers from coral reefs to seagrass beds for hunting, which eventually leads to the partitioning of seagrass foraging areas (Ogden 1997).

### 1.3 HABITAT DEVELOPMENT, SUCCESSION AND ZONATION

Reef development is the result of hard coral growth as well as other invertebrates forming a reef environment, where large and small marine species visit for food or shelter. Reef primary succession begins with corals undergoing sexual reproduction, where coral from a nearby reef releases free-swimming planulae larvae that swim until reaching a substrate suitable for the species. Suitable substrates generally tend to be a hard-bottom surface, usually of calcium-carbonate composition, and often has crustose coralline algae that induces metamorphosis of the larva through chemical cues (Baird and Morse 2004, Vermeij 2005). Successful post-settlement depends on several factors including inter-specific competition between benthic organisms, sedimentation, herbivorous species, anthropogenic impacts and natural disturbances, such as hurricanes (Tomascik 1991, Raimondi and Morse 2000, Gleason et al. 2001, Fabricius 2005, Vermeij 2006, Vermeij et al. 2006). Following successful establishment several coral species will then perform asexual reproduction or clonal growth/budding to further expand their frame, or simply continue growing through calcium carbonate deposition or cementation by coralline algae. The other main contributor of calcium carbonate is from calcareous algae (such as *Halimeda sp.*), which can either help in reef building, or will disintegrate and provide much of the sand found in coral reef systems (Nybakken 2001).

Reef development will continue with increased abundance of soft corals, sponges, tunicates, algae and hard corals. Corals with an affinity to the substrate or in habitats with advantageous abiotic factors will survive and compete with surrounding organisms. Inter-specific competition is one of the main controls on growth and success of several benthic organisms, as they are often competing for light and space. Cryptic coral species commonly

compete with sponges and tunicates for space in areas with low-light, while hermatypic corals often compete with algae in exposed, well-lit areas (Vermeij 2006). Several coral species in the Caribbean (with the exception of *Porites astreoides* and *Madracis mirabilis*) have shown defensive strategies with direct contact to algae, including damaging plants temporarily or even permanently by disrupting energy production (Nugues et al. 2004).

In addition to biotic controls in reef formation, physical and chemical constraints also limit reef development. Coral typically grows in warm, clear, shallow environments along continental shelves in low latitude regions. Optimal growth requirements generally include temperatures ranging from 18–36 °C, depths from 0-60 m, light levels no less than 1-2 % of surface intensity, salinity levels between 33-36 ‰, low sedimentation levels and limited emergence into air and wave action (Hubbard 1997, Nybakken 2001). These requirements vary for each species, causing certain species assemblages to develop in varying types of reef.

Zonation typically occurs throughout most marine ecosystems, with characteristic species found along gradients of depth, light, exposure or even water turbulence (Nybakken 2001). Coral reefs demonstrate a predictable pattern of decreasing number of species with depth, although highest average number of species is greatest at intermediate depths. Some zones can be characterized by a single species, such as *Acropora palmata* in shallow reef crests, which is more resistant to wave action with its wide, flat branches, while thinner branched *Acropora cervicornis* occurs in deeper water where water movement is more intermediate (Goreau 1959). In addition, there are also coral species zones based on similar morphological characteristics with depth. For example, branching corals are generally found in higher abundances and diversity in shallow water reef crests and patch reefs (ranging from

0-10m), at mid-depths (~20 m) along reef slopes an even mix of branching, foliaceous (or plate-like) and massive (boulder style) corals occurs, while at deeper depths (> 25 m) along reef escarpments a switch to foliaceous corals happens. These plate-like corals abound at greater depths due to increasing surface area in order to receive sufficient levels of light for growth, as levels of radiation decrease with depth (Liddell and Ohlhorst 1987, Jackson 1991).

Mangrove forests and seagrass beds throughout the Caribbean also develop in characteristic zonation patterns (Nybakken 2001). The red mangrove *Rhizophora mangle* is nearest to the shore and often partially submerged, the black mangrove *Avicennia germinans* is the next species landward which is only covered by water during spring and storm tides, while the white mangrove *Laguncularia racemosa* is found several metres away from the ocean, and is considered mostly terrestrial. The ability to tolerate water submersion from varying tidal regimes and drought-like conditions is driving typical mangrove zonation seen throughout the Caribbean and Western Atlantic. Seagrass beds also have vertical species zonation patterns that are based on light availability, which is directly a result of depth. Short, broad-leaved seagrasses, such as *Halophila decipiens* are found at deepest depths up to 30 m, while narrow, longer leafed plants, such as *Thalassia testudinum* and *Syringodium filiforme* are found abundantly in intermediate depths up to 20 m. The slightly shorter and narrower leaves of *Halodule wrightii* are found in shallower zones, where there is abundant light but often stronger currents and larger wave action (Littler and Littler 2000).

While both vegetation types are found within the seascape, how they disperse, develop and grow varies considerably between mangrove and seagrass species. Within the Caribbean, mangrove species generally flower and produce a hard, cone-shaped fruit with an embryo inside, called a propagule. Mangrove propagules will drop into the ocean and float

almost 2-5 kilometres until it finds a sediment bank to deposit into and take root (Sengupta et al. 2005). Root formation varies with species, but within *R. mangle*, characteristic prop roots develop which can cause the current to slow and increase deposition of suspended particles and sand. Over time, leaves begin to drop and become trapped within the root structure, causing anaerobic decomposition and abundance of organic detritus. In order for the tree to survive in anoxic conditions, root structures have evolved mechanisms to obtain oxygen by either developing outside of the water, as in prop roots, or send out pneumatophores from the end of roots into the air, as seen in *A. germinans*. The detritus collecting among the roots further develops into dense sediment, which will host a variety of green algae species, as well as seagrass species.

Seagrasses are angiosperms found completely submerged in marine environments. Although not actually from the grass family Poaceae, seagrasses (from one of four families: Posidoniaceae, Zosteraceae, Hydrocharitaceae, or Cymodoceaceae) developed their name from the visual similarities as meadows of grass. Seagrass patches are usually extensive in size, and form from long, tall leaf blades that look similar to grass blades. Seeds of the common Caribbean seagrass *T. testudinum* are distributed with currents and can travel up to 3 kilometres, while fruits can travel up to 15 kilometres (Kaldy and Dunton 1999) allowing successful pollination and dispersal. In addition to sexual reproduction, seagrasses also reproduce clonally through horizontal propagation of the rhizome below ground. Rhizomes produce shoots horizontally at rhizome nodes, which can bear leaves and leaf sheaths that are identical to the original plant. Seagrass species vary with the number of shoots produced, as well as rhizome diameter and elongation rates (Marba and Duarte 1998). The dense leaf structure created by clonal reproduction helps stabilize fine sediments, maintaining overall

water quality while also creating patches up to several kilometres wide and up to thousands of square kilometres with combined species and reproductive modes (Iverson and Bittaker 1986).

## 1.4 THE DISCOVERY

While walking along an inter-island coastal causeway (a bermed road, obstructing the flow of water between the open ocean and Bahía de Perros) connecting Cayo Guillermo to Cayo Coco, a surprising discovery was made in a small inlet where oceanic and coastal waters mixed on a daily basis. Only metres away from the road were hundreds of fish swimming underneath the man-made bridge, with large naturally created pools on either side containing bright coral reef fish. Upon closer investigation, two bridges with similar style inlets along the roadway also demonstrated ecosystem traits similar to natural reefs, with scleractinian coral species flourishing, along with healthy algae, sponges, tunicates, a variety of gastropods as well as commercially important crustaceans, including the Caribbean spiny lobster and the West Indian sea egg urchin. The truly unanticipated part of this discovery was that the human-induced bridge reefs were surrounded by dense mangrove forests and thick patches of seagrass beds in surrounding waters, several kilometres from the mature fringing reefs in the open ocean. Connectivity had proven to play a dominant role in this new developing seascapes, with each inlet reef-site found in a zone with a unique level of association to the open ocean, based on varying density levels of mangrove forest. One zone had no mangroves present, the second had a moderate mangrove forest density with a direct connection and the third was surrounded by mangrove forest growth with only an indirect connection to the open ocean. One could not help but question how these reef sites

developed? Are they similar to the natural reefs physically and ecologically? And do they connect through productivity and the export and import of organic matter?

## **1.5 RATIONALE**

Throughout the Caribbean no documented sites have demonstrated similar attributes as the bridge reef sites described in this study. An inland bay naturally occurring in Curaçao demonstrated coral growth in a physically-similar marginal habitat lagoon (Vermeij et al. 2007), yet the coral community development, and region in general, had little influence from human activities. In Bermuda, coral had grown in a harbour where a causeway was erected in the late 19<sup>th</sup> century, yet after dumping, the creation of a landfill site and development of an airstrip, coral mass mortality occurred, killing several large, old corals (Flood et al. 2005). Although no causeways were present between islands in New Providence, Bahamas, patch reefs and coral- and sponge-dominated hard bottoms, similar to those seen in Cayo Coco, experienced mortality following development on the island (Sealey 2004). While Alcolado (1991) commented on the state of the Sabinal-Camaguey Archipelago, with reference to the causeway focused in this study, little was mentioned about the growth and successful development of corals along the roadway (Alcolado 1991). This site demonstrates a new niche in coral community ecology, which may become increasingly more common with continued development of islands and cays globally.

These bridge reef sites are unique due to the presence of coral, seagrass and mangroves in such a localized area. Usually these ecosystems are the main interacting components found in the tropical seascape, but not in such small areas (Ogden 1997). Several studies have shown the importance of all three habitats for ontogenetic migrations of

coral reef fish between these habitats (Nagelkerken et al. 2001, de la Moriniere et al. 2003, Zeller et al. 2003, de la Moriniere et al. 2004, Dorenbosch et al. 2004, Layman et al. 2004, Nagelkerken and van der Velde 2004a, b, Chittaro et al. 2005, Mumby 2006), however few have shown the importance or feasibility of scleractinian coral species surviving in all three habitats (Lirman et al. 2003, Perry and Larcombe 2003, Vermeij et al. 2007). Although the coral growing in the bridge reefs are relatively small colonies and mostly non-framework building species, their abundance and survival in such a diverse habitat deserves closer investigation.

In light of increasing rates of reef degradation, restoration projects have become major areas of interest, both scientifically and commercially (Chin and Simmons 1994, Clark and Edwards 1999, Badalamenti et al. 2002, Seaman 2002, Sherman et al. 2002). Artificial reefs have become commonplace throughout the Florida Reef Tract along the keys, and also in the Red Sea off the coast of Israel (Rilov and Benayahu 2000, Walker et al. 2002, Perkol-Finkel and Benayahu 2004, Leeworthy et al. 2006, Perkol-Finkel et al. 2006, Thanner et al. 2006). Although they do not mimic all biophysical traits of natural reefs, they can be regarded as new frameworks for reef survival (Carr and Hixon 1997, Chou 1997, Badalamenti et al. 2002). The reefs in Cayo Coco could also be considered a form of artificial reef, yet their creation has been completely natural in that following inlet-causeway construction, no effort to ‘seed’ the site or prepare it for possible colonization was ever made.

Cuba is an important part of the social fabric of Caribbean culture due to its substantial size within the Greater Antilles, yet very little ecological data from this country is available to the international scientific community, especially concerning coral community structures of Cayo Coco and Cayo Guillermo. Coral community compositions from only the

two extreme portions of Cuba have been assessed, with one study near Naval Station, Guantanamo Bay, at the southeast corner, and another study at Maria la Gourda in the most southwest area of the island (Chiappone et al. 2001, Alcolado et al. 2003). The north coast of Cuba is an area that is not only ecologically similar to the Bahamian Archipelago and Florida, with shallow continental reefs surrounded by healthy mangrove forests and seagrass patches, but could also act as a major supply bank of coral and fish larvae to other parts of the Caribbean, through major oceanic currents (Roberts 1997).

In addition to the lack of information on coral ecology, there is also a deficiency of data on the coastal vegetation surrounding these cays. Mangrove and seagrasses are important for various reasons, including high levels of primary productivity (Robertson et al. 1991, Amarasinghe and Balasubramaniam 1992, Alongi 1994, Koch and Madden 2001), potential carbon storage pools (Twilley et al. 1992, Duarte et al. 2005), numerous coastal protection benefits (Twilley et al. 1992, Field 1995, Duarte et al. 2005) and natural water filters through deposition and burial of sediment (Duarte and Cebrian 1996). To appreciate the significance of these vegetation types, we need to understand how organic matter is exported throughout the seascape. Carbon isotope analysis is a valuable tool in determining organic matter sources, long after decomposition has occurred. Past studies concentrated on evaluating biomass and productivity of mangrove and seagrass vegetation within Cuba (Lalanarueda and Gosselck 1986, Fiala and Hernandez 1993, Martinez-Daranas et al. 2005), but no isotopic analyses have been made on modern sediments or leaves of these vegetation types.

Although there are still gaps in our understanding of the coastal carbon balance, it is understood that mangrove and seagrass ecosystems play a role in primary productivity

through *in situ* decomposition, as well as storing and exporting organic material (Duarte and Cebrian 1996). By using stable carbon isotope analysis, the carbon flow in these regions can be determined as there are significant differences in mangrove and seagrass carbon 13 ( $\delta^{13}\text{C}$ ) content (Zieman et al. 1984, Fleming et al. 1990). These differences are based on variations in utilization of atmospheric CO<sub>2</sub> and fixation processes, as well as rate-limiting diffusion barriers that prevent isotopic selectivity, especially found in seagrasses (Fleming et al. 1990). By collecting sediment and organic matter content from varying locations, autochthonous marine (seagrass) contributions can be disseminated from allochthonous terrestrial (mangrove) components in a particular region within a seascape, based on characteristic  $\delta^{13}\text{C}$  values for each vegetation type.

## 1.6 RESEARCH OBJECTIVES

While both chapters have very different research themes, each explain the overall objective of how the bridge reefs developed, and how they are connected to surrounding communities. The two chapters are meant to demonstrate that habitats within the seascape are inter-related through varying mechanisms and that development is often multi-dimensional.

### 1.6.1 Chapter Two

This chapter deals explicitly with the coral community structure of the bridge reefs, natural reefs, mangrove channels and seagrass beds and the abiotic factors shaping them within the seascape. The main goal is to investigate if varying levels of connectivity to the open ocean essentially affect coral development at the bridge reef communities. The two

central questions asked were: 1) if the three varying levels of connectivity to the open ocean are responsible for differences in coral species diversity and physical environment; and 2) how the bridge reef habitats are connected to surrounding marine habitats within the seascape. Specific questions asked for topic 1 include:

- What are the physical differences between each bridge reef?
- What are the differences in coral communities at each bridge reef?
- What are the differences in benthic communities at each bridge reef?
- How does the varying levels of connectivity affect all three factors overall?

Topic 2 also asked similar questions:

- Which natural habitats are the bridge reefs most similar to with respect to coral?
- Which natural habitats are the bridge reefs most similar to with respect to physical habitat structure?
- Which natural habitats are the bridge reefs most similar to with respect to benthic coverage?
- Using Canonical Correspondence Analysis, can the factors most important to overall habitat similarities be identified?

Within each site, depth, temperature, salinity, total dissolved solids, conductivity, water current speed, dissolved oxygen, site complexity and turbidity levels were measured. The four water chemistry variables measured (salinity, total dissolved solids, conductivity and dissolved oxygen) were chosen due to their importance in the physiological development of coral. For example, salinity levels ranging from 32 – 37 ‰ are considered optimal for coral growth. The five physical variables measured (depth, temperature, site complexity, water current speed and turbidity) were also chosen because some must be within the optimal

range for coral development (temperature, depth and turbidity), while others are useful for determining structural site similarities and allowing coral to colonize (site complexity and water current speed).

Quadrats were used at each site for measuring both coral community structure and benthic coverage. The number of coral species and abundance of each were counted at all sites, and was the main factor compared between all sites using multi-variate statistics. The benthic coverage was also characterized to determine site differences, as well as provide an overall composition of the site.

### *1.6.2 Chapter Three*

Chapter three uses  $\delta^{13}\text{C}$  as a tracer to determine the main sources of organic carbon at the bridge reef sites. This is a pilot study using a novel technique to determine the main sources of organic matter at a site, since studies have often used  $\delta^{13}\text{C}$  for monitoring gradients in mangrove and seagrass particulate organic matter, yet not as a tracer (Hemminga et al. 1994). By sourcing organic matter contributions and determining C/N ratios, indications can be made on the levels of primary productivity occurring in the bridge reefs and surrounding sites, which signifies food web structures, trophic dynamics and the importance of habitat linkages. This will be one of the first steps in determining the role of mangrove and seagrass vegetation in the modern-day carbon budget for Cayo Coco and Cayo Guillermo.

## 1.7 REFERENCES

- Alcolado, P. M. 1991. Ecological assessment of semienclosed marine water bodies of the Archipelago Sabana-Camaguey (Cuba) prior to tourism development projects. *Marine Pollution Bulletin* **23**:375-378.
- Alcolado, P. M., B. Martinez-Daranas, G. Menendez-Macia, R. del Valle, M. Hernandez, and T. Garcia. 2003. Rapid assessment of coral communities of Maria la Gorda, southeast Ensenada de Corrientes, Cuba (Part 1: stony corals and algae). *Atoll Research Bulletin*:269-278.
- Alongi, D. M. 1994. Zonation and seasonality of benthic primary production and community respiration in tropical mangrove forests. *Oecologia* **98**:320-327.
- Amarasinghe, M. D., and S. Balasubramaniam. 1992. Net primary productivity of 2 mangrove forest stands on the northwestern coast of Sri-Lanka. *Hydrobiologia* **247**:37-47.
- Badalamenti, F., R. Chemello, G. D'Anna, P. H. Ramos, and S. Riggio. 2002. Are artificial reefs comparable to neighbouring natural rocky areas? A mollusc case study in the Gulf of Castellammare (NW Sicily). *Ices Journal of Marine Science* **59**:S127-S131.
- Baird, A. H., and A. N. C. Morse. 2004. Induction of metamorphosis in larvae of the brooding corals *Acropora palifera* and *Stylophora pistillata*. *Marine and Freshwater Research* **55**:469-472.
- Bell, S. S., M. S. Fonseca, and W. J. Kenworthy. 2008. Dynamics of a subtropical seagrass landscape: links between disturbance and mobile seed banks. *Landscape Ecology* **23**:67-74.

- Bruno, J. F. 1998. Fragmentation in *Madracis mirabilis* (Duchassaing and Michelotti): How common is size-specific fragment survivorship in corals? *Journal of Experimental Marine Biology and Ecology* **230**:169-181.
- Carr, M. H., and M. A. Hixon. 1997. Artificial reefs: The importance of comparisons with natural reefs. *Fisheries* **22**:28-33.
- Chiappone, M., K. Sullivan-Sealey, G. Bustamante, and J. Tschirky. 2001. A rapid assessment of coral reef community structure and diversity patterns at Naval Station Guantanamo Bay, Cuba. *Bulletin of Marine Science* **69**:373-394.
- Chin, G. D., and R. Simmons. 1994. Evaluating artificial reefs at Parteau Cove Provincial Park. *Bulletin of Marine Science* **55**:1332.
- Chittaro, P. M., P. Usseglio, and P. Sale. 2005. Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. *Environmental Biology of Fishes* **72**:175-187.
- Chou, L. M. 1997. Artificial reefs of Southeast Asia - Do they enhance or degrade the marine environment? *Environmental Monitoring and Assessment* **44**:45-52.
- Clark, S., and A. J. Edwards. 1999. An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. *Aquatic Conservation-Marine and Freshwater Ecosystems* **9**:5-21.
- Claro, R., and K. C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research* **14**:91-106.

- de la Moriniere, E. C., I. Nagelkerken, H. van der Meij, and G. van der Velde. 2004. What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Marine Biology* **144**:139-145.
- de la Moriniere, E. C., B. J. A. Pollux, I. Nagelkerken, M. A. Hemminga, A. H. L. Huiskes, and G. van der Velde. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Marine Ecology-Progress Series* **246**:279-289.
- Dorenbosch, M., M. C. van Riel, I. Nagelkerken, and G. van der Velde. 2004. The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuarine Coastal and Shelf Science* **60**:37-48.
- Duarte, C. M., and J. Cebrian. 1996. The fate of marine autotrophic production. *Limnology and Oceanography* **41**:1758-1766.
- Duarte, C. M., J. J. Middelburg, and N. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**:1-8.
- Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* **50**:125-146.
- Fiala, K., and L. Hernandez. 1993. Root biomass of a mangrove forest in Southwestern Cuba (Majana). *Ekologia-Bratislava* **12**:15-30.
- Field, C. D. 1995. Impact of expected climate change on mangroves. *Hydrobiologia* **295**:75-81.
- Fleming, M., G. Lin, and L. d. S. L. Sternberg. 1990. Influence of mangrove detritus in an estuarine ecosystem. *Bulletin of Marine Science* **47**:663-669.

- Flood, V. S., J. M. Pitt, and S. R. Smith. 2005. Historical and ecological analysis of coral communities in Castle Harbour (Bermuda) after more than a century of environmental perturbation. *Marine Pollution Bulletin* **51**:545-557.
- Foster, N. L., I. B. Baums, and P. J. Mumby. 2007. Sexual vs. asexual reproduction in an ecosystem engineer: the massive coral *Montastraea annularis*. *Journal of Animal Ecology* **76**:384-391.
- Galindo, H. M., D. B. Olson, and S. R. Palumbi. 2006. Seascape genetics: A coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology* **16**:1622-1626.
- Gleason, D. F., D. A. Brazeau, and D. Munfus. 2001. Can self-fertilizing coral species be used to enhance restoration of Caribbean reefs? *Bulletin of Marine Science* **69**:933-943.
- González-Díaz, P., E. de la Guardia, and G. González-Sansón. 2003. Efecto de efluentes terrestres sobre las comunidades bentónicas de arrecifes coralinos de ciudad de la Habana, Cuba. *Revista de Investigaciones Marinas* **24**:193-204.
- Goreau, T. F. 1959. The ecology of Jamaican coral reefs .1. Species composition and zonation. *Ecology* **40**:67-90.
- Grober-Dunsmore, R., T. K. Frazer, W. J. Lindberg, and J. Beets. 2007. Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. *Coral Reefs* **26**:201-216.
- Hemminga, M. A., F. J. Slim, J. Kazungu, G. M. Ganssen, J. Nieuwenhuize, and N. M. Kruyt. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology-Progress Series* **106**:291-301.

- Hovel, K. A., and H. M. Regan. 2008. Using an individual-based model to examine the roles of habitat fragmentation and behavior on predator-prey relationships in seagrass landscapes. *Landscape Ecology* **23**:75-89.
- Hubbard, D. K. 1997. Reefs as dynamic systems. Pages 43-67 in C. Birkeland, editor. *Life and death of coral reefs*. Chapman & Hall, Toronto.
- Iverson, R. L., and H. F. Bittaker. 1986. Seagrass distribution and abundance in Eastern Gulf of Mexico coastal waters. *Estuarine Coastal and Shelf Science* **22**:577-602.
- Jackson, J. B. C. 1991. Adaptation and Diversity of Reef Corals. *Bioscience* **41**:475-482.
- Kaldy, J. E., and K. H. Dunton. 1999. Ontogenetic photosynthetic changes, dispersal and survival of *Thalassia testudinum* (turtle grass) seedlings in a sub-tropical lagoon. *Journal of Experimental Marine Biology and Ecology* **240**:193-212.
- Kendall, M. S., K. R. Buja, J. D. Christensen, C. R. Kruer, and M. E. Monaco. 2004. The seascape approach to coral ecosystem mapping: An integral component of understanding the habitat utilization patterns of reef fish. *Bulletin of Marine Science* **75**:225-237.
- Kitheka, J. U. 1997. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. *Estuarine Coastal and Shelf Science* **45**:177-187.
- Koch, M. S., and C. J. Madden. 2001. Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangroves. *Marine Ecology-Progress Series* **219**:109-119.

- Lalanarueda, R., and F. Gosselck. 1986. Investigations of the benthos of mangrove coastal lagoons in Southern Cuba. Internationale Revue Der Gesamten Hydrobiologie **71**:779-794.
- Layman, C. A., D. A. Arrington, R. B. Langerhans, and B. R. Silliman. 2004. Degree of fragmentation affects fish assemblage structure in Andros Island (Bahamas) estuaries. Caribbean Journal of Science **40**:232-244.
- Leeworthy, V. R., T. Maher, and E. A. Stone. 2006. Can artificial reefs alter user pressure on adjacent natural reefs? Bulletin of Marine Science **78**:29-38.
- Liddell, W. D., and S. L. Ohlhorst. 1987. Patterns of reef community structure, North Jamaica. Bulletin of Marine Science **40**:311-329.
- Lirman, D., B. Orlando, S. Macia, D. Manzello, L. Kaufman, P. Biber, and T. Jones. 2003. Coral communities of Biscayne Bay, Florida and adjacent offshore areas: diversity abundance, distribution, and environmental correlates. Aquatic Conservation-Marine and Freshwater Ecosystems **13**:121-135.
- Littler, D. S., and M. M. Littler. 2000. Caribbean Reef Plants. OffShore Graphics Inc., Washington, D.C.
- Maal-Bared, R. 2006. Comparing environmental issues in Cuba before and after the Special Period: Balancing sustainable development and survival. Environment International **32**:349-358.
- Marba, N., and C. M. Duarte. 1998. Rhizome elongation and seagrass clonal growth. Marine Ecology-Progress Series **174**:269-280.

- Martinez-Daranas, B., P. M. Alcolado, and C. M. Duarte. 2005. Leaf production and shoot dynamics of *Thalassia testudinum* by a direct census method. *Aquatic Botany* **81**:213-224.
- Mumby, P. J. 2006. Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales. *Biological Conservation* **128**:215-222.
- Mumby, P. J., A. J. Edwards, J. E. Arias-Gonzalez, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**:533-536.
- Nagelkerken, I., S. Kleijnen, T. Klop, R. van den Brand, E. C. de la Moriniere, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology-Progress Series* **214**:225-235.
- Nagelkerken, I., and G. van der Velde. 2004a. Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? *Marine Ecology-Progress Series* **274**:143-151.
- Nagelkerken, I., and G. van der Velde. 2004b. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Marine Ecology-Progress Series* **274**:153-159.
- Nugues, M. M., L. Delvoye, and R. P. M. Bak. 2004. Coral defence against macroalgae: differential effects of mesenterial filaments on the green alga *Halimeda opuntia*. *Marine Ecology-Progress Series* **278**:103-114.

- Nybakken, J. W. 2001. Marine Biology: An Ecological Approach, 5 edition. Addison Wesley Longman Inc, Toronto.
- Ogden, J. C. 1997. Ecosystem interactions in the tropical coastal seascape. Pages 288-297 *in* C. Birkeland, editor. Life and death of coral reefs. Chapman & Hall, Toronto.
- Ogden, J. C., R. Brown, and N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian patch reefs. *Science* **182**:715-717.
- Ogden, J. C., and J. C. Zieman. 1977. Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. Pages 377-382 *in* D. L. Taylor, editor. Proceedings of the Third International Coral Reef Symposium, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.
- Paine, R. T., and S. A. Levin. 1981. Inter-Tidal Landscapes - Disturbance and the Dynamics of Pattern. *Ecological Monographs* **51**:145-178.
- Perez, L. 1995. The Population of Cuba - the Growth and Characteristics of Its Labor-Force. *Columbia Journal of World Business* **30**:58-65.
- Perkol-Finkel, S., and Y. Benayahu. 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. *Coral Reefs* **23**:195-205.
- Perkol-Finkel, S., N. Shashar, and Y. Benayahu. 2006. Can artificial reefs mimic natural reef communities? The roles of structural features and age. *Marine Environmental Research* **61**:121-135.
- Perry, C. T., and P. Larcombe. 2003. Marginal and non-reef-building coral environments. *Coral Reefs* **22**:427-432.

- Pittman, S. J., C. Caldow, S. D. Hile, and M. E. Monaco. 2007. Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. *Marine Ecology-Progress Series* **348**:273-284.
- Raimondi, P. T., and A. N. C. Morse. 2000. The consequences of complex larval behavior in a coral. *Ecology* **81**:3193-3211.
- Randall, J. E. 1965. Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. *Ecology* **46**:225-260.
- Rilov, G., and Y. Benayahu. 2000. Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Marine Biology* **136**:931-942.
- Robbins, B. D., and S. S. Bell. 1994. Seagrass landscapes - a terrestrial approach to the marine subtidal environment. *Trends in Ecology & Evolution* **9**:301-304.
- Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**:1454-1457.
- Robertson, A. I., P. A. Daniel, and P. Dixon. 1991. Mangrove forest structure and productivity in the Fly River Estuary, Papua-New-Guinea. *Marine Biology* **111**:147-155.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18-32.
- Schaffelke, B., J. Mellors, and N. C. Duke. 2005. Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. *Marine Pollution Bulletin* **51**:279-296.
- Scoffin, T. P. 1970. Trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology* **40**:249-&.

- Sealey, K. S. 2004. Large-scale ecological impacts of development on tropical islands systems: comparison of developed and undeveloped islands in the central Bahamas. *Bulletin of Marine Science* **75**:295-320.
- Seaman, W. 2002. Unifying trends and opportunities in global artificial reef research, including evaluation. *Ices Journal of Marine Science* **59**:S14-S16.
- Sengupta, R., B. Middleton, C. Yan, M. Zuro, and H. Hartman. 2005. Landscape characteristics of Rhizophora mangle forests and propagule deposition in coastal environments of Florida (USA). *Landscape Ecology* **20**:63-72.
- Sherman, R. L., D. S. Gillian, and R. E. Spieler. 2002. Artificial reef design: void space, complexity, and attractants. *Ices Journal of Marine Science* **59**:S196-S200.
- Thanner, S. E., T. L. McIntosh, and S. M. Blair. 2006. Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. *Bulletin of Marine Science* **78**:57-70.
- Tomascik, T. 1991. Settlement-Patterns of Caribbean Scleractinian Corals on Artificial Substrata Along a Eutrophication Gradient, Barbados, West-Indies. *Marine Ecology-Progress Series* **77**:261-269.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice. Springer-Verlag, New York.
- Twilley, R. R., R. H. Chen, and T. Hargis. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air and Soil Pollution* **64**:265-288.
- Vermeij, M. J. A. 2005. Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. *Marine Ecology-Progress Series* **295**:123-133.

- Vermeij, M. J. A. 2006. Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. *Coral Reefs* **25**:59-71.
- Vermeij, M. J. A., N. D. Fogarty, and M. W. Miller. 2006. Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral Montastraea faveolata. *Marine Ecology-Progress Series* **310**:119-128.
- Vermeij, M. J. A., P. R. Frade, R. I. R. Jacinto, A. O. Debrot, and R. P. M. Bak. 2007. Effects of reproductive mode on habitat-related differences in the population structure of eight Caribbean coral species. *Marine Ecology-Progress Series* **351**:91-102.
- Walker, B. K., B. Henderson, and R. E. Spieler. 2002. Fish assemblages associated with artificial reefs of concrete aggregates or quarry stone offshore Miami Beach, Florida, USA. *Aquatic Living Resources* **15**:95-105.
- Zeller, D., S. L. Stoute, and G. R. Russ. 2003. Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. *Marine Ecology-Progress Series* **254**:269-280.
- Zieman, J. C., S. A. Macko, and A. L. Mills. 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. *Bulletin of Marine Science* **35**:380-392.

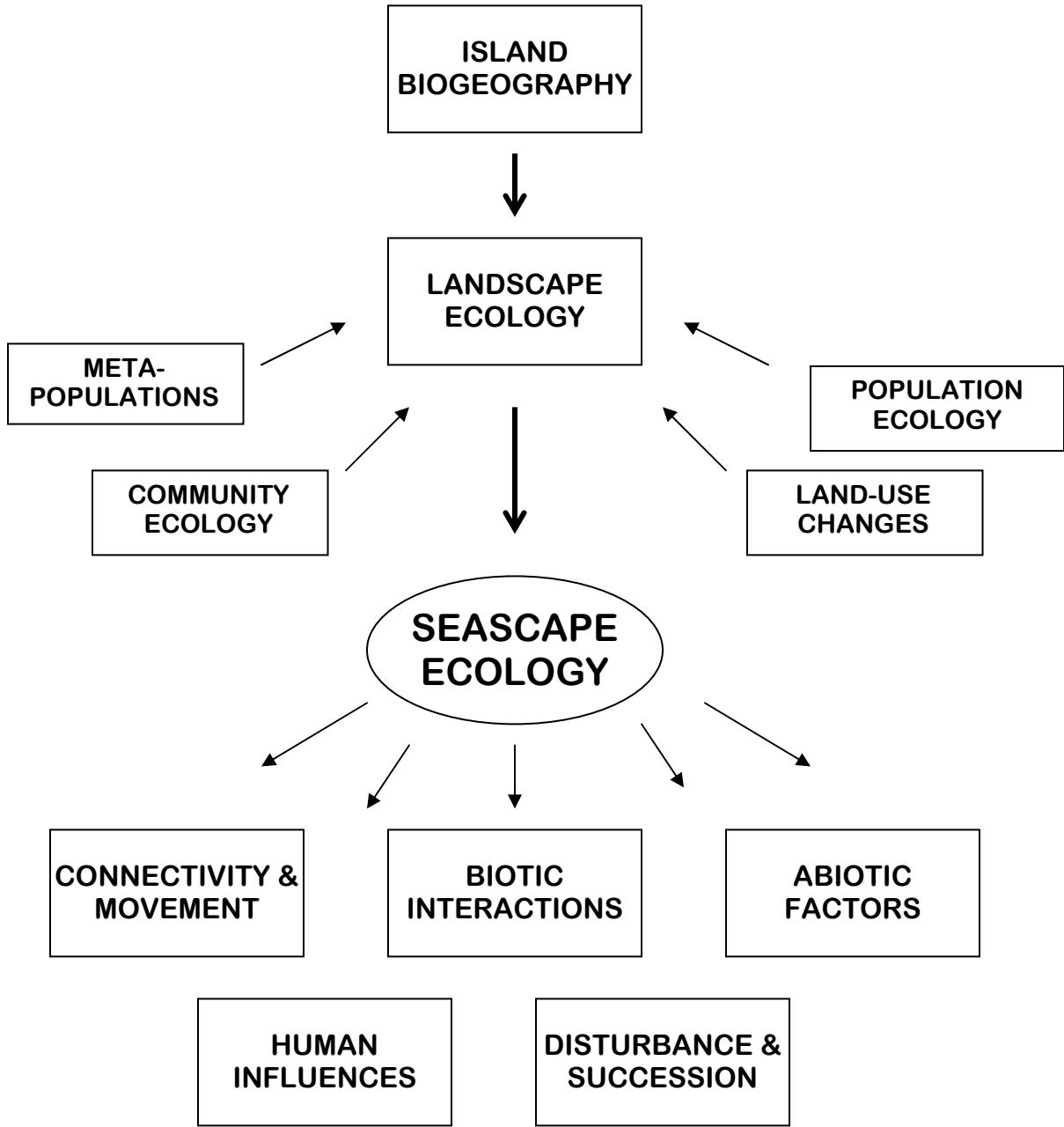


Figure 1.1. The traditional view of landscape ecology, and how it has developed into seascape ecology. Stemming from seascape ecology are the main components driving this new field.

## **CHAPTER 2:**

### **Unexpected reef formations under a coastal causeway in Cayo Coco and Cayo Guillermo, Cuba**

#### **1. INTRODUCTION**

Reef establishment requires development of a structural framework. Within the Caribbean, framework-building corals are responsible for the carbonate structure upon which coral larvae are recruited onto and grow from, and typically come from the *Montastraea*, *Agaricia*, *Meandrina* and *Diploria* genera (Hubbard 1997). Corals occasionally grow outside of a reef and can form communities within marginal habitats that lack a reef framework and have less than optimal physical environments.

Marginal habitats are characterized by being in extremely shallow, turbid sites, where salinity and temperature values approach the environmental limits for coral survival, and substrates can vary from soft, mud sediments, to seagrass and mangrove dominated regions (Perry and Larcombe 2003). Corals populating these regions commonly undergo internal fertilization to effectively reproduce in the less-than-perfect habitats. Brooding an internal planula, compared with broadcast spawning gametes, is thought to be preferred in marginal habitats as it can produce a more resilient, larger planula, spend less time as a planktonic larva, and have faster growth rates post-settlement (Szmant 1986, Smith 1992). These characteristics are generally thought to increase the probability of successful recruitment and survivorship in areas where environmental conditions are considered beyond physical tolerances.

In addition to successful reproduction in reef formation, the supply and transport of coral larvae is of equal importance for their establishment. The scale at which coral larvae

travels varies from local (tens of metres) to regional (tens of kilometres) (Edmunds and Bruno 1996). Coral recruitment relies upon a supply bank of reproductively mature adults that undergo annual coral spawning/release of fertilized gametes or larvae on nearby reefs (Roberts 1997). Although coral larvae actively swim to substrates once spawned (some preferentially choose a substrate and some indiscriminately) (Carlon and Olson 1993) oceanic currents are ultimately responsible for supplying both neighbouring reefs and regions with new recruits (Roberts 1997). Ocean currents can be driven by wind-based processes or by tidal ebb and flow (Smith 2004).

In coastal regions, tidal currents can be the driving force of mixing water between back reefs and continental shelves, especially in the presence of tidal channels. Shallow waters and channels typically have stronger tidal-driven currents compared to deep, open ocean and can be an order of magnitude stronger than wind-driven currents (de Boer et al. 2000, Smith 2004). These ocean currents provide efficient mixing of oceanic water, improving larvae transport for colonization of reefs (Smith and Stoner 1993).

In north-central Cuba, between Cayo Coco and Cayo Guillermo, new reef communities are forming under bridges along a coastal causeway connecting these two cays. Tidal currents play a strong role in forming this seascape, with lagoons sharing coastline with the island of Cuba on one side of the causeway, and tidal channels found between mangrove forests and natural fringing reefs along the fore-reef area on the other side of the bridges. An added dimension of uniqueness to the bridge zones is the fact they have individual levels of connectivity to the open ocean: one zone has a direct connection; one also has a direct connection, but is disrupted by the presence of dense mangrove forest; and the third is only indirectly connected through mangrove tidal channels. The main goal of this study is to

determine how the bridge reefs formed within the seascape. Objectives are twofold: (1) to assess whether the three varying levels of connectivity to the open ocean affect coral species diversity in the bridge reefs; and (2) to evaluate how the bridge reef habitats are connected to surrounding marine habitats within the seascape. Measurements characterizing the physical habitats in which all reef communities were found were taken, as well as surveys of species community structure and benthic composition.

## 2. METHODS

### 2.1 Study Sites

Study sites are found in the Sabana-Camagüey Archipelago (regionally known as Jardines del Rey) in the north-central province Ciego D'Avila, Cuba (Figure 2.1). The causeway connecting Cayo Coco to Cayo Guillermo was built in 1989 and runs perpendicular to three study zones delineated in Figure 2.2. Sites were chosen based on these zones, which have varying density levels of mangrove forest and overall connectivity to the open ocean: Zone 1 (most westerly) has no mangroves present, Zone 2 has a moderate mangrove forest density with a direct connection, and Zone 3 is only moderately connected due to profuse mangrove forest growth. Research sites in the zones were selected based on the four main habitat types: bridge reefs, mangrove channel reefs, seagrass beds and natural reefs. The exact locations of each site and habitat type explanations are found in Table 2.1 and Figure 2.1.

### 2.2 Study Systems

#### 2.2.1 Bridge Reefs

The bridge reef (BR) sites are formed around small bridges along the causeway, as a result of submerged limestone rock and debris (such as steel beams and tires) that partially form the substrate. These reefs contain coral in areas close to the bridge, but not directly below due to lack of light. A variety of sponges and tunicates are found directly under the structure, while *Thalassia testudinum* and a range of algae species are found outside the inlets, slightly past the coral-dominated areas. The bridge in Zone 1 is 10.0 m along the length of the road and consists of one inlet (Figure 2.3a). The inlet dimensions are consistent

at each site, with length (perpendicular to the road) of 13.2 m and width (parallel to the road) of 7.7 m. Scouring caused sand-substrate pools to occur on both the north (circumference = 50.6 m) and south (circumference = 90.4 m) side of the causeway (Figure 2.3b). Deepest points in the pools are 3.0 m on the north and 3.9 m on the south. Directly surrounding the pools, water levels are less than 1 m on the north side, and less than 0.6 m on the south (at high tide). At low tide several species of fish are often caught in the pools until water levels are high enough to swim over the surrounding sand flats to the open ocean. The bridge in Zone 2 is the longest (length along road of 98.5 m) and contains 11 inlets separated by columns 1.15 m wide (Figure 2.4), while the bridge in Zone 3 is of intermediate size (length along road of 63.1 m) with seven inlets (Figure 2.5). Surrounding the BR sites, *Rhizophora mangle* mangrove stands are found in varying densities, both along the side of the road and in the water.

### 2.2.2 Mangrove Channels

The mangrove channels (MC) are naturally carved out within coastal *R. mangle* forests (Figure 2.6a) seaward of the bridge reefs, with coral forming patches along the substrate. The substrate is hard, flat and rock-based, with loose sand covering the surface. Many of the corals are found towards the centre of the channels, with dense mangrove forest on either side (Figure 2.6b). Surrounding the coral are seagrass patches or sporadic clumps of various algal types, such as *Pencillllus* spp., *Laurencia* spp. or *Caulerpa* spp. The channels connect to the open ocean through a 6 m deep channel found in Zone 2 (Figure 2.6c).

### 2.2.3 Seagrass Beds

Seagrass (SG) habitats are north of the mangrove channels and are generally found in sandy bottom regions in the back reef lagoon. Water depth is generally shallow, with only two seagrass species present: *T. testudinum* (predominantly) and *Syringodium filiforme*. Many of the SG patches are interspersed with *Porites porites* coral fragments. *T. testudinum* leaves are occasionally covered with carbonate-based epiphytes and zoophytes and are often covered in loose sediment. Many of the SG habitats share benthic space with varying algal types also present in the MC habitat.

### 2.2.4 Natural Reefs

Each natural reef (NR) habitat varies in their form and structure, and is found in reef zones characteristic for the Cayo Coco – Cayo Guillermo region. The natural reef closest to the shore in Zone 1 is a patch reef (NR1PR), which is found in a back reef lagoon consisting primarily of *Diploria* spp. coral heads. The next habitat type seaward is the reef crest (NR1RC), which is in the fore reef zone and is a shallow habitat with clear water. In Zone 2 on a deep terrace in the fore reef zone, spur and groove reef habitat type (NR2SG) is found, characterized by a mix of soft corals, such as sea fans and sea whips, and stony corals, with sandy substrate grooves found between spurs. In Zone 3 the reef habitat is on a medium-depth reef slope (NR3RS) in the fore reef zone, and contains more foliaceous corals, such as *Agaricia* spp., as well as corals from the *Montastraea* complex (*M. annularis*, *M. franksii* and *M. faveoloata*).

## 2.3 In-Situ Observations

In order to approximate habitat connectivity, a variety of biotic and abiotic factors were measured. Diversity and abundance of coral, benthic coverage, and physical and environmental factors for all sites were measured during a 3 week field campaign between February 24, 2007 and March 16, 2007. Many of the sites were evaluated on calm, clear days, often between north-easterly cold fronts, which repeatedly brought strong winds, rain and cooler temperatures, followed by rougher sea conditions. Although this period fell within the dry season (typically December through May), occasional cold fronts can affect this region due to continental weather influences from North America. June through November is typical of rainy season weather effects, usually brought on by cyclonic activity or convection from warm sea surface temperatures and solar radiation.

### *2.3.1 Environmental Variability*

The physical environment was characterized at each site by measuring several factors, either through snorkelling in shallow sites, or SCUBA in deeper sites. Four water chemistry variables were measured: conductivity, salinity, total dissolved solids (TDS), and dissolved oxygen. Conductivity ( $\pm 0.5 \text{ mS cm}^{-1}$ ), salinity (0.2% full scale) and TDS were measured at each site with the YSI EC300 probe, calibrated daily to a standard conductivity of 1413  $\mu\text{S/cm}^3$ . Measurements were taken from approximately 2 m below the surface in all sites except NR2 and NR3, which were taken at approximately 8 m below the surface. Dissolved oxygen was measured with a Hach HQ10 Portable LDO Dissolved Oxygen Meter at approximately 2 m below the surface, and was measured in every site except for MC2 and MC3, due to equipment failure. Point measurements of all variables were taken at random

locations within each site during high tide. The BR2 and BR3 sites were separated into two areas, north and south, and five replicates of each variable were recorded, while the BR1 site was separated into four areas, north and south pool and north and south entrance, with five replicates of each variable measured in every area. All SG, MC and NR sites had 10 replicates for each variable.

Five physical water variables were also measured: current speed, site complexity, depth, temperature and turbidity. The current speed was measured with a General Oceanics Mechanical Flowmeter (model 2030R), which recorded speeds faster than  $10 \text{ cm s}^{-1}$  by rotating a standard rotor in a clockwise direction 1 m below the surface for 1 minute, indicating the number of counts per second. The speed was calculated as the following:

$$\text{DISTANCE (m)} = \frac{\text{Difference in COUNTS} * 26\,873}{999\,999} \text{ (the Rotor Constant)}$$

$$\text{SPEED (cm s}^{-1}\text{)} = \frac{\text{DISTANCE} * 100}{60 \text{ s}}$$

The site complexity was measured using a 2 m metal linked chain, loosely placed on the substrate, capturing all the contours. A measuring tape was then tautly placed next to the chain and the length was recorded. The ratio of tape length to chain length was then calculated as the complexity, with 1 indicating a flat surface, and 0 indicating a complex surface. Depth was measured at high tide for each site, using a graduated measuring stick ( $\pm 0.05 \text{ m}$ ) for shallow sites ( $< 4 \text{ m}$  deep), and for sites requiring SCUBA, a Suunto Mosquito (200900 model) dive computer ( $\pm 1\%$  of full scale or better) was used for recording depth. Temperature was measured with the same probe measuring Conductivity/Salinity/TDS (YSI EC300) ( $\pm 0.2 \text{ }^{\circ}\text{C}$ ) in the same fashion as above. The turbidity of samples taken from the water column was measured on the surface with the Lamotte Turbidity Meter (2020e) ( $\pm 2\%$ ).

The meter was calibrated prior to use with 0 and 1 NTU calibration solutions, and was set for 10 readings per sample. Point measurements of all variables were taken at random locations at each site during high tide. Each BR site was separated into two areas, north and south, and five replicates of each variable were recorded, with the exception of measurements for depth and temperature, which followed the protocol of the water chemistry measurements, with 5 replicates each in the BR1 pools and entrances. All SG, MC and NR sites had 10 replicates for each variable.

### *2.3.2 Coral Communities*

In sites where scleractinian coral was found, abundance and richness of corals was documented based on 0.5 x 0.5 m quadrats along random line transects perpendicular to the shoreline. In BR sites, transects were conducted both north and south of the bridge, within 5 m of the structure, while in the MC and NR habitats, transects were conducted at the start of reef zones. The number of quadrats used were based on asymptotes achieved in species-area curves of cumulative number of species vs. quadrats sampled (Chiappone et al. 2001) at the BR sites (Figure 2.7). Although asymptotes were not reached for the NR sites, the main concern was to capture coral diversity at the BR sites, and the diversity in only a comparably-sized region in the natural reefs. 25 quadrats were determined to be an adequate sampling size, and the spacing between each sampling unit was the length of two fin kicks by the same observer (approximately 2 m), making transects approximately 61 m long. Observations were made in the BR sites with snorkelling, while all other sites required the use of SCUBA equipment.

Within each quadrat, each scleractinian coral species was identified (as well as corals within the milleporina order) and the number of colonies were counted. For each colony of each species, the size was measured along the axis of longest diameter (cm) ( $\pm 5$  cm), and any colony smaller than 5 cm was recorded as  $< 5$  cm, however for analysis purposes, these corals were calculated as 3 cm.

### 2.3.3 Benthic Composition

To quantify the substrate of each site,  $0.5 \times 0.5$  m quadrats were randomly placed through each site and the percent coverage of the following groups were recorded: sand, algae, coral, rock, seagrass, sponges/tunicates or other. Sponges and tunicates were grouped together as several of the species looked similar *in-situ* but required laboratory analysis for accurate identification. Any object observed from the Other category was described in detail and included in the inventory. BR2 and BR3 sites had 20 random quadrats each on the north side of the bridge, south side of the bridge and directly under the bridge. The BR1 site had 20 quadrats each in the north pool, south pool, north entrance, south entrance and directly under the bridge. Benthic coverage was also characterized at the MC and NR sites with 20 quadrats for each site.

## 2.4 Statistical Analysis

Trends in data were examined using box-plots and Hierarchical Cluster Analysis (HCA) (group average linkage method using relative Euclidean distance measurements) to determine site assemblages based on coral, physical and benthic observations. Since data on physical and biological parameters did not meet the criteria for parametric statistics

(normality, homogeneity of variances and independence), these data were evaluated to detect the similarity of community structures using Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA), with PC-Ord Software (McCune and Mefford 1999) (see Tables 2.2 and 2.3 for codes used in ordination plots). All DCAs were run under Q-mode, with R-mode also verified to determine if trends were similar. For simplicity, Q-mode results are demonstrated, and outliers are removed from figures on specific graphs depending on general trends (see figure legends). Eigenvalue scores are displayed and discussed, as it is a good representation of the dispersion of the species scores on the ordination axis, with values over 0.5 denoting a good separation of species or sites along the axis (ter Braak 1995).

Correspondence of sites to coral species and physical variability or benthic coverage in CCA required the use of mean physical variables/benthic coverage replicates per site. Uni-variate statistics (graphical interpretation of box-plots and standard error) were applied to physical variables and benthic coverage averages, and showed variability was minimal and means were a reasonable choice to use for CCA. Row and column scores were standardized in CCA by centering and normalizing; scaling of ordination scores represented a compromise of optimizing columns and rows; and site scores for graphing were derived from species. Monte Carlo tests were also run in CCA, testing the null hypothesis that there was no relationship between matrices, providing a *P* value that was the proportion of randomized runs with species-environment correlations greater than or equal to the observed species-environment correlation.

### 3. RESULTS

#### 3.1 Inter-Bridge Comparisons

##### 3.1.1 Environmental Variability

Across the three bridges, conductivity, salinity and TDS demonstrated similar trends due to conductivity measurements stemming from salinity measurements, which were linked closely to the total dissolved solids present in water samples. The BR1 and BR3 sites had continuously higher values for each variable compared to the BR2 sites (Figure 2.8 a-c), with little variability. Dissolved oxygen demonstrated an overall decline from west to east (Figure 2.8d), with BR1 having highest values and BR3 lowest.

Current was less than  $10 \text{ cm s}^{-1}$  at BR3, and speeds were fastest in the north side of BR1 (maximum speed of  $44.52 \text{ cm s}^{-1}$ ) and similarly fast along the south sides of BR1 and BR2 (maximum speeds of 12.95 and  $30.81 \text{ cm s}^{-1}$ , respectively; Figure 2.8e). BR2N also had relatively fast speeds (maximum  $4.41 \text{ cm s}^{-1}$ ) but was consistently slower than the BR1 site speeds.

There was a large amount of boulders present in the entrances of BR1, as represented by the complexity of BR1N and BR1S (Figure 2.8f) yet the smoothness of the scoured pools north and south of the entrances reduced the overall sites' ruggedness. The complexity of BR1 however, was not nearly as rugged as BR2, with BR2N demonstrating the largest amount of complexity due to numerous boulders and deeply scoured pools next to each other at the entrances of each inlet. BR3 was the least complex site, with fairly flat substrates surrounding the bridge on either side. BR2 and BR3 demonstrated a trend of deeper water along the north sides of the bridges (Figure 2.8g). In BR1 only the pools were deep, with no

discernible difference between the north and south side, while the entrances in the north side were shallower.

Temperature measurements taken at high tide demonstrated considerably higher values at BR1 and similarly low temperatures at BR2 and BR3 sites (Figure 2.8h). The turbidity of each site showed a clear declining trend with zone. BR1 demonstrated the highest amount of turbidity, while BR3 had the lowest levels of suspended particles (Figure 2.8i).

By grouping all environmental variables together in HCA, the dendrogram suggests that the pool habitats of BR1 can be grouped as unique sites (close to 100% internal resemblance), as can the north and south sides of the BR3 site (close to 100% internal resemblance) (Figure 2.9). The north and south sides at BR3 share attributes with BR2N (resembling more than 90%). The entrances of BR1 also resemble a grouping, with BR2S sharing similar attributes to the entrance grouping (close to 100%). BR2S-1 and BR1NE-1 demonstrate extreme differences from the rest of the clusters, with no clustering to all other sites. As seen by using DCA (Figure 2.10), the BR1 sites and BR2S were characterized by faster current speeds. Higher turbidity values were dominant in BR1 sites, while the opposite was found in BR3 and BR2N. Separation of site scores, based on correlation to environmental variables along axis 1 and 2 was not strong (eigenvalue scores: axis 1 = 0.0369; axis 2 = 0.0034).

### *3.1.2 Coral Communities*

Coral community richness varied between the three zones with no coral present in BR1, 10 species in BR2 and only 3 species in BR3 (Table 2.3). BR3S and BR3N sites had

lower coral species diversity than the BR2 sites, with only 4 and 5 quadrats containing coral species, respectively. Along axis 1 of the coral community DCA in bridge reef sites (Figure 2.11), BR3 is separated from BR2. This separation is due to only three coral species found in BR3 (*Manincina areolata*, *P. porites* and *Siderastrea radians*), which were also found in BR2 with relatively similar abundances and sizes (Figure 2.12a-d). All other species were found in BR2. Overall separation of species was considered good for axis 1 (eigenvalue score 0.6354), while axis 2 was not as widely spread (eigenvalue score 0.1129).

### 3.1.3 Benthic Composition

The bridge reefs demonstrated different coverage patterns from each other and also within each bridge site. The pools of BR1 had highest sand coverage along the substrate, while the entrances and under-bridge area predominantly consisted of rock and rock with algae in the SE (Figure 2.13a). The substrate of BR2 was more variably covered, with an almost even distribution of coverage types in both the north and south sides. Exceptions existed with the under-bridge area containing high coverage of sponges/tunicates, the north area having higher incidences of seagrasses and the south area algae (Figure 2.13b). BR3 was a much sandier site, but also had predominant algal coverage in both sides of the bridge, seagrass in the north region and higher abundances of rocks and tunicates under the bridge (Figure 2.13c). BR2N/S contained the highest percent coverage of coral out of the three bridge areas and quantity of seafloor rock was highest in the BR1 site. All sites demonstrated highest percent coverage of tunicates/sponges under the bridges, while seagrass predominated in the north sides of both BR2 and BR3.

Although the same types of coverage exist throughout each bridge reef, the HCA demonstrates that differences in quantities are observed, with only a few site similarity groupings (Figure 2.14). The dendrogram suggests that BR1UB and NE are the closest grouped sites (nearly 100% internal resemblance), while the pools of BR1 are also similar habitats (more than 90% internal resemblance). The south sides of BR2 and BR3 are also similar (more than 80% resemblance) as are the under-bridge areas of BR2 and BR3 (close to 80% internal resemblance). The DCA plot (Figure 2.15) confirms these groupings with the BR1UB and BR1NE grouping related to the high level of rock coverage, seen along axis 1. The pool grouping of BR1 is characterized by a sandy substrate, with some obvious other coverage types also found in these sites (mostly dead organic matter, such as *T. testudinum* leaves, palm fronds and *R. mangle* leaves). Moderate seagrass coverage is found in both BR2N and BR3N, yet data clouding is loose due to the presence of coral also found in these sites. Algae coverage type surrounds BR2S and BR3S in the ordination, but coral is also present in both sites. Tunicates and sponges group closely with BR2UB and BR3UB, due to higher abundances in darker areas. Overall site separation along axis 1 was moderate (eigenvalue score 0.4734), while site separation along axis 2 was poor (eigenvalue score 0.3593).

## 3.2 Inter-Habitat Comparisons

### 3.2.1 Environmental Variability

NR sites tended to have lower conductivity, salinity and total dissolved solids, while SG habitats had intermediate levels, and MC and BR sites varied (Figure 2.16a-c). Zone 1 sites generally had overall higher dissolved oxygen levels, while zone 2 and 3 did not follow

any distinct trend. BR2 was higher than the NR2SG site, while BR3 was lower than the NR3 site, and SG3 site was higher than both (similar to SG1 levels) (Figure 2.16d).

Current was less than  $10 \text{ cm s}^{-1}$  in all sites except for BR1, BR2, MC2 and MC3, with similar speeds in both MC sites and variably fast speeds in BR1 and BR2 (Figure 2.16e). Highest levels of structural complexity were observed in the BR2, NR3S and NR1RC sites. All other sites were relatively flat, with NR1PR and NR2SG less flat than the remaining sites (Figure 2.16f). The NR2SG and NR3RS sites were distinctly deeper than all other sites, including the natural reefs in zone 1. All other sites were at shallower depths (Figure 2.16g). Temperature varied at all sites (although not corresponding to depth), with the coolest temperatures in BR3, MC3, BR2 and MC2. The warmest temperatures were in zone 1 (Figure 2.16h). Turbidity was fairly low in most sites, with BR1 having the highest (and most variable) amounts of particulate matter, and the BR2 and MC2 sites having second highest levels present in samples (Figure 2.16i).

Site groupings are strong based on physical variables in HCA, with NR2SG and NR3RS showing the closest grouping (close to 100% internal resemblance) (Figure 2.17). Other groupings that are strong (more than 90% resemblance) and demonstrate similar habitats are BR1NP and BR1SP, MC2 and MC3, BR3N and BR3S, SG1 and NR1PR and SG3 with NR1RC. These site groupings are displayed in the DCA (Figure 2.18), with NR2SG and NR3RS grouped with depth, due to these sites' deeper characteristics. The BR1NE and BR2S grouping is characterized by data clouding of current, due to strongest levels of current in these sites. Overall separation of site scores along both axes is considered poor (eigenvalue scores: axis 1 = 0.0462, axis 2 = 0.0074).

### 3.2.2 Coral Communities

As Figure 2.12 e-j demonstrates, overall coral species diversity was higher in the natural reef sites NR1RC, NR2SG and NR3RS, with 12-14 species present at each site. NR1PR and MC3 sites were also similar in diversity with 8 species each. Coral colony abundances were highest however in NR1PR and MC3. Size of colonies were small in most sites, ranging from >3cm – 30cm averages, with the exception of *Diploria clivosa* colonies in NR1PR and *Millepora complanata* in NR1RC, reaching maximum colony sizes of 100cm and 80cm, respectively.

Site groupings in HCA demonstrate strong similarity between NR1RC and NR2SG (close to 100% internal resemblance) (Figure 2.19). MC3 and NR1PR are also considered similar sites, with close to 95% resemblance and BR2N similar to this grouping by greater than 90% internal resemblance. The grouped BR3 sites (which had less than 75% resemblance to each other) were not similar to any other sites, based on coral abundances and diversity, with only three species present.

Several coral species congregate in one or more sites throughout the seascape. The DCA plot (Figure 2.20) demonstrates similarities in the BR3 and MC sites, based on the main species assemblages of *M. areolata* and *S. radians*, while BR2S also shares some similarities to these sites, yet is slightly different based on *Porites furcata*, *Millepora alcicornis* and *Porites divaricata*. These sites are also grouped with BR2N and NR1PR along axis 1, with BR2N and NR1PR containing *Porites astreoides*, *Porites* sp., *P. porites* and *D. clivosa*. NR1RC demonstrates similar patterns to BR2N and NR1PR, but is distinct based on the presence of *M. complanata*, *Diploria strigosa*, *Montastraea* sp. and *Meandrina meandrites*. The NR2 and NR3 sites are quite different from the other sites, with unique

assemblages compared to the BR and MC sites. Eigenvalue score for axis 1 denotes good dispersion of species, reflecting a strong relationship between species and sites, while axis 2 is moderate (eigenvalue scores: axis 1 = 0.5419; axis 2 = 0.2591).

CCA (Figure 2.21) implies that depth is the strongest environmental factor responsible for the distribution of coral (axis 1 correlation coefficient = 0.849). Coral species gathering around NR2SG, NR3RS and NR1RC are all species that are found solely in these sites, which are of deeper depths than other sites. Turbidity is the next important environmental variable (axis 1 correlation coefficient = -0.710) responsible for the centering of coral species between MC2 and BR2N sites, with *F. fragum* as the main coral species present in highest levels of turbidity. Current speed is also an important environmental factor (axis 1 correlation coefficient = -0.636), with the coral species surrounding BR2 sites and NR1PR found in faster current (BR2) and higher wave action (NR1PR), while MC sites sharing axis 2, also experienced fast water current. Conductivity, salinity and TDS demonstrate correlation coefficients of 1.00 in raw correlations among variables in the second matrix and were therefore grouped as one variable jointly. Using Monte Carlo analysis for comparing species-environment correlations demonstrates a significant relationship between matrices ( $P = 0.013$ ).

### 3.2.3 Benthic Composition

Benthic composition was varied for each site, yet all sites had relatively low amounts of tunicates/sponges and other coverage types (Figure 2.22 a-f). MC2 was characterized by high amounts of sand, while MC3 had both high levels of sand and algae. All natural reef sites had high levels of algae, except for NR3RS, which had higher amounts of rock. By

combining the bridge reef observations in HCA (Figure 2.23), the most noticeable groupings were with BR1SP and MC2 (greater than 95% internal resemblance), BR3S and MC3 (greater than 90% resemblance), BR1UB and BR1NE (greater than 80% resemblance) and BR2UB and BR3UB (greater than 60% resemblance). Out of all surrounding sites, NR1RC and NR1PR were the most similar, with respect to benthic coverage (close to 100% internal resemblance).

Site groupings remain relatively the same in DCA, with only one or two sites added to each assemblage (Figure 2.24). The NR1RC and NR1PR grouping is predominant, but is also joined with BR2N, due to the mixed coverage of both coral and seagrass. Coral coverage is also predominant in NR2SG, which also has a higher abundance of rock, similar to BR1NE, BR1UB and NR3RS. BR3N is predominantly surrounded by a seagrass benthic coverage, while sites BR3S and BR2S have a more mixed coverage, with algae, seagrass, sand and other present. The MC3 grouping with BR3S is based on the predominant coverage of sand, which BR1SP, BR1NP and MC2 also follows. The under-bridge habitats of BR2 and BR3 are characterized most by the high abundances of tunicates and sponges. Overall separation of site scores along both axes is only moderate, demonstrating a medium relationship between sites and coverage types (eigenvalue scores: axis 1 = 0.4129, axis 2 = 0.2897).

CCA demonstrates that coral is considered the coverage type corresponding most to coral species distributions (axis 1 correlation coefficient = 0.913), which is intuitive based on the high diversity of coral present in the natural reef sites (Figure 2.25). Sand is the next important coverage type responsible for coral species distribution (axis 1 correlation coefficient = -0.777), with MC and BR3 sites having highest coverage of sand, and coral

species *M. areolata*, *S. radians* and *F. fragum*. Tunicate/sponge coverage type has a high correlation coefficient (axis 1 = 0.768) to NR3RS, however under-bridge habitats in BR sites would normally have largest coverage of this type, yet were not included in matrices due to no coral present in these sites. Rock coverage type is considered the last of the important coverage types (axis 1 correlation coefficient = 0.734) in site separation from coral species distributions, with NR3RS (and BR1UB/NE not included) having most rock present, perhaps due to the presence of boulder-style corals, such as *Montastraea annularis* and *Montastraea cavernosa*. Monte Carlo analysis demonstrates that comparing coral species-benthic coverage correlations has no significant relationship between matrices ( $P = 0.825$ ).

## 4. DISCUSSION

### 4.1 Bridge Reef Structure and Function

#### 4.1.1 Coral Community Connectivity

Comparing coral community structure in the bridge reef sites demonstrates there is an underlying factor responsible for the evident differences in abundance and richness of coral. The high species diversity found in Zone 2 may be explained by the direct connection to the open ocean, compared with lower diversity in the indirectly connected site in Zone 3 (Table 2.3). Zone 1 however, is also directly connected yet has no coral present. This site should in fact have the highest levels of species diversity if connectivity is the main factor responsible for coral proliferation, yet because of its position in front of extremely shallow sand flats between the open ocean and the bridge reef, connectivity is actually disrupted.

The distance oceanic water travels over the shallow sand-flat area between the open-ocean and BR1 is approximately 2 kilometres, in areas less than 1 foot deep during low tide (personal observation), similar to many of the bays in the region (Claro et al. 2001). Much of the water running over this intermediate habitat heats considerably during peak sunlight hours and receives substantial UV light exposure. In addition, these extremely shallow sand flats limit the volume of flow, causing increased evaporation and perhaps even higher levels of metal ions from the sand, which may contribute to higher conductivity and salinity in BR1 (Figure 2.8a,b). The patch reef and reef crest in Zone 1 have high abundances of coral and should be a potentially large source of larvae for recruitment at the BR1 site, yet because of the unfavourable conditions between these two habitats, successful recruitment may be limited. Past studies have demonstrated that a suite of environmental variables can affect successful larval recruitment. Elevated temperatures (33° C) have shown to cause mortality

in *P. astreoides* larvae (a species seen throughout our seascape) (Edmunds et al. 2001) while larvae have also shown negative responses (such as avoidance) to higher UV light exposure levels (Gleason et al. 2006), which may be occurring in the shallow sand-flats between the BR1 site and open-ocean. High sediment levels have also been shown to increase mortality and reduce settlement rates in coral larvae (Gilmour 1999). While sediment values in BR1 are considered similar to other sites within Florida (roughly 1-3 NTU) (Kenworthy and Fonseca 1996) they are still relatively higher than the other sites. If water levels were deeper over the sand flats, coral distribution at BR1 could be equivalent or even higher than BR2 since connectivity is most direct at this site. Mangroves in Zone 2 slightly inhibit connectivity, yet also slow water speed while increasing the depth of water in front of the bridge reefs, thereby facilitating oceanic exchange via the channel.

#### *4.1.2 Physical Environmental Constraints and Controls*

Although connectivity is believed to be the underlying factor in coral community development at the bridge reef sites, the physical environment also plays a similar role in their establishment. Water current speed was found to be one of the more important physical factors shaping the bridge reef communities (Figure 2.10). While speeds were variable, they mimicked patterns seen in other tidal channels in the Bahamas with speeds ranging from 5 cm s<sup>-1</sup> to 25 cm s<sup>-1</sup> (Smith 2004). Tidal currents have been known to control levels of sediment and silt entering habitats (Stewart et al. 2000, Hoitink 2004), as well as provide oxygen and food sources, such as plankton and other nutrients to reef sites.

To a lesser extent, turbidity contributes to the community ecology of the sites, as seen in BR1 with highly turbid measurements and no coral present. Turbidity levels relate to the

amount of light entering the water column and can be influenced by sedimentation levels, algal blooms and any other particulate matter skewing light. Higher NTU values have been shown to affect corals by decreasing growth rates, disrupting colony formation and changing respiration rates due to active sediment removal by cilia and mucus (Rogers 1990).

Measured salinity levels are generally high for coral reef ecosystems (oceanic levels range from 32-37‰) but compared to prior studies of the region, salinity has dropped considerably (Alcolado 1991). The hydrodynamic regime shifted in the Sabana-Camaguey Archipelago in north-central Cuba following the construction of the coastal highways, causing weak water circulation and high salinity levels (65‰) in Bahía de Perros in 1991. After the addition of inlets, oceanic water was allowed to mix freely with the bay, thereby dropping salinity to biologically acceptable levels (Alcolado 1991, Claro et al. 2001). Previous coral studies have shown increases in salinity to 42‰ cause decreases in coral respiration and photosynthesis in *S. siderea* (Muthiga and Szmant 1987), as well as death with sustained 40‰ salinity levels in the Red Sea coral, *Stylophora pistillata*, due to reduced photosynthesis (Ferrier-Pages et al. 1999). Monitoring of the bridge reefs will need to continue, as these higher salinity levels may cause widespread coral mortality.

The difficulty with short-term field work is that several characteristics measured provide merely a snap-shot of that particular point in time, and do not capture annual changes. Many water chemistry variables can vary significantly not only from day to day, but also from low tide to high tide, as water flow changes direction through the bridges (open ocean to lagoon during high tide, and lagoon to open ocean during low tide). In addition, seasonal inputs can cause changes to turbidity levels and temperature, as northern cold fronts passing through the region bring cooler water and wave action, while summer characteristically has

calm ocean conditions and peak temperatures. Long-term data observations from data-loggers are suggested for the future to capture diurnal and annual variations

#### 4.1.3 Benthic Community Structure and Form

Benthic coverage directly influences habitat composition due to strong limitations of the physical environment. Tunicates and sponges dominate directly beneath the bridges where it is typically darker, while some are occasionally found beyond the entrances. Although the sponges and tunicates are found predominantly in dark regions, they do not need dark conditions to grow. The lack of light beneath the bridges prevents photosynthetic organisms (and organisms containing photosynthetic symbionts) from settling in these areas, providing a region where sponges and tunicates can proliferate without competing corals and algae for space. The seagrasses found mostly in front of the bridge structures however, require constant sunlight and clear water for photosynthesis, which occurs consistently on either side of the bridge structures where water current is strongest.

Although algae are abundant, they do not out-compete other benthic species, consistent with mesotrophic environments, such as the Cayo Coco-Guillermo region (see Appendix A, Gonzalez-de Zayas 2005). The BR3 zone however shows signs of intense algal competition, where the flat sandy areas in front of the bridge demonstrate higher levels of *Laurencia intricata*. This algae species is generally found in protected sandy areas up to 3 m deep and can form thick, dense algal mats (Littler and Littler 2000). Species within the genera *Laurencia* are considered drift-type macroalgae, common throughout the Greater and Lesser Antilles, Florida and the Bahamas, and have been known to cause shading over substrates and other organisms in the benthos region (Littler and Littler 2000, Biber and

Irlandi 2006). *L. intricata*, similar to *R. mangle* roots and leaves of *T. testudinum*, can significantly reduce water currents and trap and bind carbonate materials (Scoffin 1970). This algal type is strongly influenced by seasonality, with higher abundances in the winter and early spring, and can also be influenced by shifts in salinity (Josselyn 1977, Biber and Irlandi 2006). The levels of *L. intricata* will have to be monitored closely in this region, to assure that competition for light between it and corals remains moderate to low, and that blooms are only present in the winter months (when observations were made).

## **4.2 Terrestrial-Marine Continuum: Integrated Seascapes Studies**

### *4.2.1 Connecting the Bridge Reefs to the Seascapes*

The bridge reefs in Zone 2 and 3 demonstrate overall similarities to the patch reef in Zone 1 and both mangrove channel reefs, respectively. BR3 is most similar to MC2 and MC3 because of *M. areolata* and *S. radians* present in all three sites (Figure 2.20). Other similarities also include comparable salinity, conductivity and TDS levels (Figure 2.21) and a predominantly sand covered substrate (Figure 2.25). The BR2 habitats associate more towards NR1PR based on shared coral community structure, with species from *Porites*, *Diploria* and even *Millepora* (bottom left corner of Figure 2.20). Large amounts of seagrass cover both site substrates (Figure 2.25), and may encourage coral growth in other parts of the sites, due to clearer water from sediment settlement in seagrass patches (Scoffin 1970).

### *4.2.2 Coral in Marginal Habitats*

The coral species found dominating the bridge reef sites, mangrove channels and NR1PR are species typically found in marginal habitats: *M. areolata*, *P. astreoides*, *P.*

*porites* and *S. radians*. With the exception of a few less-resistant species in BR2 (*D. clivosa* and *M. alcicornis*) these species can survive in waters where most other corals experience mortality due to high sedimentation, variable salinity from tidal influences, and extreme temperature regimes. The BR2 site may be considered less of a marginal site, due to its clearer water, higher dissolved oxygen levels, slightly deeper depths and lower salinity and TDS levels (Figure 2.8).

Many of the dominant corals found in the BR sites are species that have evolved morphological characteristics over time to withstand these environments. For example, some *S. radians* colonies have grown in a spherical shape to encourage development in disturbed habitats (Lewis 1989) and have also demonstrated high resistance to changes in salinity and large amounts of sedimentation (Lirman et al. 2002). Moreover, *S. radians* and *P. astreoides* have been known to withstand high levels of sedimentation while other more sensitive species, such as *M. annularis*, demonstrate reduced coral cover in areas with high deposition rates (Torres and Morelock 2002). Other species, such as *M. areolata*, have produced self-righting capabilities to prevent death from lack of light and independent removal of sediments in disturbed habitats (Johnson 1992, Uhrin et al. 2005). Shallow waters often inhibit coral growth, yet morphs of *F. fragum* have been shown to reside in depths ranging from <1m to 3m in Panama (Carlon and Budd 2002). Within BR2N, the milleporinian coral *M. alcicornis* is found growing in two separate locations and is commonly distributed in turbulent, rough water (Lewis 2006) as is found in our BR2N site.

The mangrove channels are also characterized with mostly marginal coral species. Despite their limited ability in building typical carbonate-based reef structures, many of these species are likely responsible for contributing larvae to the bridge reefs, and ultimately

creating the coral communities. With the exception of *Eusamilia fastigiata* and *M. annularis*, the corals in the mangrove channels are reproductive brooders, implying fully developed coral larvae travel only a short distance to reach an appropriate substrate and settle (Smith 1992). Since the distance between the mangrove channels and bridge reefs is short (less than 2 km from each habitat type), it is feasible that most of the coral recruits at the bridge reefs were from brooded larvae of mangrove channel corals. Broadcast spawning corals are generally not found in marginal habitats; however the presence of *D. clivosa* in BR2N is likely due to successful larval recruitment of broadcast spawned gametes from the *D. clivosa* colonies in the patch reef. Spawning gametes of *E. fastigiata* and *M. annularis* from the mangrove channels and other *Diploria* spp. from the patch reefs and natural reefs may also eventually colonize the bridge reefs in the future. Successful recruitment of these species will depend on meeting their individual physiological requirements, which are directly related to the physical environment.

#### 4.2.3 The Natural Reefs of the Cayo Coco – Cayo Guillermo Reef Tract

The patch reef in Zone 1 demonstrates an atypical coral habitat compared to the other natural reef habitats of the seascape, with several *Diploria* spp. coral colonies and coral heads. Patch reefs on average can vary significantly in size, depth, shape and species composition. In the southern Bahamas island chain, this was typified with patch reefs in tidal channels having less abundant coral than patch reefs surrounding islands and cays, similar to our study (Chiappone et al. 1996). Essentially the mangrove channel reefs are tidal channel patch reefs that similarly demonstrate less abundant coral than the NR1PR. Dominant coral species present both in NR1PR and the Bahamian patch reefs include *M. complanata*, *P. astreoides*

and *P. porites* (Chiappone et al. 1996). Patch reefs in a semi-enclosed harbour with a causeway in Bermuda also shared similar species composition, with several *D. strigosa* and *Diploria labyrinthiformes* colonies (Flood et al. 2005). Species within the *Diploria* genus typically are found in depths as shallow as 1.5 m, although *D. clivosa* is the only species most common in shallower depths (Humann and Deloach 2002). Surprisingly, *D. strigosa* colonies in NR1PR were found in depths shallower than 1 m with coral heads exposed to air during low tide. *Diploria* spp. have been found at similar depths in other patch reefs in Florida and Bermuda, however no studies have discussed exposure to air during low tide (Fricke and Meischner 1985, Ginsburg et al. 2001).

In the ordinations comparing all sites, natural reefs were most often grouped separately from the other habitat sites. The spur-and-groove reef of Zone 2 and reef slope of Zone 3 were closely grouped together as a result of the coral species found at these sites, which were always in deeper water (Figure 2.21). These species are not typical of extreme deep water reefs but are commonly found in mid-depth habitats throughout the Caribbean and Cuba, and avoid shallow marginal habitats (Chiappone et al. 2001, González-Díaz et al. 2003, Acosta and de la Guardia 2004, de la Guardia et al. 2004). The reef crest was typical of other reef crests in the Caribbean, displaying a combination of Strigosa-Palmata and Palythoa-Millepora zonation patterns. These zones are typically characterized with strong wave action at the fore and rear parts of the reef, containing *Porites* spp. and *M. Annularis*, with *Acropora palmata*, *D. strigosa* and *M. alcicornis* species in the break zone (Geister 1977). Although *A. palmata* was not present in our quadrats, a few colonies were observed at the site, indicating healthy colonies not affected by white band disease, that has killed several *A. palmata* colonies throughout the Caribbean (Peters 1997).

## 5. CONCLUSIONS

Connectivity seems ultimately responsible for the development of coral at the bridge reefs. The direct connection present in BR1 should have encouraged successful coral development; however shallow water over the sand flats likely disrupts the flow of water, and ultimately the coral larva supply. The direct connection to the open ocean through the mangrove forests in Zone 2 encourages the high diversity of coral found at BR2. The mangrove prop roots slow the speed of water through the channels and deepen water levels between the natural reefs and the bridge reefs, allowing coral larvae to colonize the site. BR3 has less coral diversity than BR2, likely due to less than optimal physio-chemical conditions at the site from dense mangrove forests surrounding BR3, and only an indirect connection to natural reefs in the open ocean.

Within the seascape, BR2 is most similar to the patch reef in Zone 1 with similar coral community structure, benthic coverage and physical conditions, while BR3 shows most similarities to both mangrove channel sites. Larval dispersal from the mangrove channels and natural reefs is crucial for coral colonization at the BR sites. The mangrove channel reefs likely supplied most of the coral to BR3, while the patch reef likely supplied coral to the BR2 site. The coral that settled at the bridge reefs likely colonized as a result of physiologically meeting the less-than-optimal environmental conditions and finding suitable substrates to settle onto.

If recommendations were to be made for development of similar bridge reefs between other cays in the Sabana-Camáüey archipelago, we would suggest the following factors be met when constructing new causeways:

- Large natural reefs directly in front of new causeways, to supply coral larvae.
- Presence of mangrove tidal channels to deepen water levels by slowing currents, in addition to providing coral larvae that can survive in marginal habitats.
- Have many inlets along causeways to encourage little disruption to the hydrodynamics of the region, allowing optimal physio-chemical conditions for coral growth.
- And lastly provide sufficient amounts of natural limestone rock or dead coral framework that mimics hard substrates seen in natural reefs, upon which coral can recruit.

These bridge reefs are now an important part of the Cayo Coco – Cayo Guillermo seascape that many organisms live in, visit or utilize for survival. Although many of the coral species are marginal habitat species, they are contributing to the ecology of the region, and should be monitored for continued development and growth. While the survival of many reefs in the Caribbean is threatened by human actions, this study demonstrates human development has actually increased the number of reef communities in Jardines del Rey, and may continue to do so for many years to come.

## 6. REFERENCES

- Acosta, A. V., and E. de la Guardia. 2004. Estructura de la comunidad de corales en el arrecife costero de Boca de Canasí, la Habana, Cuba. *Revista Investigaciones Marinas* **25**:15-22.
- Alcolado, P. M. 1991. Ecological assessment of semienclosed marine water bodies of the Archipelago Sabana-Camaguey (Cuba) prior to tourism development projects. *Marine Pollution Bulletin* **23**:375-378.
- Biber, P. D., and E. A. Irlandi. 2006. Temporal and spatial dynamics of macroalgal communities along an anthropogenic salinity gradient in Biscayne Bay (Florida, USA). *Aquatic Botany* **85**:65-77.
- Carlon, D. B., and A. F. Budd. 2002. Incipient speciation across a depth gradient in a scleractinian coral? *Evolution* **56**:2227-2242.
- Carlon, D. B., and R. R. Olson. 1993. Larval dispersal distance as an explanation for adult spatial pattern in 2 Caribbean reef corals. *Journal of Experimental Marine Biology and Ecology* **173**:247-263.
- Chiappone, M., K. M. Sullivan, and C. Lott. 1996. Hermatypic scleractinian corals of the southeastern Bahamas: A comparison to western Atlantic reef system. *Caribbean Journal of Science* **32**:1-13.
- Chiappone, M., K. Sullivan-Sealey, G. Bustamante, and J. Tschirky. 2001. A rapid assessment of coral reef community structure and diversity patterns at Naval Station Guantanamo Bay, Cuba. *Bulletin of Marine Science* **69**:373-394.
- Claro, R., K. C. Lindeman, and L. R. Parenti, editors. 2001. *Ecology of the Marine Fishes of Cuba*. Smithsonian Institution Press, Washington.

- de Boer, W. F., L. Rydberg, and V. Saide. 2000. Tides, tidal currents and their effects on the intertidal ecosystem of the southern bay, Inhaca Island, Mozambique. *Hydrobiologia* **428**:187-196.
- de la Guardia, E., P. González-Díaz, and S. C. Iglesias. 2004. Estructura de la comunidad de grupos bentónicos sésiles en la zona de buceo de Punta Francés, Cuba. *Revista Investigaciones Marinas* **25**:81-90.
- Edmunds, P. J., and J. F. Bruno. 1996. The importance of sampling scale in ecology: Kilometer-wide variation in coral reef communities. *Marine Ecology Progress Series* **143**:165-171.
- Edmunds, P. J., R. D. Gates, and D. F. Gleason. 2001. The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. *Marine Biology* **139**:981-989.
- Ferrier-Pages, C., J. P. Gattuso, and J. Jaubert. 1999. Effect of small variations in salinity on the rates of photosynthesis and respiration of the zooxanthellate coral *Stylophora pistillata*. *Marine Ecology Progress Series* **181**:309-314.
- Flood, V. S., J. M. Pitt, and S. R. Smith. 2005. Historical and ecological analysis of coral communities in Castle Harbour (Bermuda) after more than a century of environmental perturbation. *Marine Pollution Bulletin* **51**:545-557.
- Fricke, H., and D. Meischner. 1985. Depth Limits of Bermudan Scleractinian Corals - a Submersible Survey. *Marine Biology* **88**:175-187.
- Geister, J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Pages 23-29 in D. L. Taylor, editor. *Proceedings of the Third International*

- Coral Reef Symposium. Rosential School of Marine and Atmospheric Science, Miami, Florida.
- Gilmour, J. 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Marine Biology* **135**:451-462.
- Ginsburg, R. N., E. Gischler, and W. E. Kiene. 2001. Partial mortality of massive reef-building corals: An index of patch reef condition, Florida Reef Tract. *Bulletin of Marine Science* **69**:1149-1173.
- Gleason, D. F., P. J. Edmunds, and R. D. Gates. 2006. Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral *Porites astreoides*. *Marine Biology* **148**:503-512.
- Gonzalez-de Zayas, R. 2005. Dynamics of salt, nutrients and organic matter in three bridges of Cayo Guillermo causeway. Unpublished Report CIEC, Cayo Coco.
- González-Díaz, P., E. de la Guardia, and G. González-Sansón. 2003. Efecto de efluentes terrestres sobre las comunidades bentónicas de arrecifes coralinos de ciudad de la Habana, Cuba. *Revista Investigaciones Marinas* **24**:193-204.
- Hoitink, A. J. F. 2004. Tidally-induced clouds of suspended sediment connected to shallow-water coral reefs. *Marine Geology* **208**:13-31.
- Hubbard, D. K. 1997. Reefs as dynamic systems. Pages 43-67 in C. Birkeland, editor. *Life and death of coral reefs*. Chapman & Hall, Toronto.
- Humann, P., and N. Deloach. 2002. *Reef coral identification: Florida, Caribbean, Bahamas*, 2nd edition. New World Publications, Inc., Jacksonville, Florida.

- Johnson, K. G. 1992. Population dynamics of a free-living coral: recruitment, growth and survivorship of *Manicina-Areolata* (Linnaeus) on the Caribbean coast of Panama. Journal of Experimental Marine Biology and Ecology **164**:171-191.
- Josselyn, M. N. 1977. Seasonal changes in the distribution and growth of *Laurencia poitei* (Rhodophyceae, Ceramiales) in a subtropical lagoon. Aquatic Botany **3**:217-229.
- Kenworthy, W. J., and M. Fonseca. 1996. Light requirements of seagrasses *Halodule wrightii* and *Syringodium filiforme* derived from the relationship between diffuse light attenuation and maximum depth distribution. Estuaries **19**:740-750.
- Lewis, J. B. 1989. Spherical growth in the Caribbean coral *Siderastrea radians* (Pallas) and its survival in disturbed habitats. Coral Reefs **7**:161-167.
- Lewis, J. B. 2006. Biology and ecology of the hydrocoral *Millepora* on coral reefs. Pages 1-55 in A. Southward, C. Young, and L. Fuiman, editors. Advances in Marine Biology. Academic Press.
- Lirman, D., D. Manzello, and S. Macia. 2002. Back from the dead: the resilience of *Siderastrea radians* to severe stress. Coral Reefs **21**:291-292.
- Littler, D. S., and M. M. Littler. 2000. Caribbean Reef Plants. OffShore Graphics Inc., Washington, D.C.
- McCune, B., and M. J. Mefford. 1999. PC-Ord. Multivariate Analysis of Ecological Data. in. MjM Software, Gleneden Beach, Oregon.
- Muthiga, N. A., and A. M. Szmant. 1987. The effects of salinity stress on the rates of aerobic respiration and photosynthesis in the hermatypic coral *Siderastrea siderea*. Biological Bulletin **173**:539-551.

- Perry, C. T., and P. Larcombe. 2003. Marginal and non-reef-building coral environments. *Coral Reefs* **22**:427-432.
- Peters, E. C. 1997. Diseases of Coral-Reef Organisms. Pages 114-139 in C. Birkeland, editor. *Life and Death of Coral Reefs*. Chapman & Hall, Toronto.
- Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**:1454-1457.
- Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**:185-202.
- Scoffin, T. P. 1970. Trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology* **40**:249-&.
- Smith, N. P. 2004. Transport processes linking shelf and back reef ecosystems in the Exuma Cays, Bahamas. *Bulletin of Marine Science* **75**:269-279.
- Smith, N. P., and A. W. Stoner. 1993. Computer simulation of larval transport through tidal channels: role of vertical migration. *Estuarine Coastal and Shelf Science* **37**:43-58.
- Smith, S. R. 1992. Patterns of coral recruitment and postsettlement mortality on Bermudas reefs - comparisons to Caribbean and Pacific reefs. *American Zoologist* **32**:663-673.
- Stewart, L. K., A. D. Heap, and K. J. Woolfe. 2000. Evaluating the influence of tidal currents on the distribution of silt in Nara Inlet, central Great Barrier Reef, Australia. *Sedimentary Geology* **136**:59-69.
- Szmant, A. M. 1986. Reproductive Ecology of Caribbean Reef Corals. *Coral Reefs* **5**:43-53.
- ter Braak, C. J. F. 1995. Ordination. Pages 91-173 in R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, editors. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.

- Torres, J. L., and J. Morelock. 2002. Effect of terrigenous sediment influx on coral cover and linear extension rates of three Caribbean massive coral species. Caribbean Journal of Science **38**:222-229.
- Uhrin, A. V., C. L. Slade, and J. G. Holmquist. 2005. Self righting in the free-living coral *Manicina areolata* (Cnidaria : Scleractinia): Morphological constraints. Caribbean Journal of Science **41**:277-282.

Table 2.1. Site locations and habitat types

<b>Zone</b>	<b>Site</b>	<b>Habitat Type</b>	<b>Latitude (N)</b>	<b>Longitude (W)</b>
1	BR1NE	Bridge Reef North Entrance		
	BR1NP	Bridge Reef North Pool		
	BR1UB	Bridge Reef Under Bridge	22° 33'39.92	78° 38'12.37
	BR1SP	Bridge Reef South Pool		
	BR1SE	Bridge Reef South Entrance		
	SG1	Seagrass Bed/Lagoon	22° 34'09.67	78° 37'22.22
	NR1-PR	Natural Reef – Patch Reef	22° 34'12.14	78° 36'33.00
	NR1-RC	Natural Reef – Reef Crest in Fore Reef	22° 35'44.19	78° 35'15.60
	BR2N	Bridge Reef North	22° 31'53.26	78° 36'22.12
2	BR2S	Bridge Reef South		
	MC2	Mangrove Channel	22° 32'05.18	78° 36'08.79
	NR2-SG	Natural Reef – Spur and Grooves in Deep Terrace	22° 35'33.75	78° 34'13.15
	BR3N	Bridge Reef North	22° 31'35.62	78° 35'59.07
3	BR3S	Bridge Reef South		
	MC3	Mangrove Channel	22° 31'57.16	78° 35'51.12
	SG3	Seagrass Bed/Lagoon	22° 32'50.60	78° 34'55.34
	NR3-RS	Natural Reef – Reef Slope Medium Depth in Fore Reef	22° 35' 18.08	78° 32'39.86

Table 2.2. Abbreviations of environmental variables measured and benthic coverage types used in ordination plots.

<b>Environmental Variable</b>	<b>Abbreviation</b>	<b>Benthic Coverage Type</b>	<b>Abbreviation</b>
Complexity (Rugosity)	Rug	Algae	A
Conductivity	Con	Coral	C
Current Speed	Flo	Rock	R
Depth	D	Other	O
Dissolved Oxygen	DO	Sand	SA
Salinity	Sal	Seagrass	SG
Temperature	T	Tunicate/Sponge	TS
Total Dissolved Solids	TDS		
Turbidity	Tur		

Table 2.3. Scleractinian and Milliporinian coral colony abundances, based on 0.5x0.5m quadrats at each site (n=25)

Species	Abbreviation	BR2N	BR2S	BR3N	BR3S	MC2	MC3	NR1RC	NR1PR	NR2SG	NR3RS
<i>Agaricia agarcites</i>	Aa							2		2	2
<i>Agaricia sp.</i>	As							3		1	1
<i>Diploria clivosa</i>	Dc	1						1	12		
<i>Diploria labyrinthiformes</i>	Dl									2	
<i>Diploria strigosa</i>	Ds							2	2		1
<i>Eusamilia fastigiata</i>	Ef						1				6
<i>Favia fragum</i>	Ff	1	2			2					
<i>Madracis decactis</i>	Md									1	
<i>Manicina areolata</i>	Ma	1	3	4	7	12	7				
<i>Meandrina meandrites</i>	Mm							1			
<i>Millepora alcicornis</i>	MLa		1								
<i>Millepora cervicornis</i>	MLce									1	
<i>Millepora complanata</i>	MLco							4	2		
<i>Montastraea annularis</i>	MOa						1	1			5
<i>Montastraea cavernosa</i>	MOc							1		2	16
<i>Montastraea sp.</i>	MOs							1			
<i>Mussa anglosa</i>	MUa									1	
<i>Porites astreoides</i>	Pa	19	36			16	28	1	53	8	9
<i>Porites divaricata</i>	Pd	6	55				7		1		1
<i>Porites furcata</i>	Pf		1								
<i>Porites porites</i>	Pp	14	13	12	8		12	9	24	1	8
<i>Porites sp.</i>	Ps	17					1	1	14	1	
<i>Scolymia sp.</i>	SCs										1
<i>Siderastrea radians</i>	Sr	1	1	4	2	2	7	2	2	1	8
<i>Siderastrea siderea</i>	Ss							1		15	7

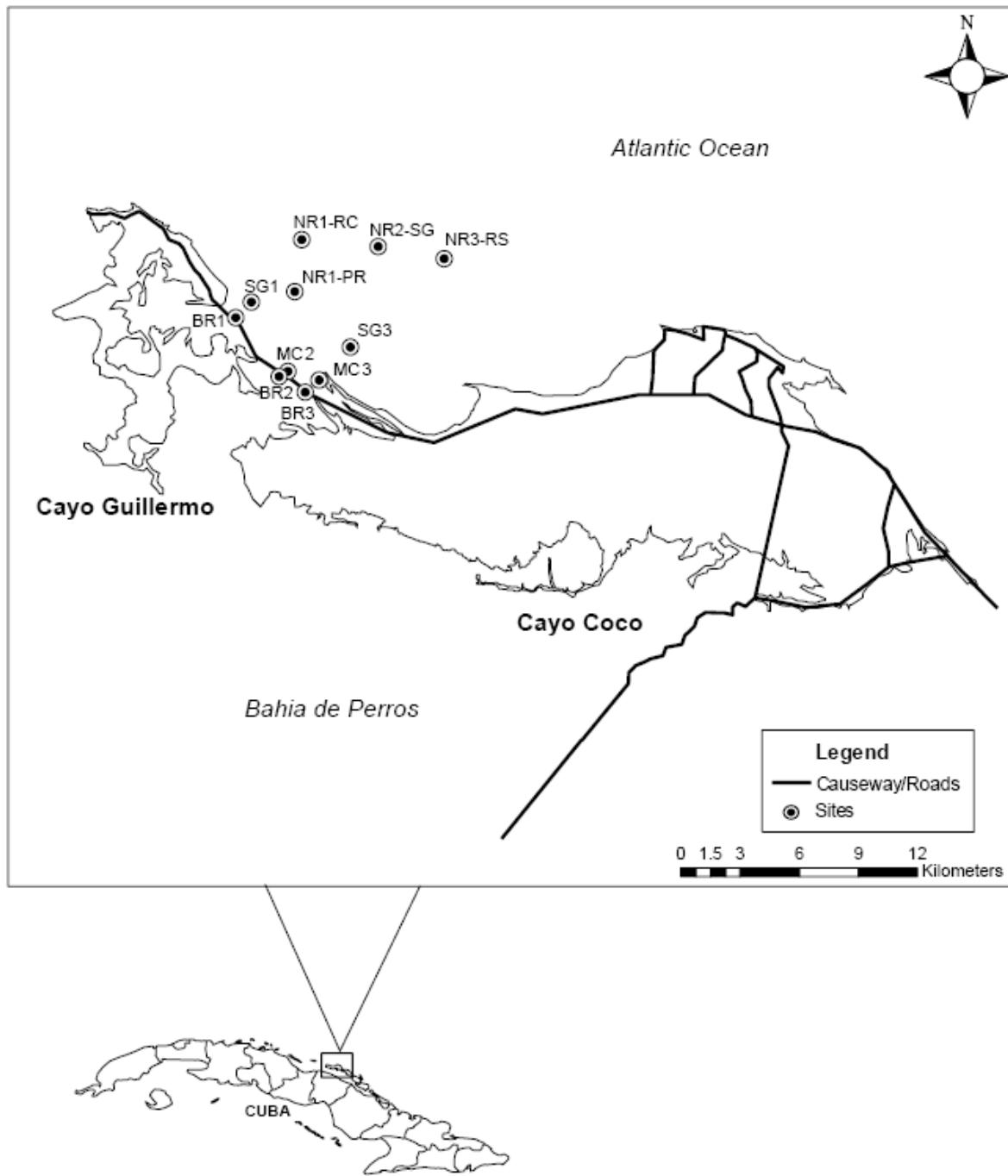


Figure 2.1. Location of study sites in Jardines del Rey, Ciego d'Avila province, Cuba. See Table 2.1 for co-ordinates of sites and site descriptions.

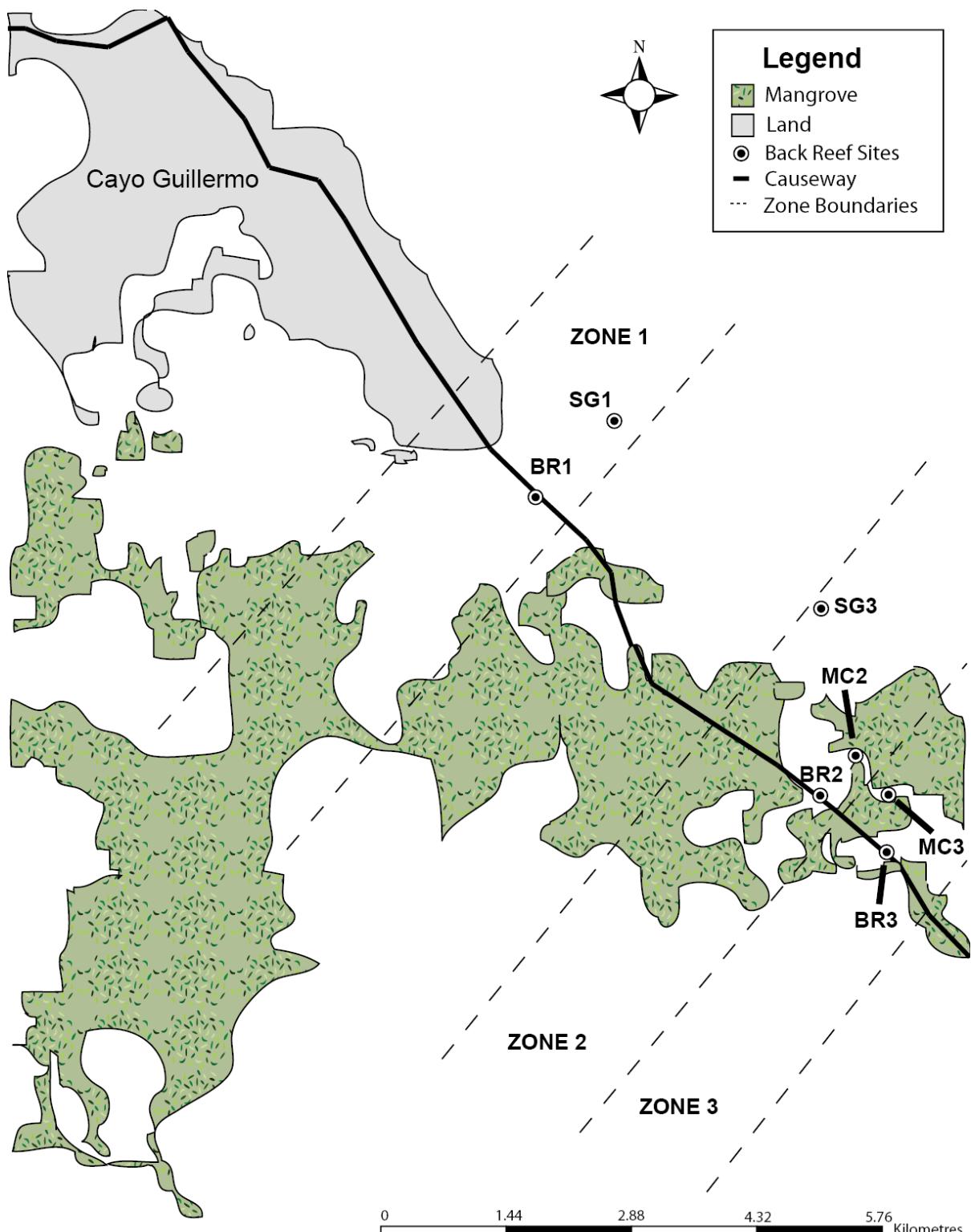


Figure 2.2. Distribution of mixed-species mangrove forests surrounding the bridge reef sites, and the delineation of zones, based on the presence of bridge sites, used in analysis.

**a)****b)**

Fig. 2.3. Characteristic view of Bridge Reef Zone 1: a) entrance area of inlet; b) scouring of pools (facing south).



Figure 2.4. Water flow entering inlets on the north side of Bridge Reef Zone 2.



Figure 2.5. Water flow entering inlets on the south side of Bridge Reef Zone 3.

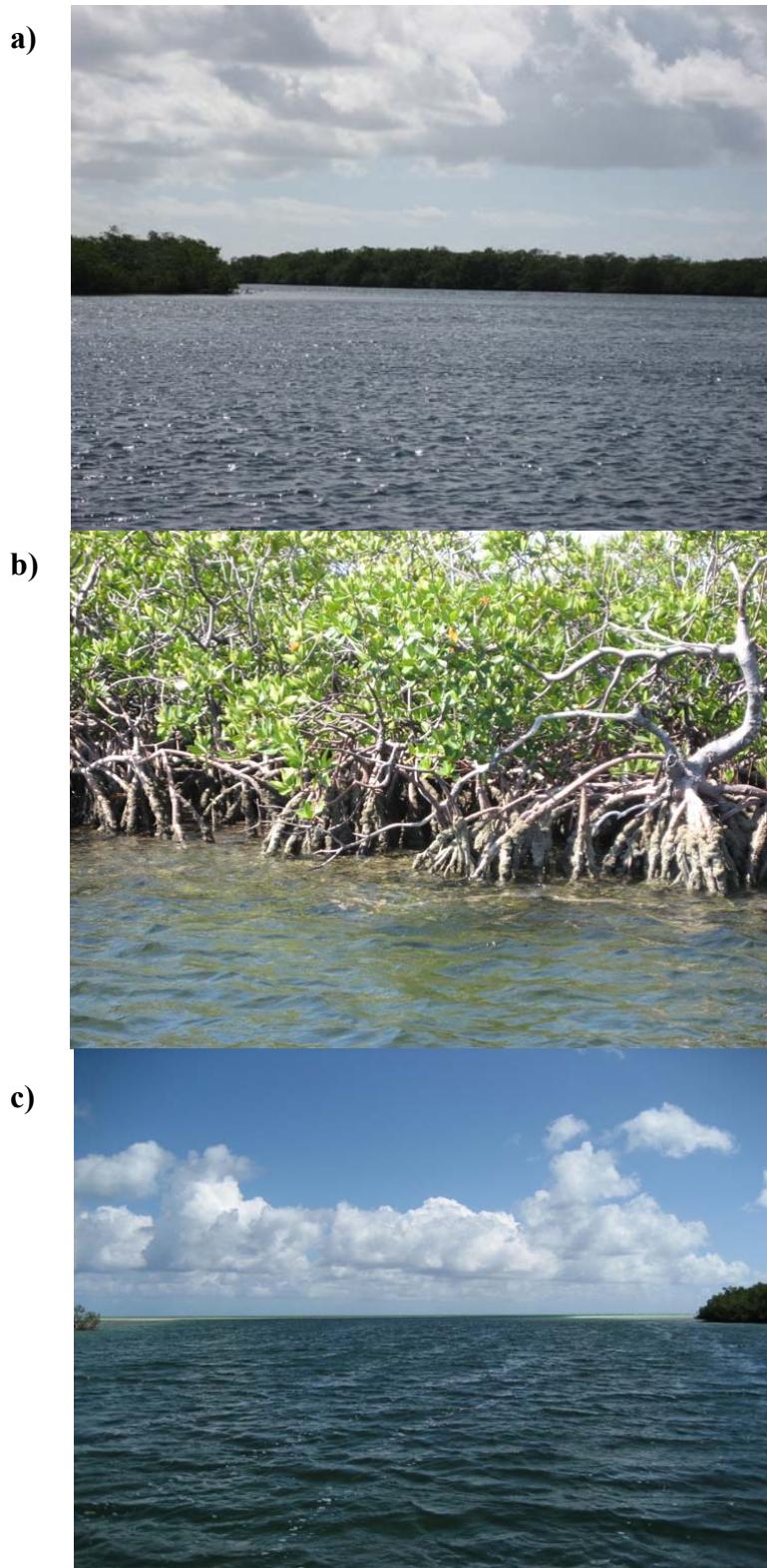


Fig. 2.6. Mangrove channel reef areas: a) interior portion approaching Bridge Reef Zone 3; b) dense mangrove forest along edges of channels; and c) initial channel looking seaward (north)

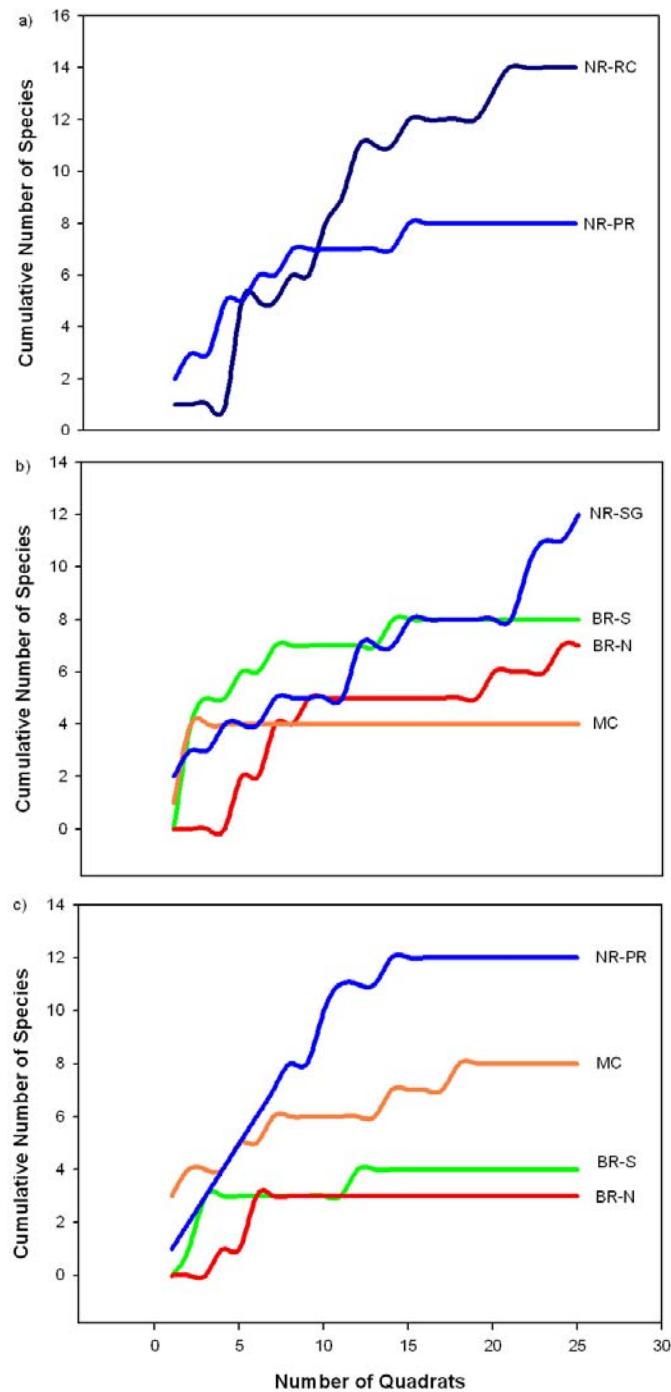
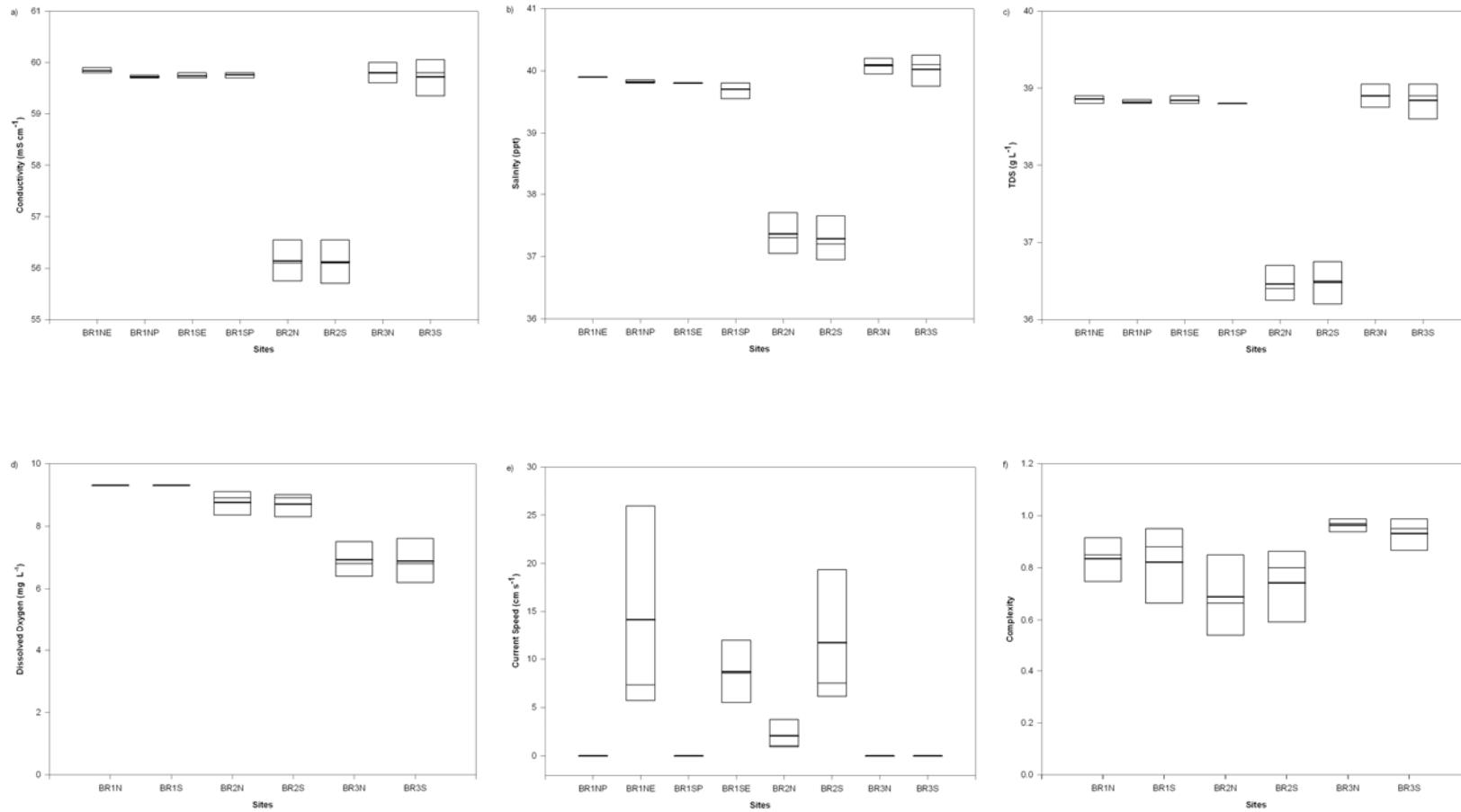


Figure 2.7. Cumulative number of coral species vs. number of quadrats sampled for reefs at (a) Zone 1, (b) Zone 2 and (c) Zone 3.



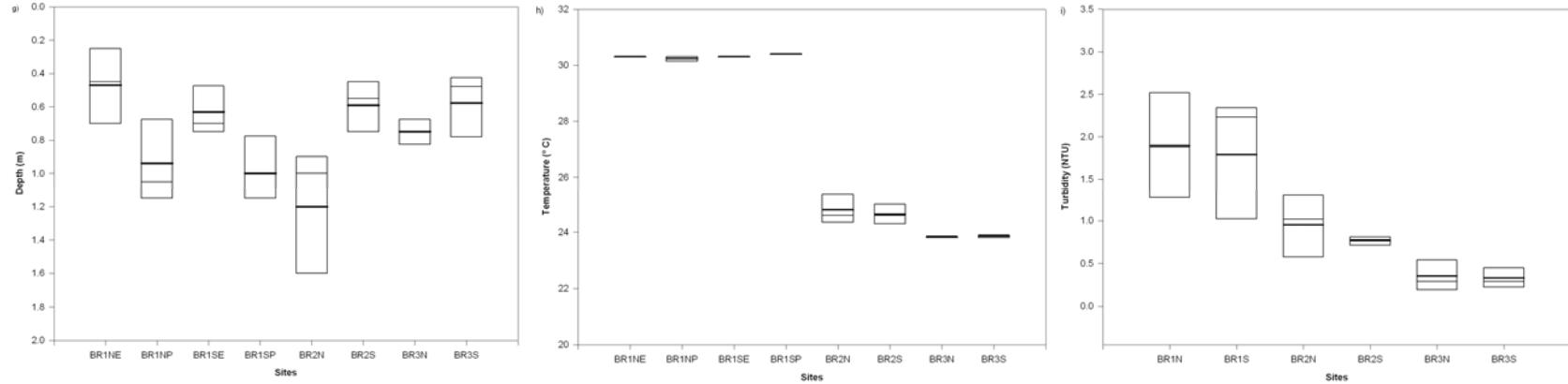


Figure 2.8. Physical-Environmental variables measured at each bridge reef site during high tide measurements: a) Conductivity ( $\text{mS cm}^{-1}$ ); b) Salinity (ppt); c) Total Dissolved Solids ( $\text{g L}^{-1}$ ); d) Dissolved Oxygen ( $\text{mg L}^{-1}$ ); e) Current speed ( $\text{cm s}^{-1}$ ); f) Complexity ratio ( $\text{m m}^{-1}$ ); g) Depth (m); h) Temperature ( $^{\circ}\text{C}$ ); i) Water turbidity (NTU). The upper and lower boundaries of the box plot indicate the 75<sup>th</sup> and 25<sup>th</sup> percentile, respectively. The thin solid line within the box is the median, and the thick solid line is the mean.

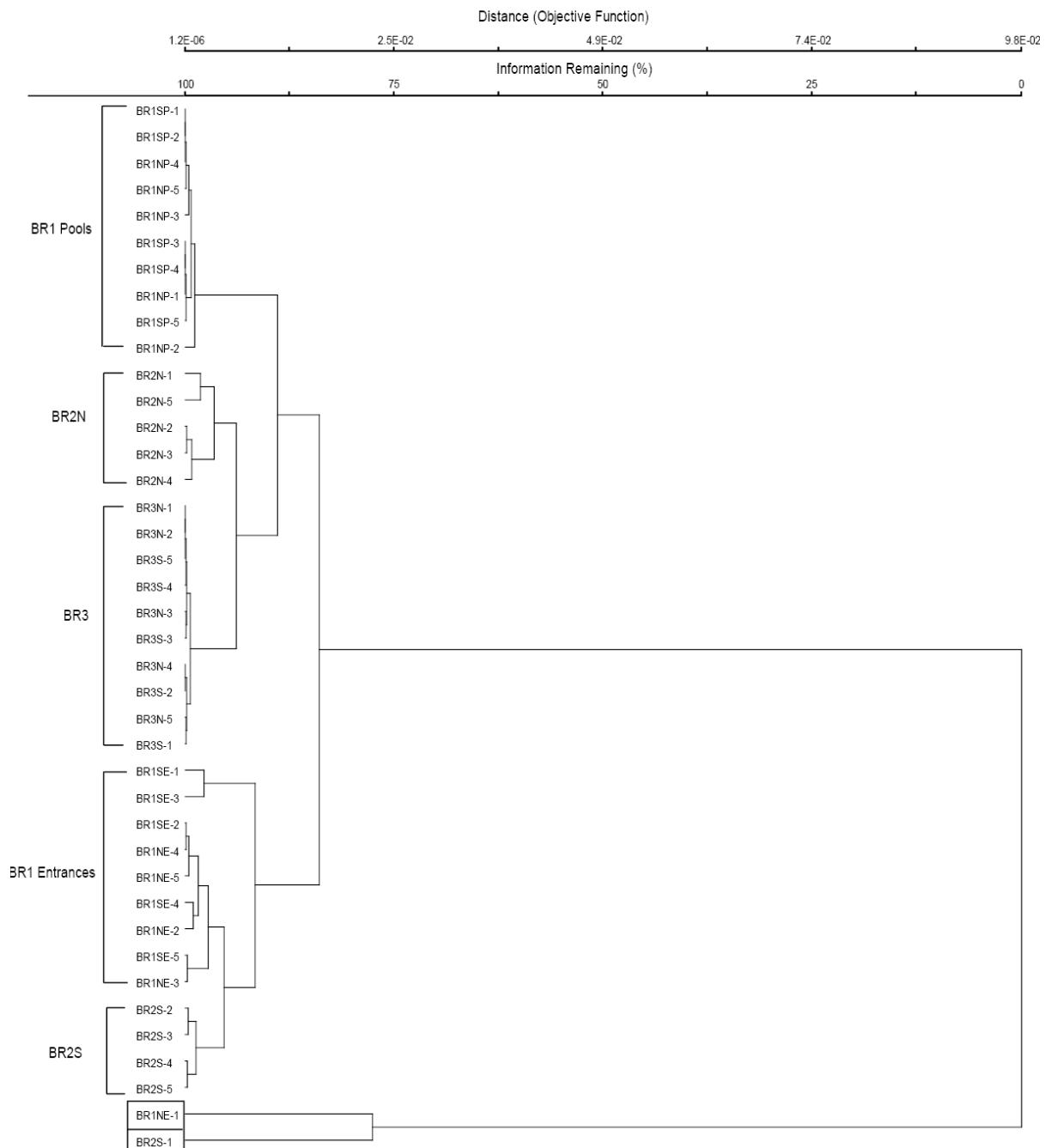


Figure 2.9. Hierarchical Cluster Analysis dendrogram of bridge reef sites, based on physical variables measured at each bridge reef, using relative Euclidean distance measurements.

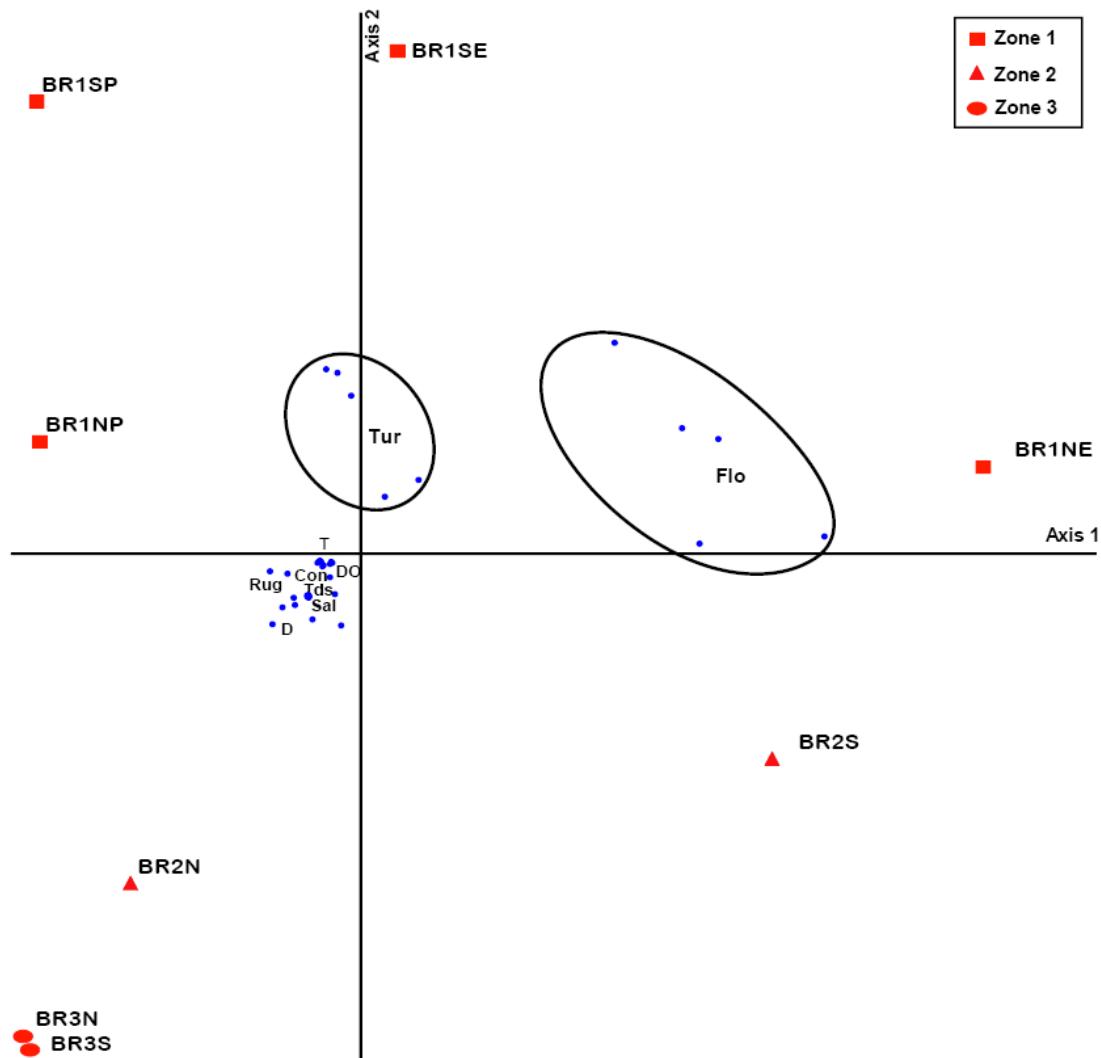


Figure 2.10. Detrended Correspondence Analysis of the Bridge Reef Sites, with physical variables used to determine site scores (eigenvalue scores: axis 1 = 0.0369; axis 2 = 0.0034)

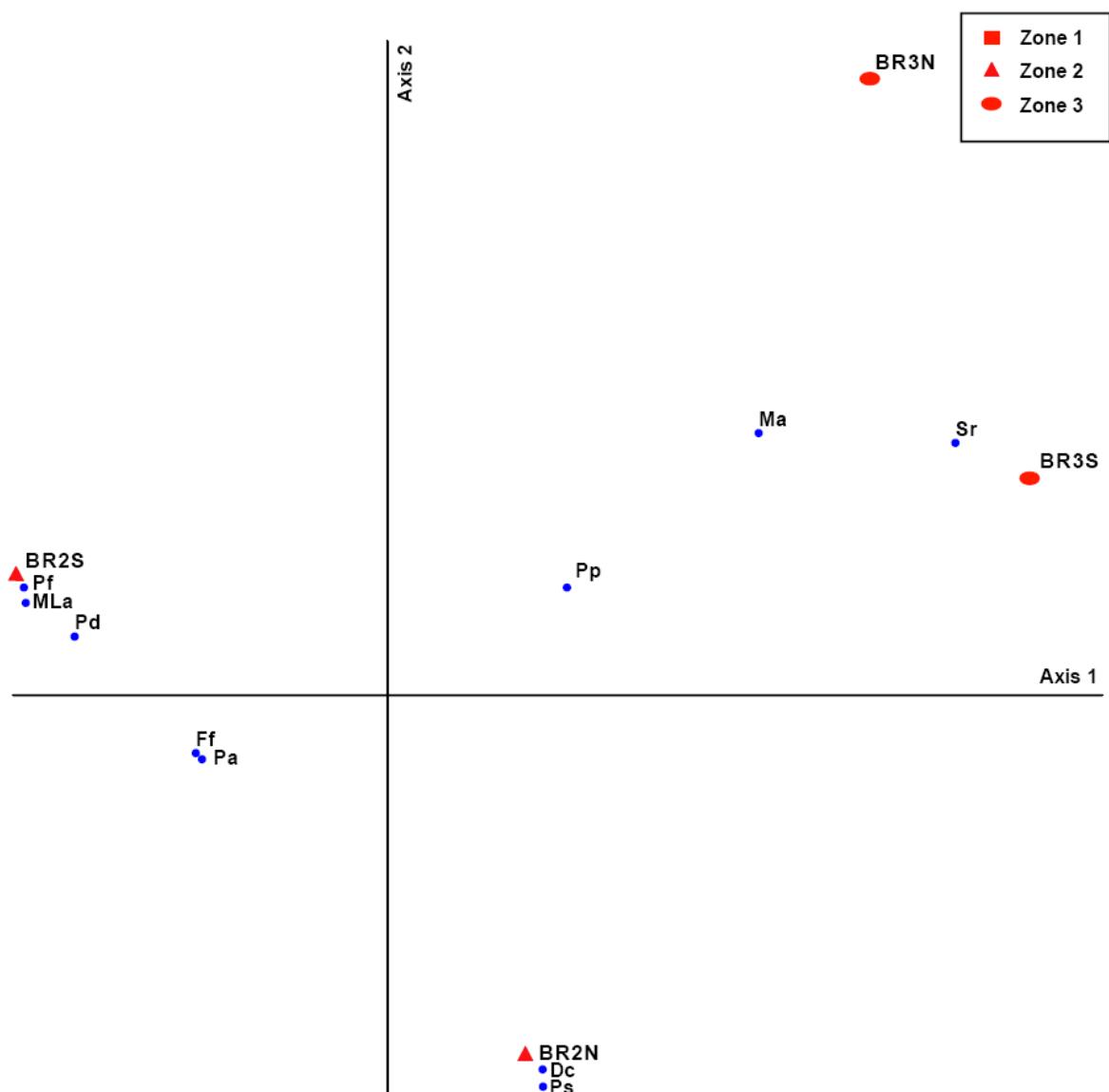
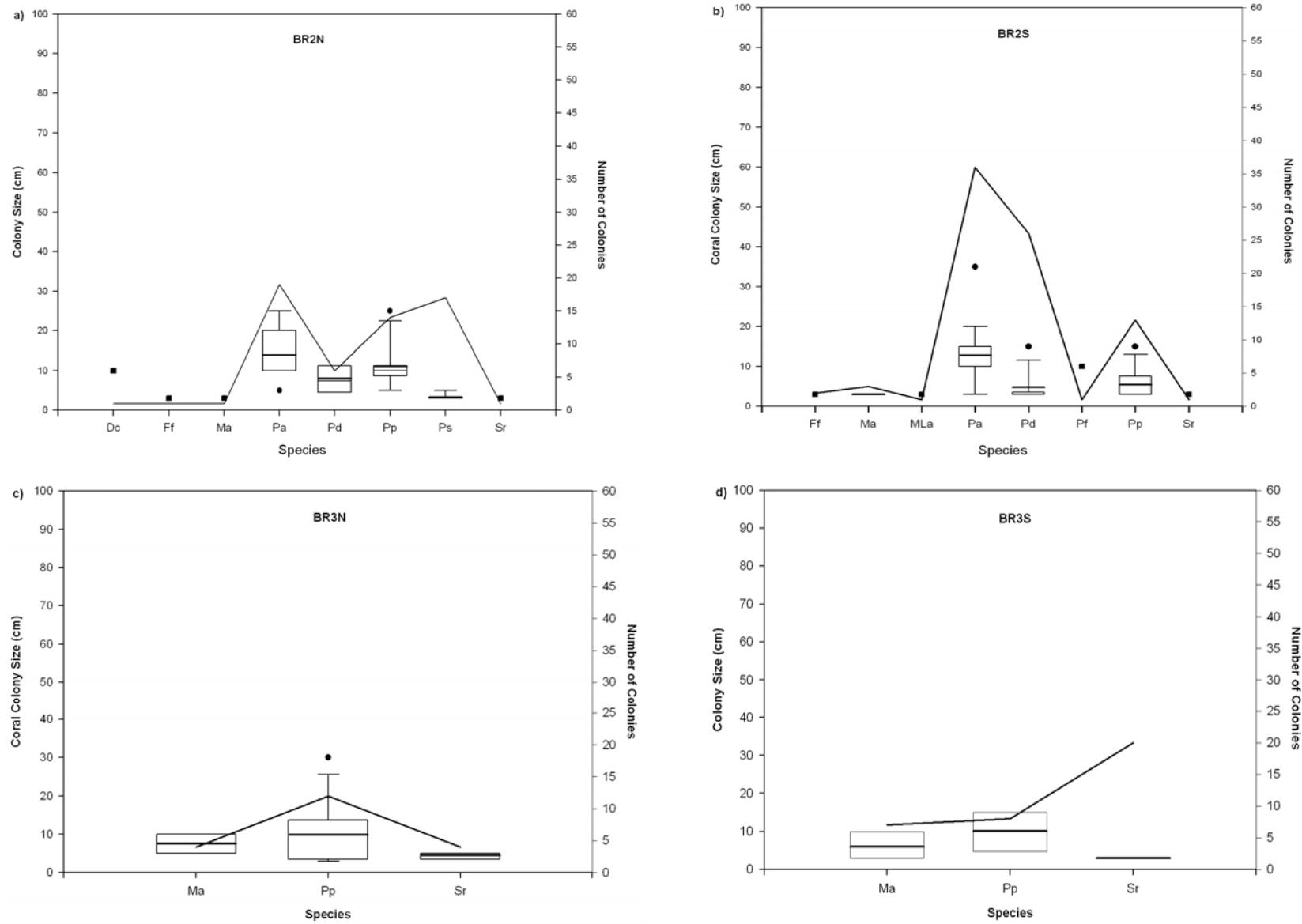
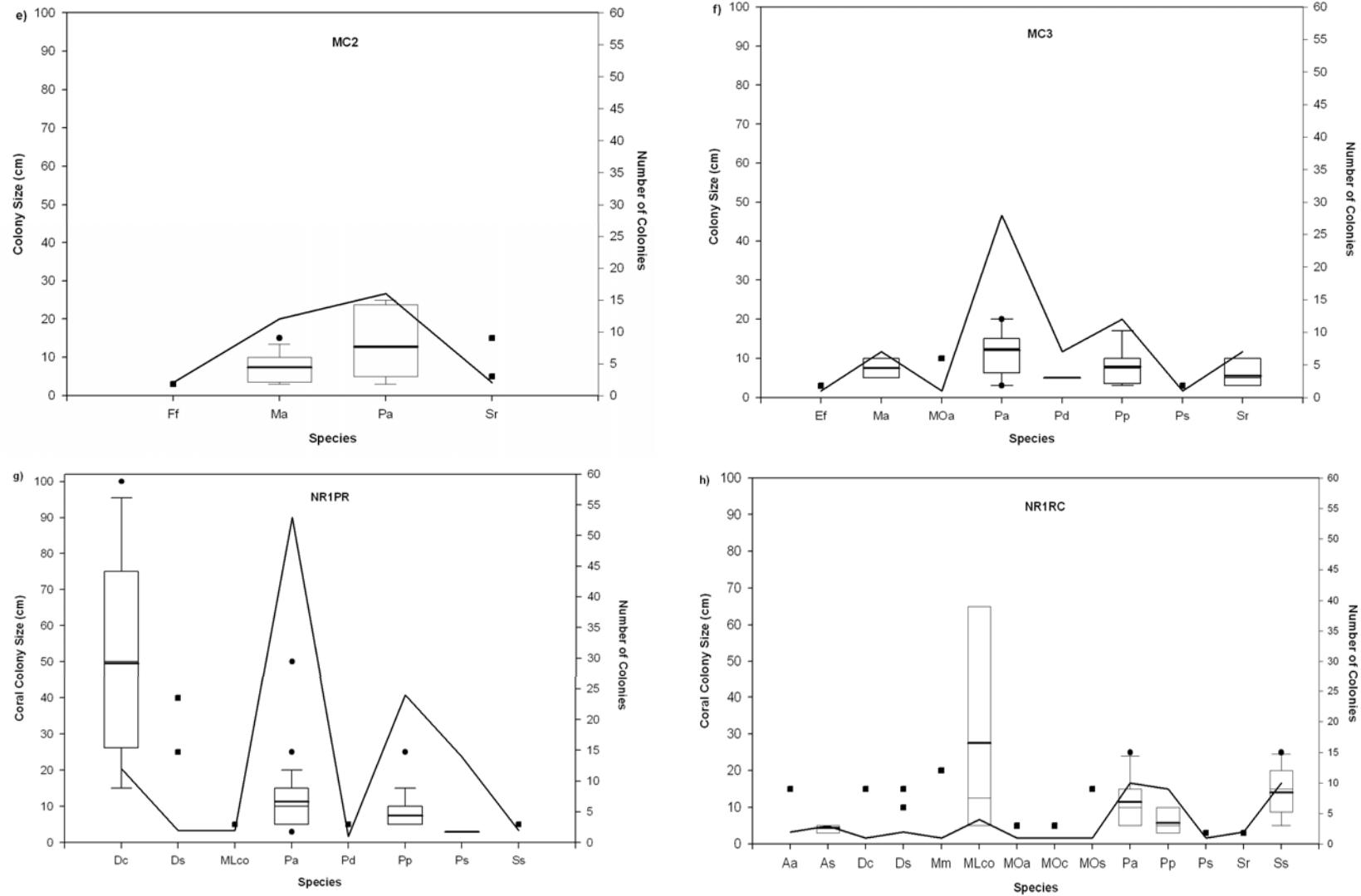


Figure 2.11. Detrended Correspondence Analysis of the Bridge Reef Sites, with replicated coral quadrats used to determine species scores, based on coral species abundances (eigenvalue scores: axis 1 = 0.6354; axis 2 = 0.1129).





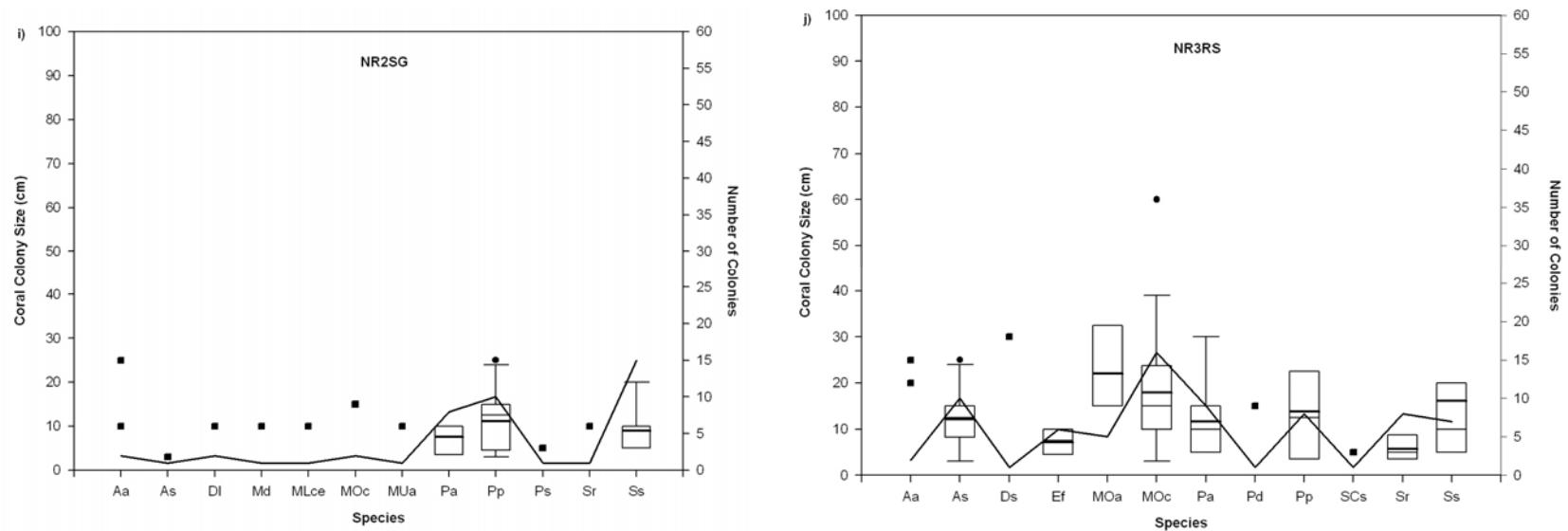
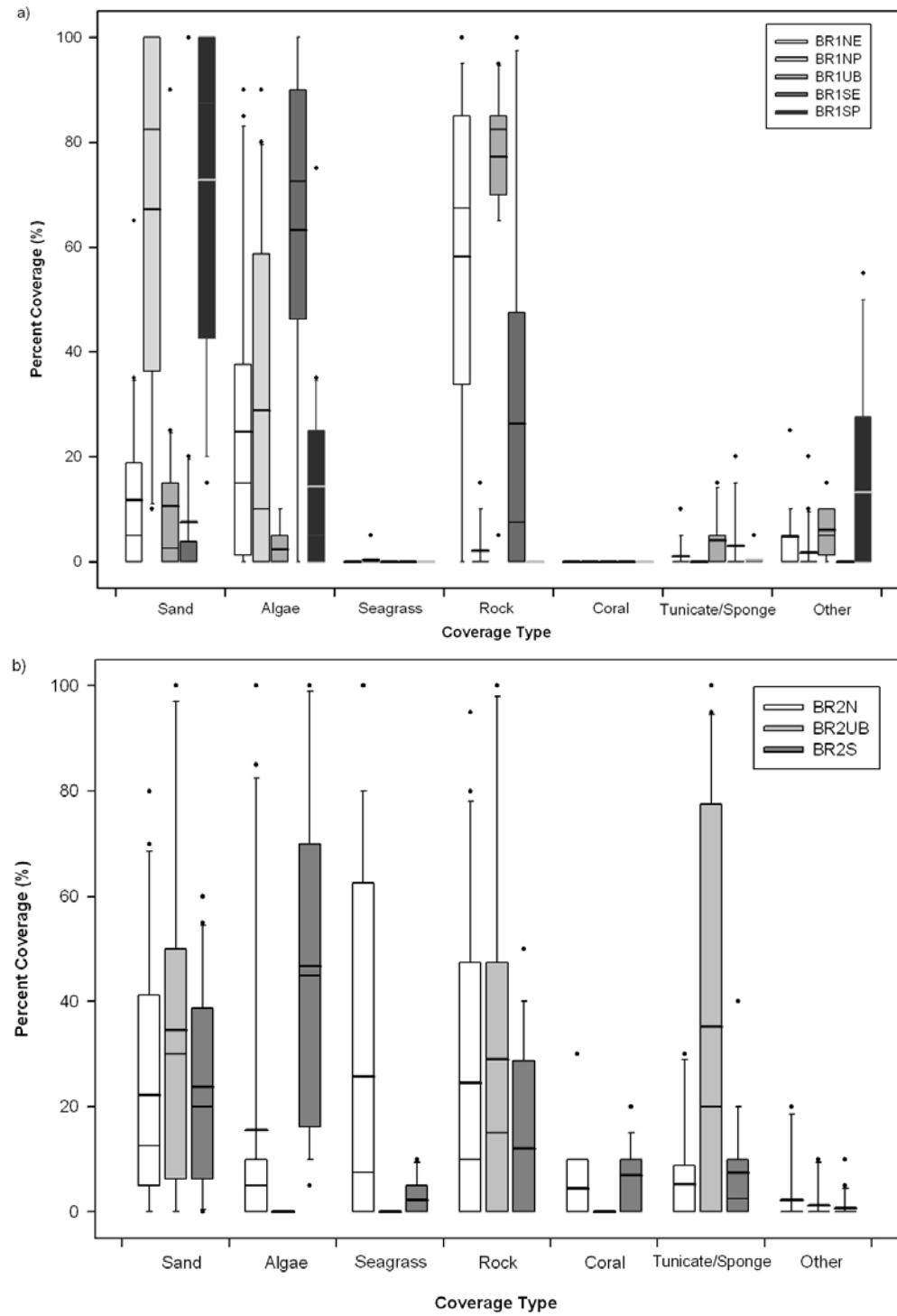


Figure 2.12. Coral colony size and number of colonies counted for entire transect ( $n = 25$  quadrats) at each site. Box plots represent colony size, and line plots represent the number of colonies present at the individual site. The upper and lower boundaries of the box plot indicate the 75<sup>th</sup> and 25<sup>th</sup> percentile, respectively. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Outliers (circles) and low number of colonies (<3) (squares) are plotted as individual points.



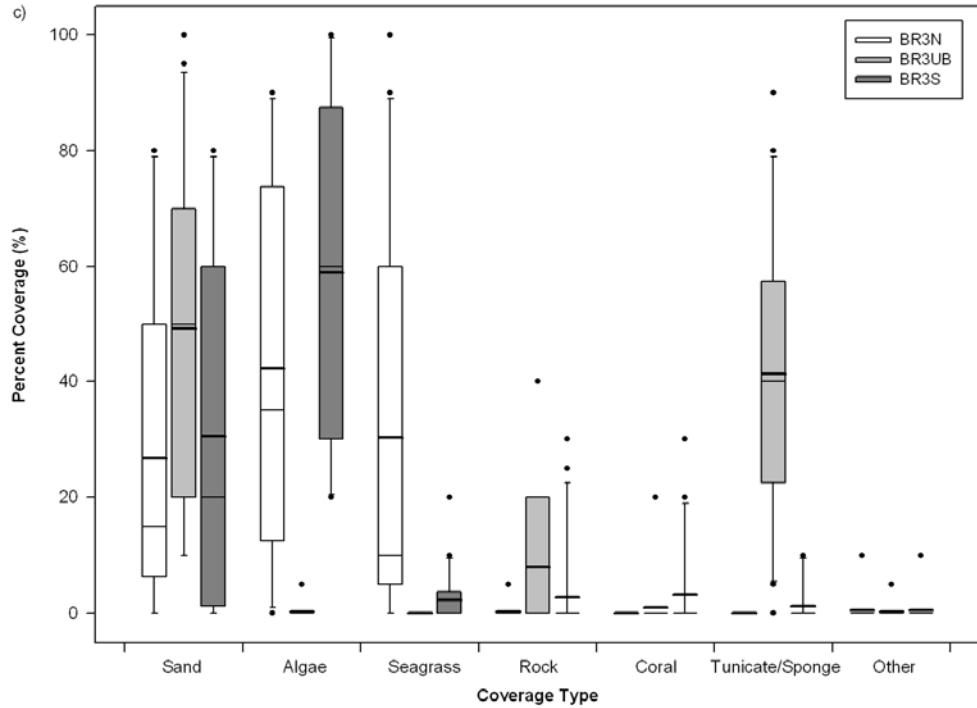


Figure 2.13. Benthic coverage for a) Zone 1, b) Zone 2, c) Zone 3. Box plots represent percent coverage variation for each coverage type, with the lower boundary of the box indicating the 25<sup>th</sup> percentile and the upper boundary of the box the 75<sup>th</sup> percentile. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Outliers (circles) are plotted as individual points.

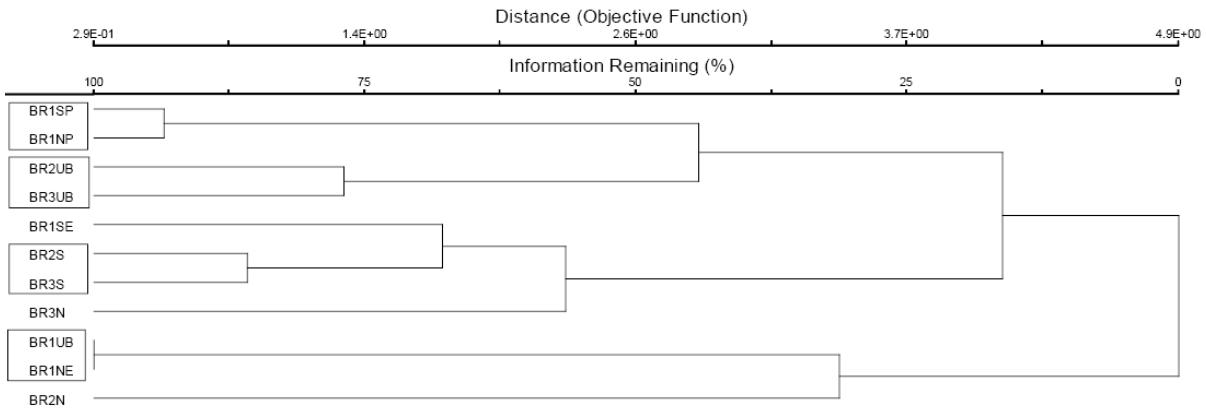


Figure 2.14. Hierarchical Cluster Analysis dendrogram, using relative Euclidean distance measurements, of bridge reef sites, based on percent benthic coverage quadrats measured at each bridge reef.

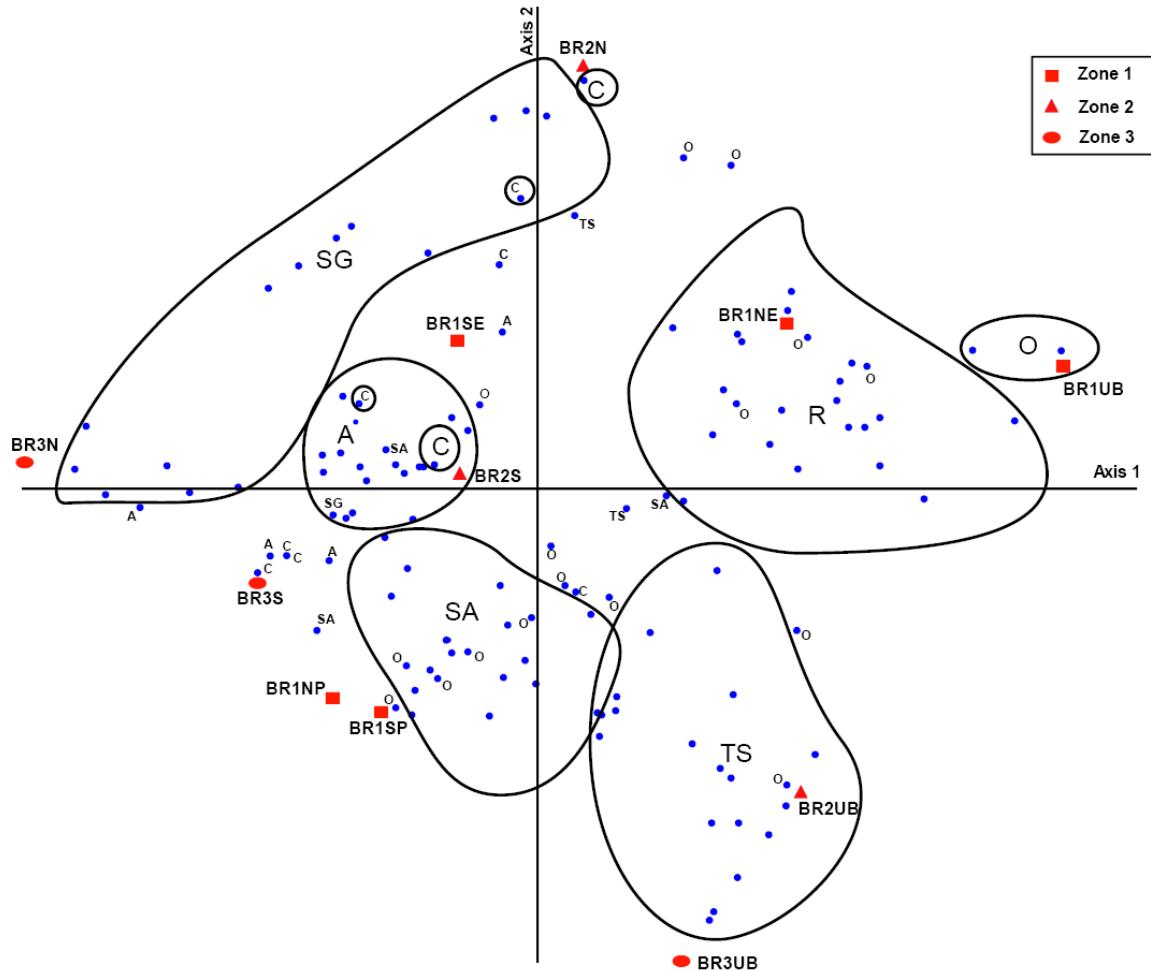
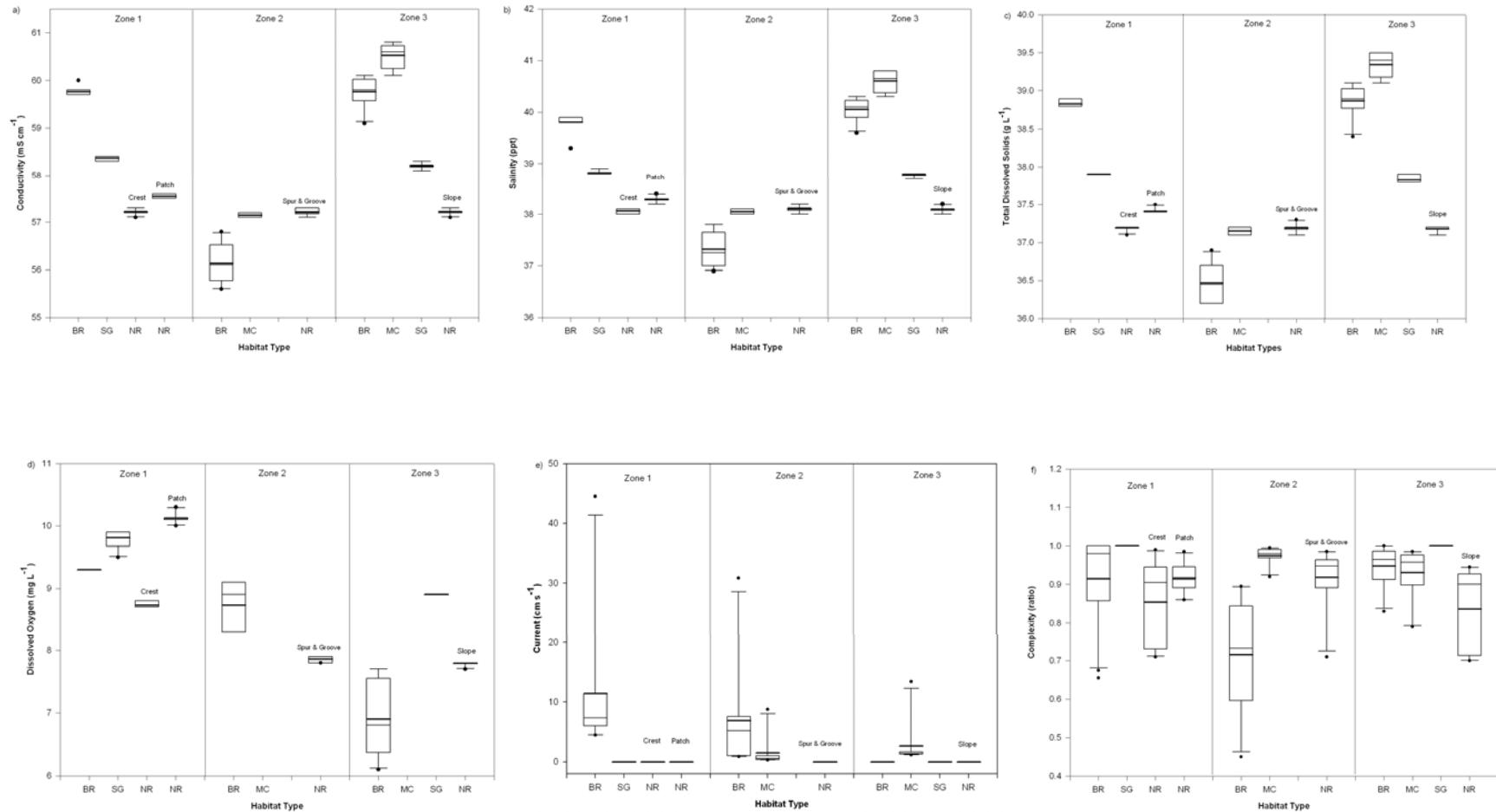


Figure 2.15. Detrended Correspondence Analysis of the Bridge Reef Sites, with replicated percent benthic coverage quadrats used to determine site scores (eigenvalue scores: axis 1 = 0.4734; axis 2 = 0.3593). Outlying benthic coverage ordination points were removed to better demonstrate trends, with the exception of Coral and Other coverage categories, due to their more scattered occurrences.



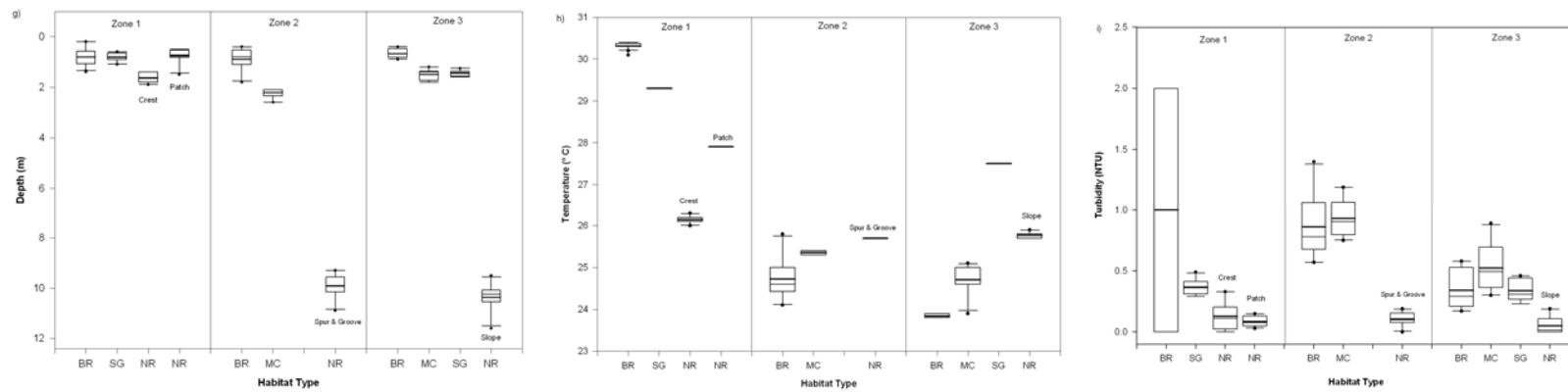


Figure 2.16. Physical-Environmental variables measured at all sites: a) Conductivity ( $\text{mS cm}^{-1}$ ); b) Salinity (ppt); c) Total Dissolved Solids ( $\text{g L}^{-1}$ ); d) Dissolved Oxygen ( $\text{mg L}^{-1}$ ); e) Current speed ( $\text{cm s}^{-1}$ ); f) Complexity ratio ( $\text{m m}^{-1}$ ); g) Depth (m); h) Temperature ( $^{\circ}\text{C}$ ); i) Water turbidity (NTU). The upper and lower boundaries of the box plot indicate the 75<sup>th</sup> and 25<sup>th</sup> percentile, respectively. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Outliers are plotted as individual points.

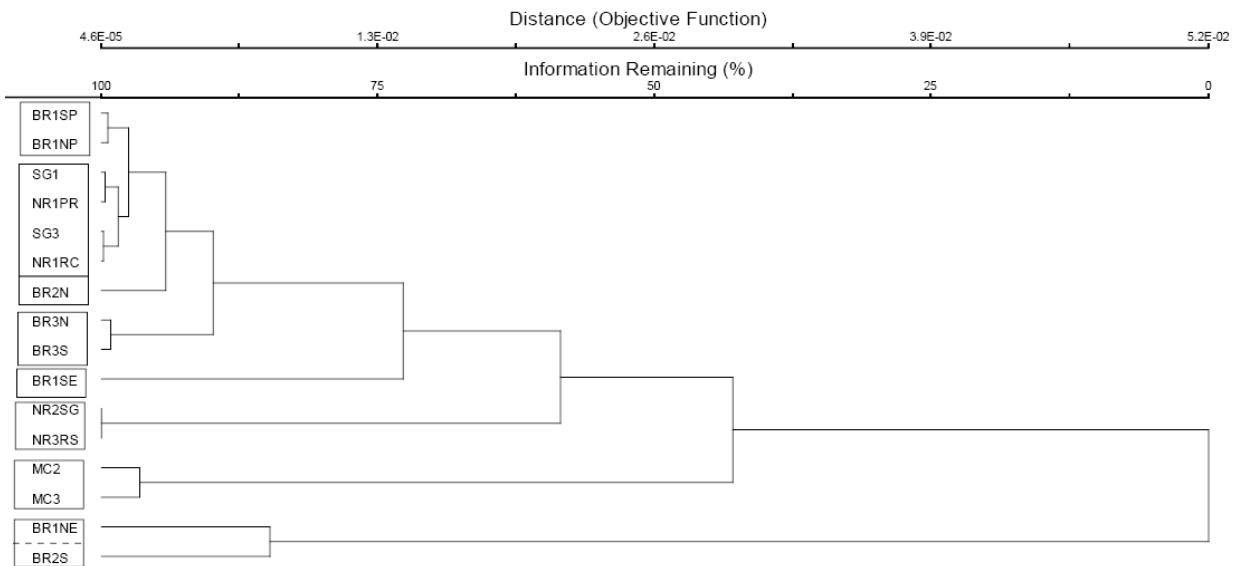


Figure 2.17. Hierarchical Cluster Analysis dendrogram of all sites, based on physical variables measured at each site, using relative Euclidean distance measurements.

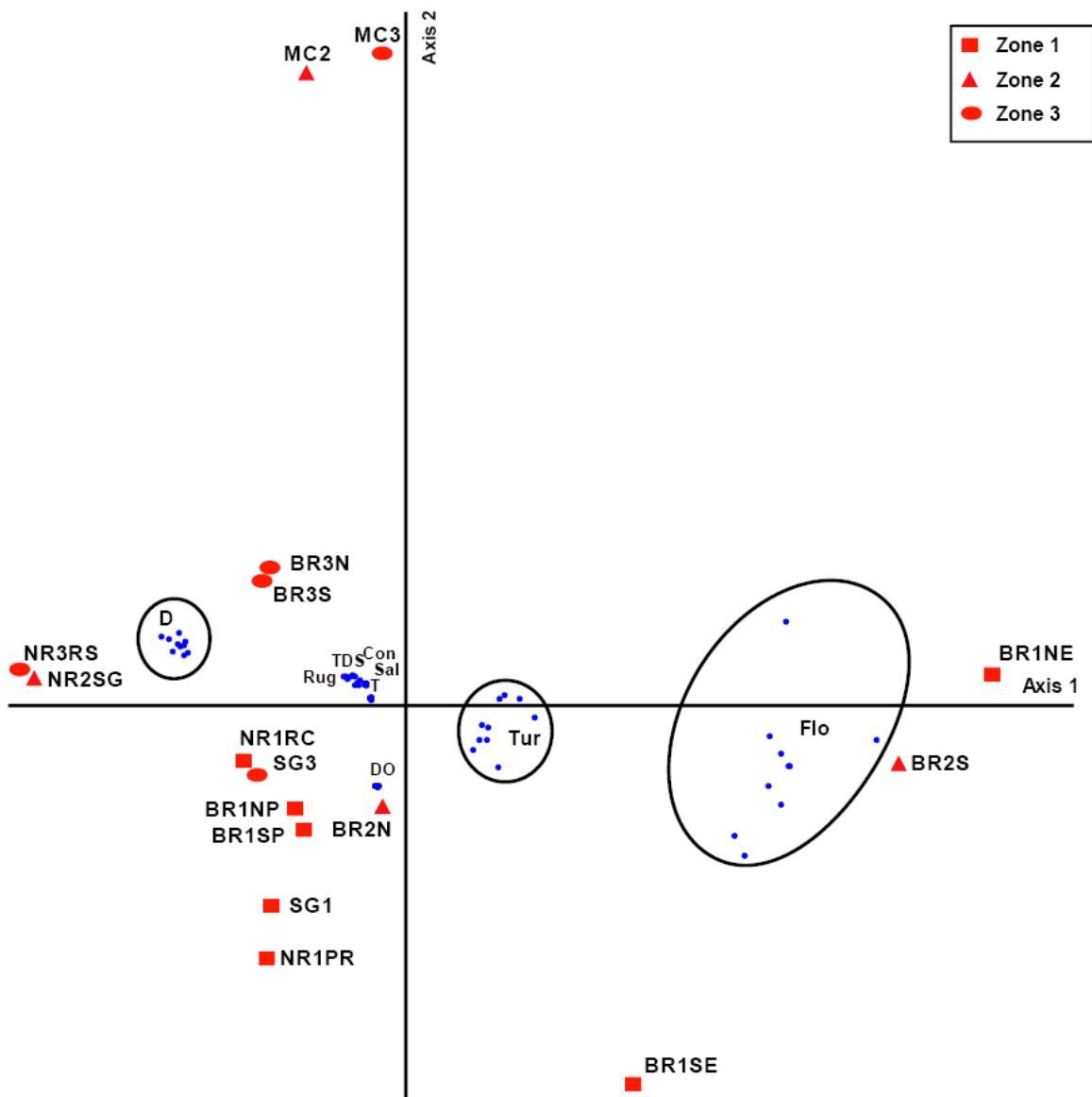


Figure 2.18. Detrended Correspondence Analysis of all sites, based on physical and environmental variables to determine site scores (eigenvalue scores: axis 1 = 0.0462; axis 2 = 0.0074)

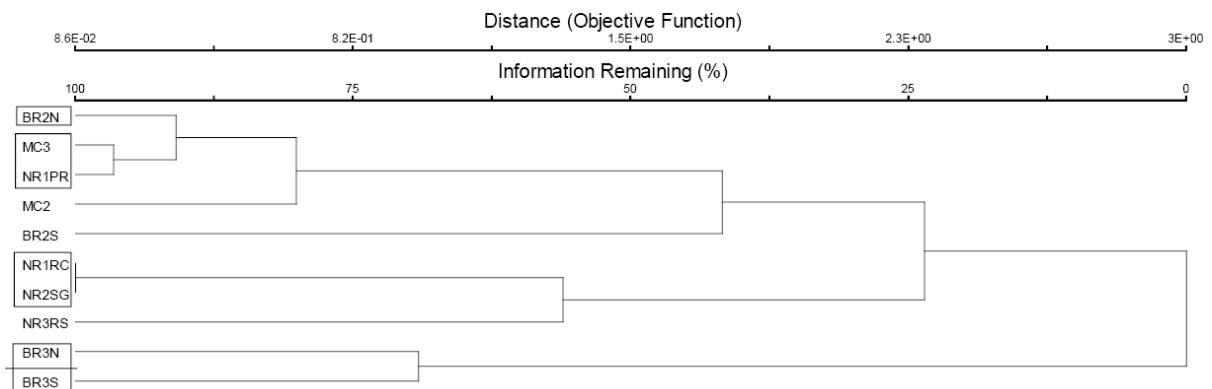


Figure 2.19. Hierarchical Cluster Analysis dendrogram of all sites, based on coral species diversity and abundances, using relative Euclidean distance measurements.

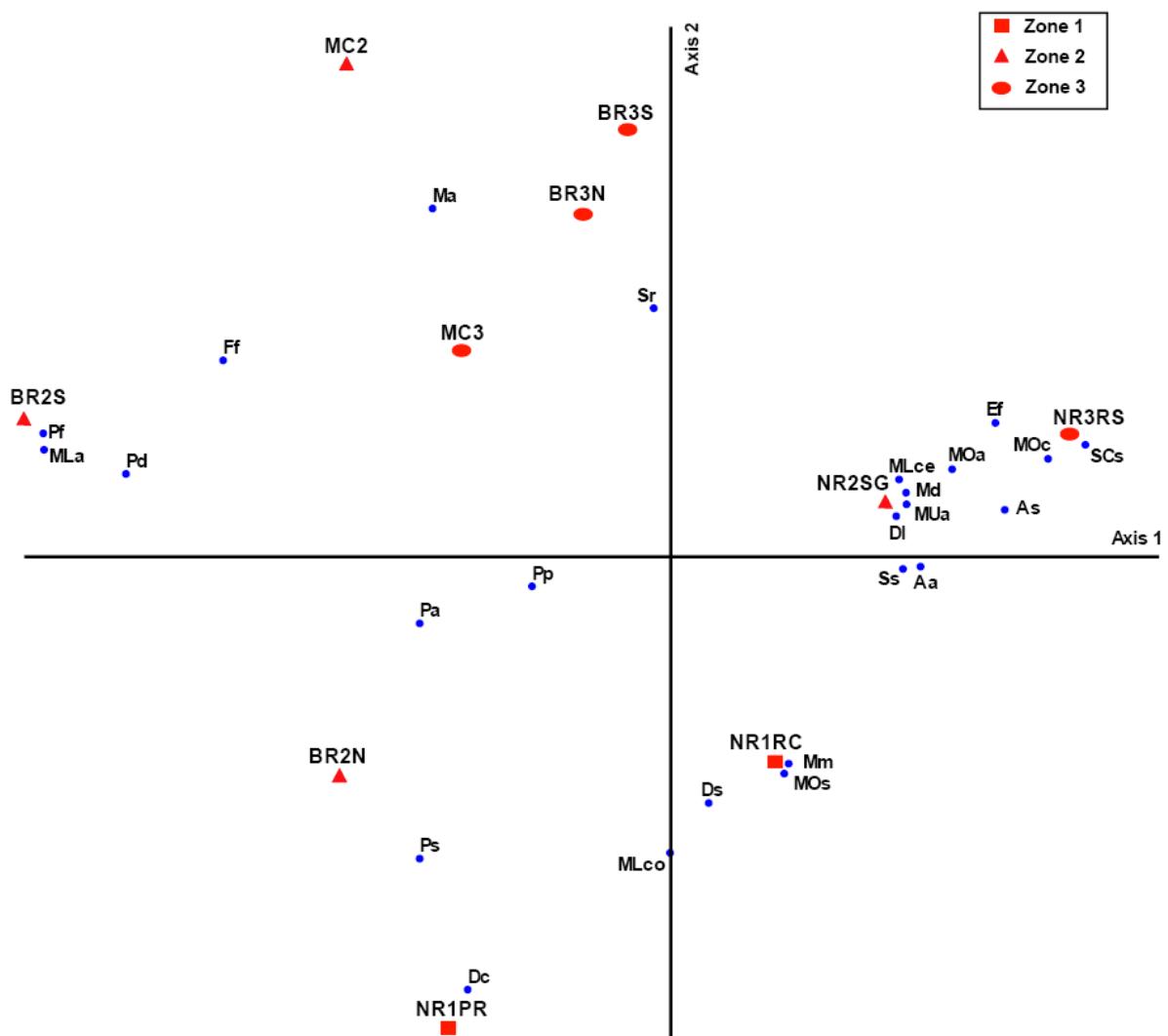


Figure 2.20. Detrended Correspondence Analysis of all sites and coral species, based on coral quadrats to determine species scores (eigenvalue scores: axis 1 = 0.5419; axis 2 = 0.2591).

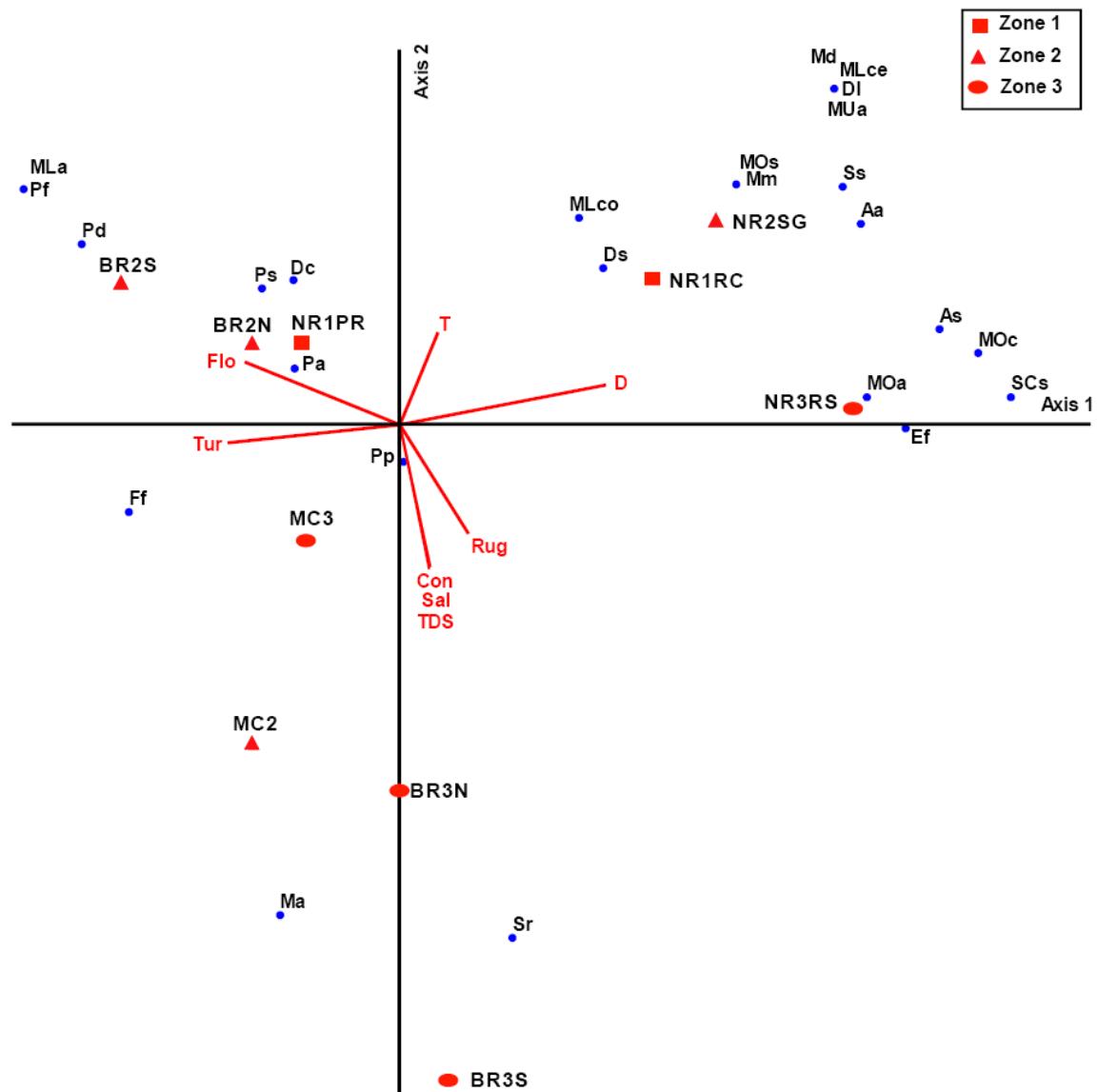
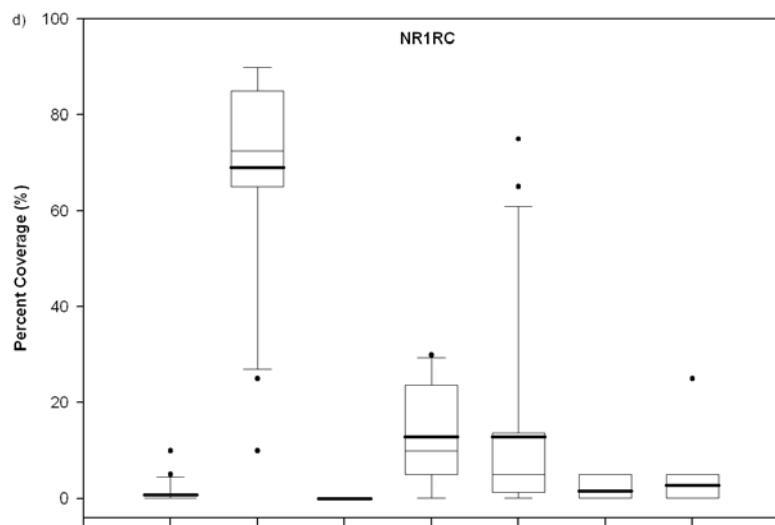
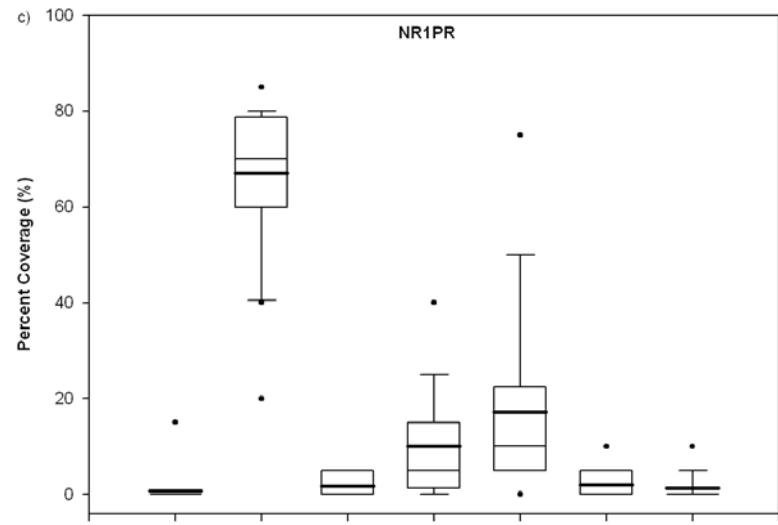
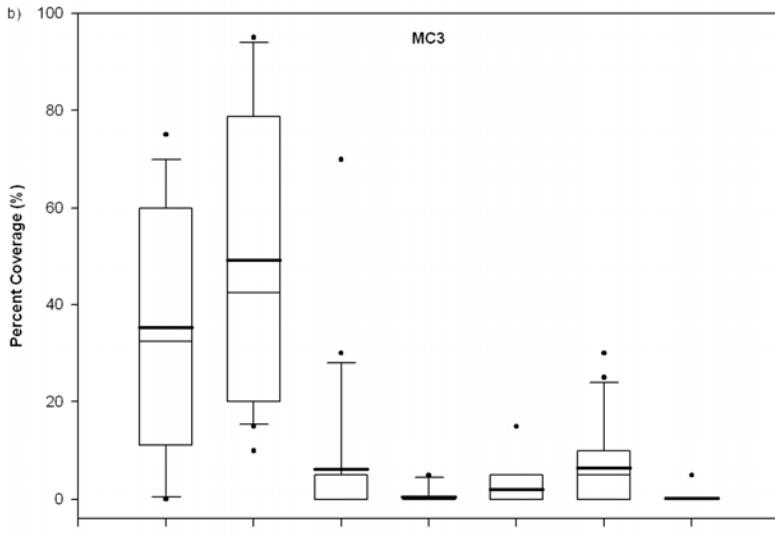
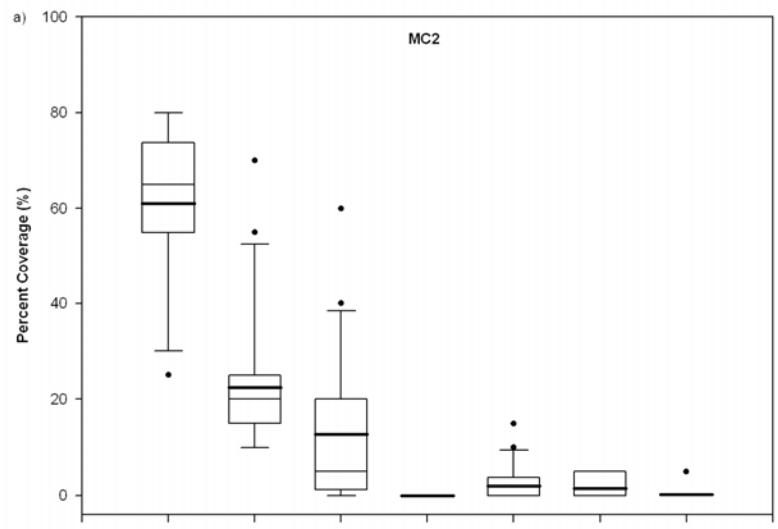


Figure 2.21. Canonical Correspondence Analysis of coral species and sites corresponding to environmental and physical variables (eigenvalue scores of axis 1 = 0.542 and axis 2 = 0.37).



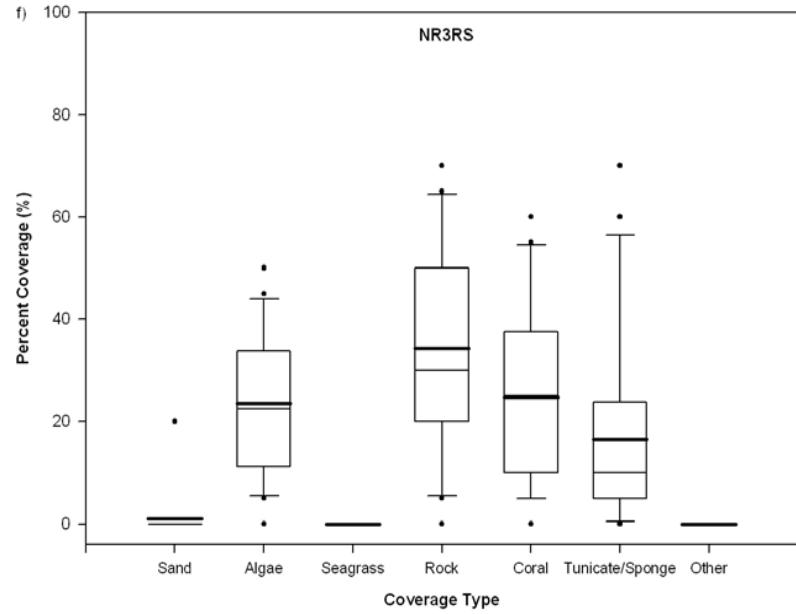
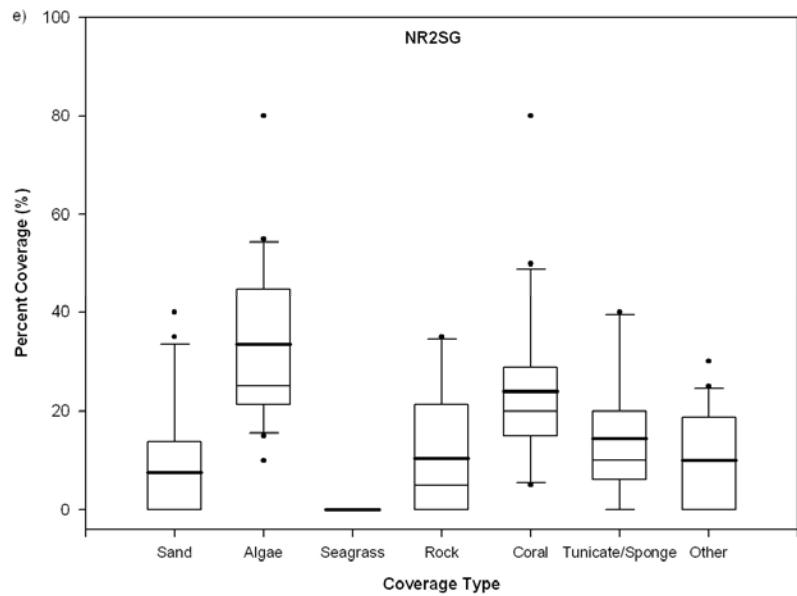


Figure 2.22. Benthic coverage for a) MC2, b) MC3, c) NR1PR, d) NR1RC, e) NR2SG, f) NR3RS. Box plots represent percent coverage variation for each coverage type, with the lower boundary of the box indicating the 25<sup>th</sup> percentile and the upper boundary of the box the 75<sup>th</sup> percentile. The thin solid line within the box is the median, and the thick solid line is the mean. The error bars above and below the box indicate the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Outliers (circles) are plotted as individual points.

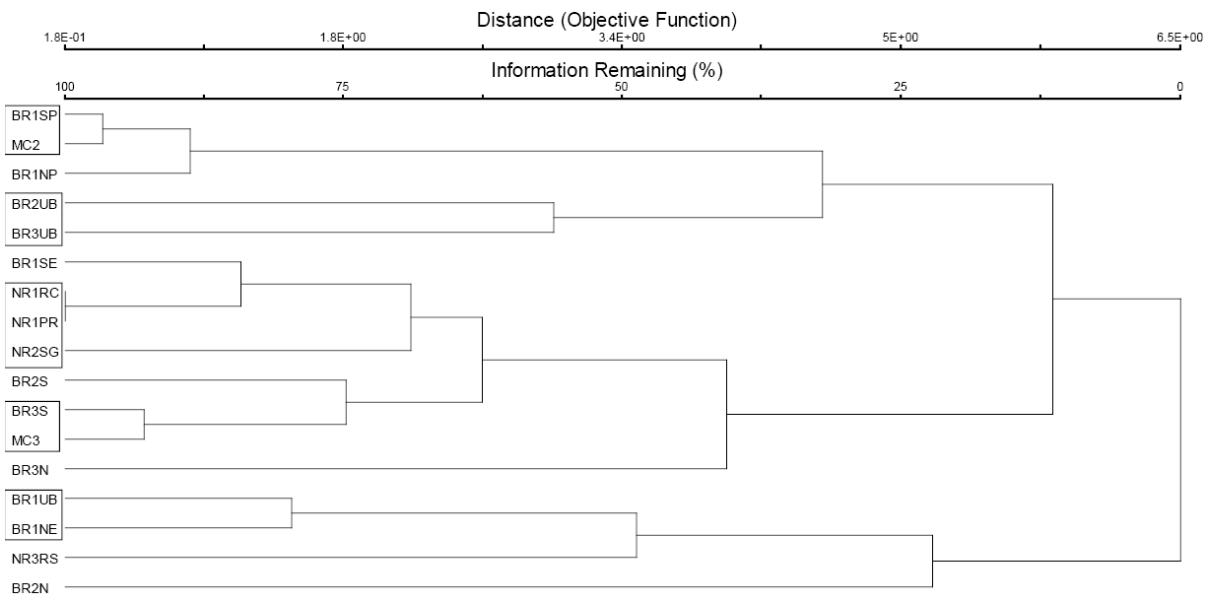


Figure 2.23. Hierarchical Cluster Analysis dendrogram of all sites based on replicated percent benthic coverage quadrats, using relative Euclidean distance measurements.

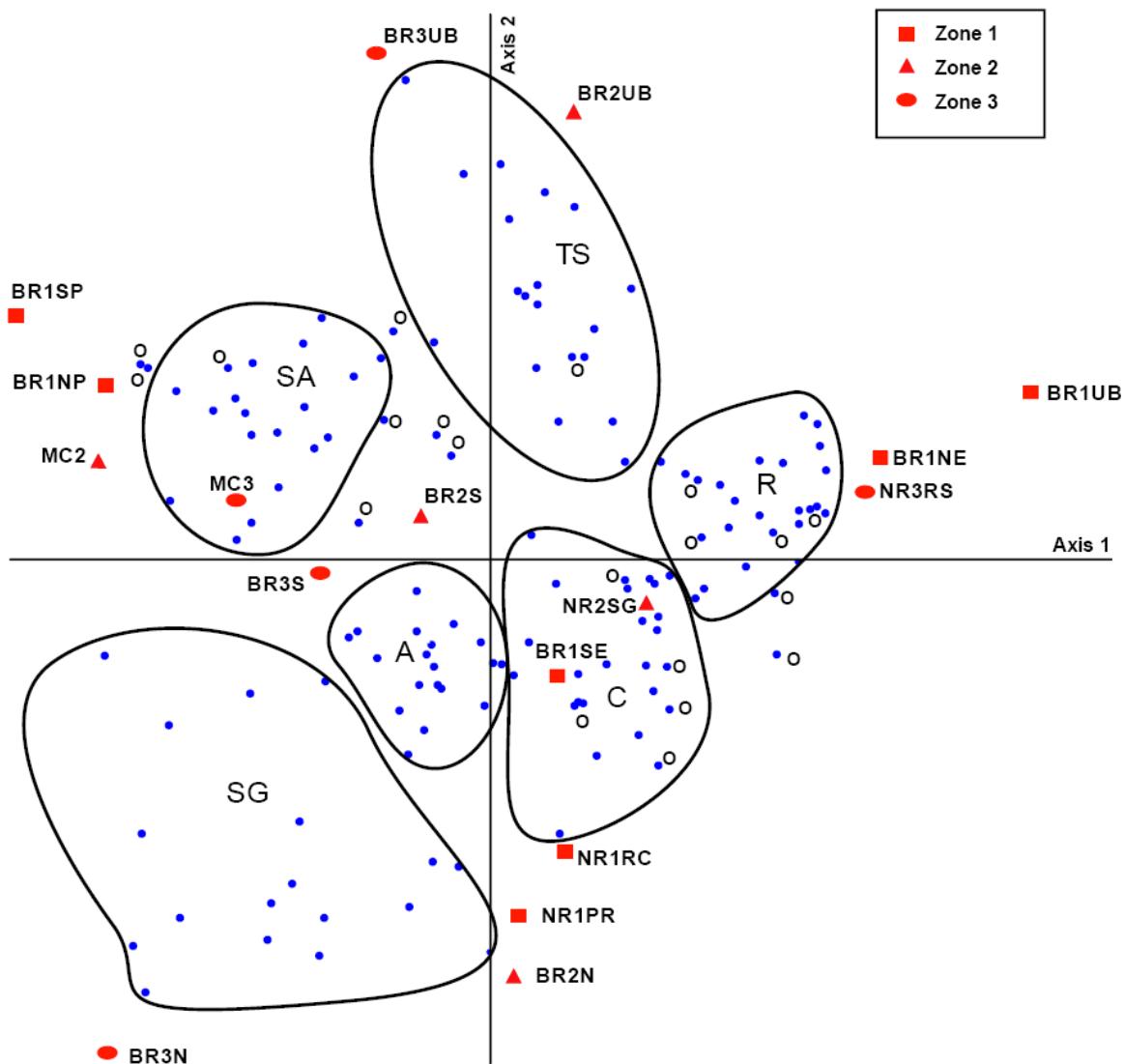


Figure 2.24. Detrended Correspondence Analysis of all sites and benthic coverage percentages, based on percent coverage quadrats to determine site scores (eigenvalue scores: axis 1 = 0.4129; axis 2 = 0.2897). Outlying benthic coverage ordination points were removed to better demonstrate trends, with the exception of Other coverage category, due to its more scattered occurrence.

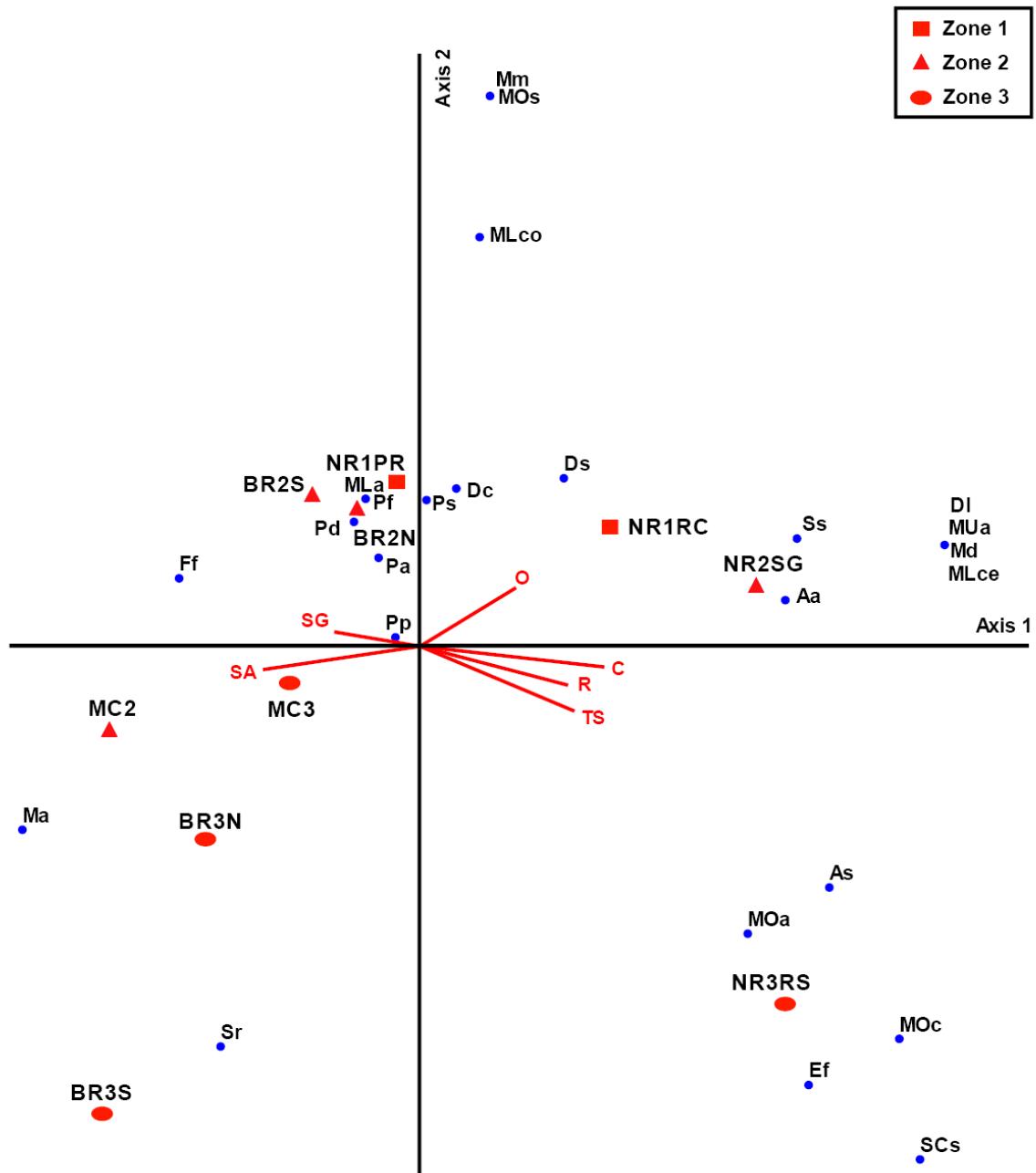


Figure 2.25. Canonical Correspondence Analysis of coral species and sites corresponding to benthic coverage types (eigenvalue scores of axis 1 = 0.419 and axis 2 = 0.323).

## **CHAPTER 3:**

### **Coastal productivity in unusual reef habitats and surrounding seascape: an application of $\delta^{13}\text{C}$ and C/N ratios**

#### **1. INTRODUCTION**

The export of organic matter is an important process occurring from terrestrial-marine interfaces to the seagrass beds and fringing reefs abounding in tropical coastal waters. Both mangrove forests and seagrass beds are highly productive ecosystems, with a large proportion of their growth contributing to active decomposition, detritus and other particulate organic matter found within sediments and suspended in the water column (Bouillon et al. 2004). Once converted to this form, organic matter becomes an important food source for several benthic organisms found in these habitats, including fish, gastropods and other herbivorous and planktivorous species (Fry et al. 1982, Marguillier et al. 1997, Kon et al. 2007). Overall amounts of carbon produced annually are variable but high (Duarte et al. 2005), and in regions with strong currents or high tidal influences, export and burial in surrounding habitats occurs (Kitheka 1997, Bouillon et al. 2003).

High levels of plant productivity require efficient levels of photosynthesis, which can be difficult in submerged or semi-submerged tidal plants. Inorganic carbon is found naturally in two forms:  $\text{C}^{12}$  and  $\text{C}^{13}$ , with the proportion of  $\text{C}^{13}$  used in the leaf during photosynthesis varying depending on species and photosynthetic pathways. By using stable carbon isotope analysis, the carbon flow in these regions can be determined as there are significant differences in mangrove and seagrass carbon 13 ( $\delta^{13}\text{C}$ ) content (Zieman et al. 1984, Fleming et al. 1990). These differences are based on variations in utilization of

atmospheric CO<sub>2</sub> and fixation processes, as well as rate-limiting diffusion barriers that prevent isotopic selectivity, especially found in seagrasses (Fleming et al. 1990)

Many studies within Africa and Asia rely on using both δ<sup>13</sup>C and carbon to nitrogen (C/N) ratios as tracers of organic matter within the seascape (Hemminga et al. 1994, Holmer and Olsen 2002, Bouillon et al. 2003, Kennedy et al. 2004), however studies within the Caribbean and Gulf of Mexico are limited with this joint approach, including no modern δ<sup>13</sup>C studies in Cuba (Peros et al. 2007). In addition to relatively characteristic values per species, C/N ratios are useful for determining levels of decomposition by looking at loss of carbon and increased amount of nitrogen from microbial biomass accumulation during decay (Wafar et al. 1997, Holmer and Olsen 2002).

In north-central Cuba, between Cayo Coco and Cayo Guillermo, new reef communities are forming under bridges along a coastal causeway connecting these two cays. Tidal currents play a strong role in forming this seascape, with lagoons sharing coastline with the island of Cuba on one side of the causeway, and tidal channels found between mangrove forests and natural fringing reefs along the fore-reef area on the other side of the bridges. Seagrass beds surround the bridge reefs, as do varying densities of mangrove forest. Juvenile reef fish that commonly stay in mangrove forests were seen sheltering beneath these bridges, amongst coral and other reef organisms typical of coral reefs. These sites represent a unique intermediate habitat, which may play an integral role in the connectivity of the seascape.

The main goals of this study are to (1) determine if δ<sup>13</sup>C can be used as a tracer to establish the main sources of organic carbon at the bridge reef sites and (2) identify the sources and levels of primary production within the Cayo Coco-Cayo Guillermo seascape. By using a combination of *Thalassia testudinum* biomass and shoot dynamics, areal

distribution of *Rhizophora mangle* mangrove stands and  $\delta^{13}\text{C}$  as an organic matter tracer, we will characterize the productivity of the region, and determine the role of the bridge reefs in seascape connectivity. These results will also be the first modern  $\delta^{13}\text{C}$  and C/N ratio coastal vegetation records for Cuba. Although  $\delta^{13}\text{C}$  values for the Caribbean seagrass and mangrove species *T. testudinum* and *R. mangle* are approximately -9 ‰ and -28 ‰, respectively, variation of isotope signatures within a species can occur (Smith and Epstein 1971, Lin et al. 1991). As a result, there is a need to determine isotopic signatures for varying regions.

## 2. METHODS

### 2.1 Study Sites

See Chapter 2, Section 2.1.

### 2.2 Study Systems

See Chapter 2, Section 2.2

### 2.3 Primary Productivity

#### 2.3.1 Seagrass Biomass and Coverage

BR, MC and SG sites containing seagrass patches were characterized by measuring percent coverage, shoot density and canopy height of *T. testudinum*, and samples were taken to determine above- and below-ground biomass in the laboratory. Two 20 m transect lines were placed approximately 10 m apart in each site (including north and south of bridges in BR sites), and 0.5 m square quadrats, containing a 10 cm x 10 cm grid, were placed every 5 m along the transect lines. At each sampling station where *T. testudinum* was present, the percent coverage was estimated, the number of shoots was counted for each grid square within the quadrat and three leaves or three clumps of leaves were measured with a ruler to determine the mean canopy height (cm).

Seagrass cores were collected at each BR, MC and SG site containing *T. testudinum* patches to determine above- and below-ground biomass. Between the two 20 m transect lines used to characterize the site, four circular cores, with a radius of 12.5 cm each, were taken from radiating lines measuring 5 m (Figure 3.1). Each core reached a maximum depth of 10 cm, and care was taken to collect all roots and rhizomes from below ground. The

sample was first placed in a mesh bag to wash the sample *in situ*, making sure little sand was present, and was then placed in a plastic sample bag, where 5% formol (formaldehyde) was added to fix the plant material for future measurements. Back in the laboratory, seagrass samples were washed with water to remove any extra sand, shells or other organisms, and seagrass leaves were dipped in 5% HCl to remove any calcium-carbonate-based epibionts. Any algae or other organisms were physically removed from the leaves, shoots, rhizomes and roots.

Each core for each site was initially weighed and placed in a drying oven set at 60 °C. After 24 hours, the sample was weighed once every hour until a constant dry weight was achieved, and no water was present. The final weight ( $\pm 0.01\text{g}$ ) represented the Dry Weight (DW) above- and below-ground biomass.

### *2.3.2 Mangrove Forest Characterization*

For characterization of the seascape, the area and perimeter of *Rhizophora mangle* stands in each zone seaward of the causeway were also estimated. By using satellite imagery from Landsat-7 ETM+, 2001, the amount of mangrove forest surrounding the bridge reefs and mangrove channels in Zone 2 and 3 was estimated through ArcMap 9.2 GIS software.

## **2.4 Isotope Sampling and Analysis**

### *2.4.1 Isotope Sampling and Preparation*

To trace terrestrial- or marine-based organic sources in each site, sediment and leaves were collected. The first 5 cm of sediment was collected in bare sandy areas by using a small trowel, and was placed in plastic sample bags. Leaves from mangrove trees and shoots from

seagrasses were gathered if they were present in the site, as well as sediment directly underneath the vegetation, and were placed in plastic sample bags. Samples were preserved on ice until they were processed.

All leaves and shoots were rinsed in the lab with 10% HCl to remove any calcium carbonate, and were then placed in a drying oven (60 °C) for over 48 hours. Post-drying, samples were ground with a mortar and pestle until a fine powder was formed. All sediment samples were continually rinsed with 10% HCl in beakers for several days until all remnants of calcium carbonate were removed and all chemical reactions had finished. Samples were spun in a centrifuge (Sorvall Legend T) to separate the acid waste from the sediment, were rinsed in water and dried in a drying oven (60 °C) for 72 hours. The sediments were ground with a mortar and pestle and placed in glass vials.

#### *2.4.2 Isotope Analysis*

Samples were sent to the University of Waterloo Environmental Isotope Laboratory for  $\delta^{13}\text{C}$  isotope sampling. Analysis was preformed with a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan/Bremen-Germany) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108 – Italy) for combustion of organic material. Values reported were expressed as the difference between the isotope ratio of the sample and that of the carbonate rock Peedee Belemnite formation for carbon (Craig 1957) in parts per million (‰), expressed as delta ( $\delta$ ). Results were corrected to carbon standards IAEA-CH6 (sugar), EIL-72 (cellulose) and EIL-32 (graphite). The carbon composition of each sample (%) was calculated based on Carlo Erba Elemental Standards B2005, B2035 and B2036  $\pm$  1%.

### 3. RESULTS AND DISCUSSION

#### 3.1 Abiotic and Biochemical Factors Affecting Seagrass Productivity

The productivity of *T. testudinum* within the bridge reef of Zone 2 ( $\sim 17$  g DW 0.05 m $^{-2}$ ) differs from that in Zone 3 ( $\sim 13$  g DW 0.05 m $^{-2}$ ) (Table 3.1). Canopy height and percent cover of *T. testudinum* between the two bridge reefs differ minimally, indicating that the overall higher productivity at BR2 is the result of greater leaf surface area available for photosynthesis (i.e. shoot density of 238 vs. 57 shoots m $^{-2}$ , Table 3.1). Abiotic (environmental) factors may also play a role in limiting the production of leaf area in *T. testudinum*. Water samples at BR3 contained higher levels of salinity relative to BR2 (Table 3.2), indicating further environmental constraints on production of seagrass leaf area at BR3. Optimal salinity levels for *T. testudinum* are generally between 30 – 40 %, based on productivity, leaf area, photosynthetic efficiency and plant survival experiments (reviewed in (Touchette 2007)). Short term salinity pulse experiments correspond with these levels, demonstrating decreases in leaf growth, leaf elongation and photosynthetic rates (Lirman and Cropper 2003, Koch et al. 2007). Hypersalinity causes changes in *T. testudinum* leaf structure possibly because of increased accumulation of soluble sugars or chloroplasts which stimulate osmosis, in addition to the salt ions denaturing plant membranes and organelles (Iyer and Barnabas 1993).

Rates of seagrass carbon turn-over are much greater at site BR2 relative to BR3 due to large differences in C/N ratios of organic matter. Generally, lower C/N ratios indicate greater rates of decomposition because there is relatively more nitrogen available for microbe activity (i.e. decomposition) (Goldman et al. 1987, Enriquez et al. 1993, Wafar et al. 1997); site BR2 has almost half the C/N of site BR3 (Table 3.3). Another factor that could

contribute to greater carbon turn-over rates is water temperature. Microbial respiration is influenced by temperature, with warmer temperatures causing higher rates of organic decomposition (Vazquez-Dominguez et al. 2007). At the time of our sampling, water temperature at BR2 was nearly 1°C warmer than at BR3 (Table 3.2).

### *3.2 Mangrove “Productivity”*

Due to physical constraints and time limitations, a comprehensive study of carbon allocation in the mangrove forest surrounding our sites was not undertaken, although measurements of C/N were taken from mangrove leaves and from underlying sediment. The C/N ratio of mangrove leaves was similar amongst all sites (BR2, BR3, MC2, and MC3) and ranged between 41 to 47 (Table 3.3). Our ratios are consistent with previous studies performed in the Caribbean and Gulf of Mexico (Anderson and Fourqurean 2003, Wooller et al. 2003, Gonreea et al. 2004).

The C/N ratio of sediments taken near mangrove trees was lower than from mangrove leaves; however this C/N reduction resulted almost primarily from a lowering of percent carbon than from percent nitrogen. The C/N ratio of mangroves at site BR3, for example was 41 (with 41% carbon and 1% nitrogen; Table 3.3). Within mangrove sediments at site BR3, C/N declines to 10, with a concomitant reduction in percent carbon to 19 but a slight increase in percent nitrogen (i.e. 1.8 relative to 1.0). The most labile carbon molecules (i.e. sugars) within mangrove detritus rapidly decomposes upon mixing with the ocean floor sediment, with N-based compounds (i.e. enzymes, phenols) taking much longer to fully decompose (Holmer and Olsen 2002).

### *3.3 Influence of Mangrove Detritus on Organic Carbon Sampled along a Cuban Seascapes*

By using stable carbon isotope analysis, we are able to trace distribution of seagrass- and mangrove-derived carbon within the coastal region. For example, the average  $\delta^{13}\text{C}$  value for sampled mangrove leaves across bridge and mangrove channel sites is -27.73 ‰, whereas for seagrasses it is -8.24 ‰. Although both mangroves and seagrasses photosynthesize via the C<sub>3</sub> pathway, the presence of carbon accumulating mechanisms (i.e. use of bicarbonate to increase CO<sub>2</sub> within the chloroplast and at the site of carboxylation) by water plants results in a less negative  $\delta^{13}\text{C}$  signature (Benedict et al. 1980, Touchette and Burkholder 2000). Terrestrial C<sub>3</sub> plants such as mangroves exhibit a more negative  $\delta^{13}\text{C}$  value because RUBISCO (the primary carboxylating enzyme in C<sub>3</sub> plants) strongly discriminates against binding of <sup>13</sup>C relative to <sup>12</sup>C (Christeller and Laing 1976, Wong et al. 1979). Due to the relative difference in  $\delta^{13}\text{C}$  signature of mangroves and seagrasses, it is possible to identify the source of carbon found within sediments at various locations along the seascapes.

Our study shows that the bridge reef site sediments contain carbon derived from a mixture of seagrasses and mangroves, however the contribution of mangrove-derived carbon significantly differs between sites. For example, BR3 ( $\delta^{13}\text{C}$  of -19.59 ‰) has a stable carbon isotope value closer to that of mangroves relative to sediments sampled at BR2 (i.e. -17.43 ‰) and BR1 ( $\delta^{13}\text{C}$  of -16.31 ‰) (Figure 3.2a). Variations in sediment  $\delta^{13}\text{C}$  between sites are mirrored by the total area of surrounding mangrove forest; for example, Zone 3 is characterized by greater mangrove area (1.7 km<sup>2</sup>) relative to Zone 2 (1 km<sup>2</sup>) and Zone 1 with none (Table 3.4).

The  $\delta^{13}\text{C}$  signature of sediments taken along our Cuban seascape, including a patch reef, reef crest, spur and groove reef and reef slope, parallel changes in the kinetic energy of water flow. Of the seascape formations mentioned previously, patch reefs have a  $\delta^{13}\text{C}$  value closer to that of mangroves (-15.15 ‰), with a trend toward decreasing influence of mangroves on carbon sediments between patch reef and reef crest (-14.14 ‰) and between reef crest and spur and groove (-13.76 ‰) (Figure 3.2d). Any suspended organic material will be less likely to precipitate in high energy environments (i.e. waves, tidal currents, winds); however, upon reaching the reef slope (-16.22 ‰), organic matter can be deposited because the slope represents a low energy environment relative to the reef crest. Patch reefs and reef crests are typically in areas of high wave action and tidal influences, due to their closeness to shore, while spur and groove reefs are typically along mid-depth or deep terraces, yet also receive significant current action, causing grooves between spurs (Roberts et al. 1992). Although currents can be complicated at deeper depths, generally reef slopes experience little wave action or tidal influences, compared to shallower environments, as a result of steep shelf inclination and depth (Roberts et al. 1977, Jackson 1991). It is well known that coastal mangroves improve the productivity of reef ecosystems (Jennerjahn and Ittekkot 2002). Our study shows similar results to Hemminga et al. (1994), with the movement of organic carbon through different seascape formations, showing a pattern of decreasing mangrove contributions to seascape formations up until the reef slope, wherein mangrove-rich organic carbon once again increases (Figure 3.3). Unlike Hemminga et al. (1994), we have shown that reefs in front of areas with high mangrove productivity demonstrate more  $^{13}\text{C}$ -depleted sediments, implying outwelling from the mangrove forest to the reef does occur.

With respect to the functioning of coastal marine systems, the occurrence of bridge reefs along the Cuban causeway add a unique step in the trophic element of seascapes. Juvenile fish generally inhabit shallow waters within the prop roots of coastal mangroves as protection from predators (Laegdsgaard and Johnson 2001, de la Moriniere et al. 2004, Dorenbosch et al. 2004, Mumby et al. 2004, Nagelkerken and van der Velde 2004a, b). As these fish mature they must make their way to the outer reefs to complete their lifecycle (see Figure 3.3). Although coastal seagrass beds offer juvenile fish protection from predators, seagrass beds do not provide the necessary food resources required by maturing fish. Once at the reef, mature fish may occasionally wander back into shallow coastal waters, however their primary habitat is within the offshore reefs (Huxham et al. 2007).

In a survey of the presence and abundance of fish found at the bridge reef sites, it was discovered that most of the fish present were mature and not juvenile (Appendix B), as would be expected if juvenile fish were to primarily use patch reefs as temporary stops along their migration towards the outer reef. Fish of various species were found in relatively large abundance, most of which were mature. Many of these mature fish displayed obvious signs of predation (multiple bite marks), which was not altogether surprising considering the abundance and size of top predators (barracuda) we encountered while snorkelling. One similar site that we explored (but which was not part of our current study) showed evidence of shark predation (i.e. decomposing shark remains were found around bridge reef formations). Without conducting experiments tagging fish and assessing their seasonal migration routes we cannot say for certain that some of the mature fish encountered were not permanent residents of the bridge reefs. It is likely that many fish were in their mature lifecycle as the bridge reefs themselves contained many characteristics of coral reef

ecosystems: crustaceans, coral, sponges, jelly fish, tunicates, and healthy reef algae (see Chapter 2).

#### 4. CONCLUSIONS

The main goal of this chapter was to determine if  $\delta^{13}\text{C}$  could be used as a tracer to determine the main sources of organic matter at the bridge reef sites. Although we were not able to clearly identify the sediment at each bridge to be specifically mangrove- or seagrass-based, we were able to demonstrate that the organic matter produced and exported to these sites was largely a mixture of sources, combined into detritus.  $\delta^{13}\text{C}$  was useful however at demonstrating if mangrove source matter was more prevalent at one site compared to another, with BR3 showing the highest influence from mangroves, compared to sites BR1 and BR2 which had substantially less surrounding mangrove forest area.

Unlike Hemminga et al. (1994) we were able to show that indeed, organic matter from mangroves can be exported to coral reef environments. Although the coral reef sites in the first two zones did not show any influence from mangroves, the reef slope in the third zone with the most mangrove forest and lowest wave/current energy, had lighter  $\delta^{13}\text{C}$  values indicative of organic mangrove source matter. This study demonstrates the importance of connectivity within the seascape, and especially highlights the role of many sources of organic matter in intermediate habitats (such as the bridge reefs), and implies the need for conservation of seagrass beds and mangrove forests in coastal communities.

## 5. REFERENCES

- Anderson, W. T., and J. W. Fourqurean. 2003. Intra- and interannual variability in seagrass carbon and nitrogen stable isotopes from south Florida, a preliminary study. *Organic Geochemistry* **34**:185-194.
- Benedict, C. R., W. W. L. Wong, and J. H. H. Wong. 1980. Fractionation of the stable isotopes of inorganic carbon by seagrasses. *Plant Physiology* **65**:512-517.
- Bouillon, S., F. Dahdouh-Guebas, A. Rao, N. Koedam, and F. Dehairs. 2003. Sources of organic carbon in mangrove sediments: variability and possible ecological implications. *Hydrobiologia* **495**:33-39.
- Bouillon, S., T. Moens, and F. Dehairs. 2004. Carbon sources supporting benthic mineralization in mangrove and adjacent seagrass sediments (Gazi Bay, Kenya). *Biogeosciences* **1**:71-78.
- Christeller, J. T., and W. A. Laing. 1976. Isotope discrimination by Ribulose 1,5-Diphosphate Carboxylase. *Plant Physiology* **57**:580-582.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochimica Et Cosmochimica Acta* **12**:133-149.
- de la Moriniere, E. C., I. Nagelkerken, H. van der Meij, and G. van der Velde. 2004. What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Marine Biology* **144**:139-145.
- Dorenbosch, M., M. C. van Riel, I. Nagelkerken, and G. van der Velde. 2004. The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuarine Coastal and Shelf Science* **60**:37-48.

- Duarte, C. M., J. J. Middelburg, and N. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**:1-8.
- Enriquez, S., C. M. Duarte, and K. Sandjensen. 1993. Patterns in decomposition rates among photosynthetic organisms - the importance of detritus C-N-P content. *Oecologia* **94**:457-471.
- Fleming, M., G. Lin, and L. d. S. L. Sternberg. 1990. Influence of mangrove detritus in an estuarine ecosystem. *Bulletin of Marine Science* **47**:663-669.
- Fry, B., R. Lutes, M. Northam, P. L. Parker, and J. C. Ogden. 1982. A  $^{13}\text{C}/^{12}\text{C}$  comparison of food webs in Caribbean seagrass meadows and coral reefs. *Aquatic Botany* **14**:389-398.
- Goldman, J. C., D. A. Caron, and M. R. Dennett. 1987. Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C-N ratio. *Limnology and Oceanography* **32**:1239-1252.
- Gonneea, M. E., A. Paytan, and J. A. Herrera-Silveira. 2004. Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years. *Estuarine Coastal and Shelf Science* **61**:211-227.
- Hemminga, M. A., F. J. Slim, J. Kazungu, G. M. Ganssen, J. Nieuwenhuize, and N. M. Kruyt. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology-Progress Series* **106**:291-301.
- Holmer, M., and A. B. Olsen. 2002. Role of decomposition of mangrove and seagrass detritus in sediment carbon and nitrogen cycling in a tropical mangrove forest. *Marine Ecology-Progress Series* **230**:87-101.

- Huxham, M., E. Kimani, J. Newton, and J. Augley. 2007. Stable isotope records from otoliths as tracers of fish migration in a mangrove system. *Journal of Fish Biology* **70**:1554-1567.
- Iyer, V., and A. D. Barnabas. 1993. Effects of varying salinity on leaves of *Zostera capensis* Setchell. I. Ultrastructural changes. *Aquatic Botany* **46**:141-153.
- Jackson, J. B. C. 1991. Adaptation and Diversity of Reef Corals. *Bioscience* **41**:475-482.
- Jennerjahn, T. C., and V. Ittekkot. 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften* **89**:23-30.
- Kennedy, H., E. Gacia, D. P. Kennedy, S. Papadimitriou, and C. M. Duarte. 2004. Organic carbon sources to SE Asian coastal sediments. *Estuarine Coastal and Shelf Science* **60**:59-68.
- Kitheka, J. U. 1997. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. *Estuarine Coastal and Shelf Science* **45**:177-187.
- Koch, M. S., S. A. Schopmeyer, C. Kyhn-Hansen, C. J. Madden, and J. S. Peters. 2007. Tropical seagrass species tolerance to hypersalinity stress. *Aquatic Botany* **86**:14-24.
- Kon, K., H. Kurokura, and K. Hayashizaki. 2007. Role of microhabitats in food webs of benthic communities in a mangrove forest. *Marine Ecology-Progress Series* **340**:55-62.
- Laegdsgaard, P., and C. Johnson. 2001. Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* **257**:229-253.

- Lin, G., T. Banks, and L. d. S. L. Sternberg. 1991. Variation in  $\delta^{13}\text{C}$  values for the seagrass *Thalassia testudinum* and its relations to mangrove carbon. *Aquatic Botany* **40**:333-341.
- Lirman, D., and W. P. Cropper. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: Field, experimental, and modeling studies. *Estuaries* **26**:131-141.
- Marguillier, S., G. vanderVelde, F. Dehairs, M. A. Hemminga, and S. Rajagopal. 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by delta C-13 and delta N-15. *Marine Ecology-Progress Series* **151**:115-121.
- Mumby, P. J., A. J. Edwards, J. E. Arias-Gonzalez, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**:533-536.
- Nagelkerken, I., and G. van der Velde. 2004a. Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? *Marine Ecology-Progress Series* **274**:143-151.
- Nagelkerken, I., and G. van der Velde. 2004b. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Marine Ecology-Progress Series* **274**:153-159.
- Peros, M. C., E. G. Reinhardt, H. P. Schwarcz, and A. M. Davis. 2007. High-resolution paleosalinity reconstruction from Laguna de la Leche, north coastal Cuba, using Sr, O, and C isotopes. *Palaeogeography Palaeoclimatology Palaeoecology* **245**:535-550.

- Roberts, H. H., S. P. Murray, and J. N. Suhayda. 1977. Physical processes on a fore-reef shelf environment. Pages 504-516 in 3rd International Coral Reef Symposium. Taylor, D. L., Rosential School of Marine and Atmospheric Science.
- Roberts, H. H., P. A. Wilson, and A. Lugofernandez. 1992. Biologic and Geologic Responses to Physical Processes - Examples from Modern Reef Systems of the Caribbean-Atlantic Region. *Continental Shelf Research* **12**:809-834.
- Smith, B. N., and S. Epstein. 1971. Two categories of  $^{13}\text{C}/^{12}\text{C}$  ratios for higher plants. *Plant Physiology* **47**:380-384.
- Touchette, B. W. 2007. Seagrass-salinity interactions: Physiological mechanisms used by submersed marine angiosperms for a life at sea. *Journal of Experimental Marine Biology and Ecology* **350**:194-215.
- Touchette, B. W., and J. M. Burkholder. 2000. Overview of the physiological ecology of carbon metabolism in seagrasses. *Journal of Experimental Marine Biology and Ecology* **250**:169-205.
- Vazquez-Dominguez, E., D. Vaque, and A. M. Gasol. 2007. Ocean warming enhances respiration and carbon demand of coastal microbial plankton. *Global Change Biology* **13**:1327-1334.
- Wafar, S., A. G. Untawale, and M. Wafar. 1997. Litter fall and energy flux in a mangrove ecosystem. *Estuarine Coastal and Shelf Science* **44**:111-124.
- Wong, W. W., C. R. Benedict, and R. J. Kohel. 1979. Enzymic fractionation of the stable carbon isotopes of carbon dioxide by Ribulose-1,5-bisphosphate Carboxylase. *Plant Physiology* **63**:852-856.

- Wooller, M., B. Smallwood, M. Jacobson, and M. Fogel. 2003. Carbon and nitrogen stable isotopic variation in *Laguncularia racemosa* (L.) (white mangrove) from Florida and Belize: implications for trophic level studies. *Hydrobiologia* **499**:13-23.
- Zieman, J. C., S. A. Macko, and A. L. Mills. 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. *Bulletin of Marine Science* **35**:380-392.

Table 3.1. Mean ( $\pm$  standard error) seagrass characteristics for sites supporting *Thalassia testudinum* meadows: Shoot density, canopy height, percent coverage and seagrass biomass (above and below ground) estimates for those sites supporting seagrass meadows

<b>Site</b>	<b>Shoot Density (shoots m<sup>-2</sup>)</b>	<b>Canopy Height (cm)</b>	<b>Percent Coverage (% 0.25 m<sup>-2</sup>)</b>	<b>Biomass (g DW 0.05 m<sup>-2</sup>)</b>
BR2	238.2 $\pm$ 14.99	17.86 $\pm$ 0.59	22.75 $\pm$ 3.37	17.26 $\pm$ 2.70
BR3	57.0 $\pm$ 5.99	18.57 $\pm$ 1.71	20.0 $\pm$ 3.06	13.25 $\pm$ 2.11
MC2	189.6 $\pm$ 20.62	18.49 $\pm$ 1.81	32.0 $\pm$ 7.42	23.86 $\pm$ 1.55
MC3	284.0 $\pm$ 19.68	21.88 $\pm$ 1.24	54.5 $\pm$ 8.21	22.64 $\pm$ 4.59
SG1	176.0 $\pm$ 10.96	17.85 $\pm$ 0.74	21.5 $\pm$ 1.50	31.56 $\pm$ 1.88
SG3	240.8 $\pm$ 22.92	13.23 $\pm$ 0.30	27.5 $\pm$ 1.71	20.21 $\pm$ 3.25

Table 3.2. Physical and Environmental Means ( $\pm$  Standard Error) for each variable measured at all sites.

	<i>BR1NP</i>	<i>BR1NE</i>	<i>BR1SP</i>	<i>BR1SE</i>	<i>BR2N</i>	<i>BR2S</i>	<i>BR3N</i>	<i>BR3S</i>
Complexity (m m <sup>-1</sup> )	0.84 $\pm$ 0.04		0.82 $\pm$ 0.07		0.68 $\pm$ 0.08	0.74 $\pm$ 0.06	0.96 $\pm$ 0.01	0.93 $\pm$ 0.03
Current (cm s <sup>-1</sup> )		14.14 $\pm$ 7.61		8.68 $\pm$ 1.51		2.07 $\pm$ 0.72	11.69 $\pm$ 4.79	0.00 $\pm$ 0.00
Depth (m)	0.96 $\pm$ 0.23	0.94 $\pm$ 0.09	0.53 $\pm$ 0.14	0.77 $\pm$ 0.08	1.2 $\pm$ 0.18	0.59 $\pm$ 0.07	0.75 $\pm$ 0.04	0.58 $\pm$ 0.09
Conductivity (Ms cm <sup>-1</sup> )	59.72 $\pm$ 0.02	59.84 $\pm$ 0.04	59.76 $\pm$ 0.02	59.74 $\pm$ 0.02	56.14 $\pm$ 0.18	56.12 $\pm$ .21	59.72 $\pm$ 0.18	59.80 $\pm$ 0.10
Salinity (‰)	39.82 $\pm$ 0.02	39.90 $\pm$ 0.00	39.70 $\pm$ 0.10	39.80 $\pm$ 0.00	37.36 $\pm$ 0.15	37.28 $\pm$ 0.17	40.02 $\pm$ 0.12	40.08 $\pm$ 0.07
Temperature (°C)	30.24 $\pm$ 0.04	30.30 $\pm$ 0.00	30.40 $\pm$ 0.00	30.30 $\pm$ 0.00	24.80 $\pm$ 0.27	24.64 $\pm$ 0.19	23.86 $\pm$ 0.02	23.82 $\pm$ 0.02
TDS (g L <sup>-1</sup> )	38.82 $\pm$ 0.02	38.86 $\pm$ 0.02	38.80 $\pm$ 0.00	38.84 $\pm$ 0.02	36.46 $\pm$ 0.10	36.48 $\pm$ 0.13	38.84 $\pm$ 0.12	38.90 $\pm$ 0.07
Turbidity (NTU)		1.89 $\pm$ 0.31		1.79 $\pm$ 0.31		0.95 $\pm$ 0.17	0.77 $\pm$ 0.02	0.35 $\pm$ 0.08
Dissolved O <sub>2</sub> (mg L <sup>-1</sup> )		9.30 $\pm$ 0.00		9.30 $\pm$ 0.00		8.76 $\pm$ 0.38	8.70 $\pm$ 0.17	6.92 $\pm$ 0.57
	<i>MC2</i>	<i>MC3</i>	<i>SG1</i>	<i>SG3</i>	<i>NR1PR</i>	<i>NR1RC</i>	<i>NR2SG</i>	<i>NR3RS</i>
Complexity (m m <sup>-1</sup> )	0.97 $\pm$ 0.01	0.93 $\pm$ 0.02	1.00 $\pm$ 0.00	1.00 $\pm$ 0.00	0.92 $\pm$ 0.01	0.85 $\pm$ 0.04	0.92 $\pm$ 0.03	0.84 $\pm$ 0.03
Current (cm s <sup>-1</sup> )	1.45 $\pm$ 0.82	2.62 $\pm$ 1.20	0.00 $\pm$ 0.00					
Depth (m)	2.21 $\pm$ 0.06	1.49 $\pm$ 0.07	0.82 $\pm$ 0.05	1.45 $\pm$ 0.04	0.76 $\pm$ 0.09	1.63 $\pm$ 0.06	9.92 $\pm$ 0.15	10.36 $\pm$ 0.17
Conductivity (Ms cm <sup>-1</sup> )	57.15 $\pm$ 0.02	60.52 $\pm$ 0.08	58.37 $\pm$ 0.02	58.20 $\pm$ 0.02	57.55 $\pm$ 0.02	57.21 $\pm$ 0.02	57.21 $\pm$ 0.02	57.21 $\pm$ 0.02
Salinity (‰)	38.05 $\pm$ 0.02	40.60 $\pm$ 0.06	38.82 $\pm$ 0.01	38.78 $\pm$ 0.01	38.29 $\pm$ 0.02	38.06 $\pm$ 0.02	38.10 $\pm$ 0.02	38.09 $\pm$ 0.02
Temperature (°C)	25.36 $\pm$ 0.02	24.70 $\pm$ 0.11	29.30 $\pm$ 0.00	27.50 $\pm$ 0.00	27.90 $\pm$ 0.00	26.14 $\pm$ 0.03	25.70 $\pm$ 0.00	25.77 $\pm$ 0.02
TDS (g L <sup>-1</sup> )	37.15 $\pm$ 0.02	39.34 $\pm$ 0.05	37.90 $\pm$ 0.00	37.83 $\pm$ 0.02	37.41 $\pm$ 0.01	37.19 $\pm$ 0.01	37.19 $\pm$ 0.02	37.18 $\pm$ 0.01
Turbidity (NTU)	0.93 $\pm$ 0.05	0.53 $\pm$ 0.06	0.37 $\pm$ 0.02	0.34 $\pm$ 0.03	0.08 $\pm$ 0.01	0.13 $\pm$ 0.04	0.11 $\pm$ 0.02	0.05 $\pm$ 0.02
Dissolved O <sub>2</sub> (mg L <sup>-1</sup> )			9.81 $\pm$ 0.05	8.90 $\pm$ 0.00	10.12 $\pm$ 0.02	8.73 $\pm$ 0.02	7.86 $\pm$ 0.02	7.79 $\pm$ 0.01

Table 3.3. C/N Ratios (% weight) for all sites measured, with mean % compositions of Carbon and Nitrogen included.

Site	Seagrass Leaves			Seagrass Sediment			Mangrove Leaves			Mangrove Sediment			Sediment		
	Ratio	% C	% N	Ratio	% C	% N	Ratio	% C	% N	Ratio	% C	% N	Ratio	% C	% N
BR1													7.81	5.75	0.74
BR2	30.65	41.80	1.36	8.17	3.07	0.38	45.30	36.10	0.83	10.15	8.28	0.82	9.86	3.30	0.33
BR3	66.37	40.96	0.62	10.37	7.41	0.71	40.76	41.41	1.02	10.06	18.46	1.84	8.81	3.33	0.38
MC2	39.01	38.43	0.99	7.82	31.87	4.08	45.10	42.36	0.94	15.20	17.59	1.16			
MC3	41.08	39.76	0.97	8.34	1.64	0.20	47.36	44.37	0.94	12.38	6.96	0.56			
SG1	50.72	32.55	0.64	8.82	20.32	2.30							6.29	16.66	2.65
SG3	48.81	40.32	0.83	8.46	2.04	0.24							6.89	9.80	1.42
NR1-PR													6.23	9.71	1.56
NR1-RC													9.23	14.96	1.62
NR2-SG															
NR3-RS															
Mean (± s.e.)	46.11 (± 5.0)	38.97 (± 1.4)	0.90 (± 0.1)	8.66 (± 0.4)	11.06 (± 5.1)	1.32 (± 0.6)	44.63 (± 1.4)	41.06 (± 1.8)	0.93 (± 0.1)	11.95 (± 1.2)	12.82 (± 3.1)	1.09 (± 0.3)	7.87 (± 0.6)	9.07 (± 2.0)	1.24 (± 0.3)

Table 3.4. Perimeter (km) and area ( $\text{km}^2$ ) of mangrove forest (*Rhizophora mangle*) surrounding bridge reefs and mangrove channels in Zones 2 and 3, based on satellite imagery from Landsat-7 ETM+, 2001.

<b>Site</b>	<b>Perimeter (km)</b>	<b>Area (<math>\text{km}^2</math>)</b>
Zone 2	12.29	1.13
Zone 3	10.28	1.71

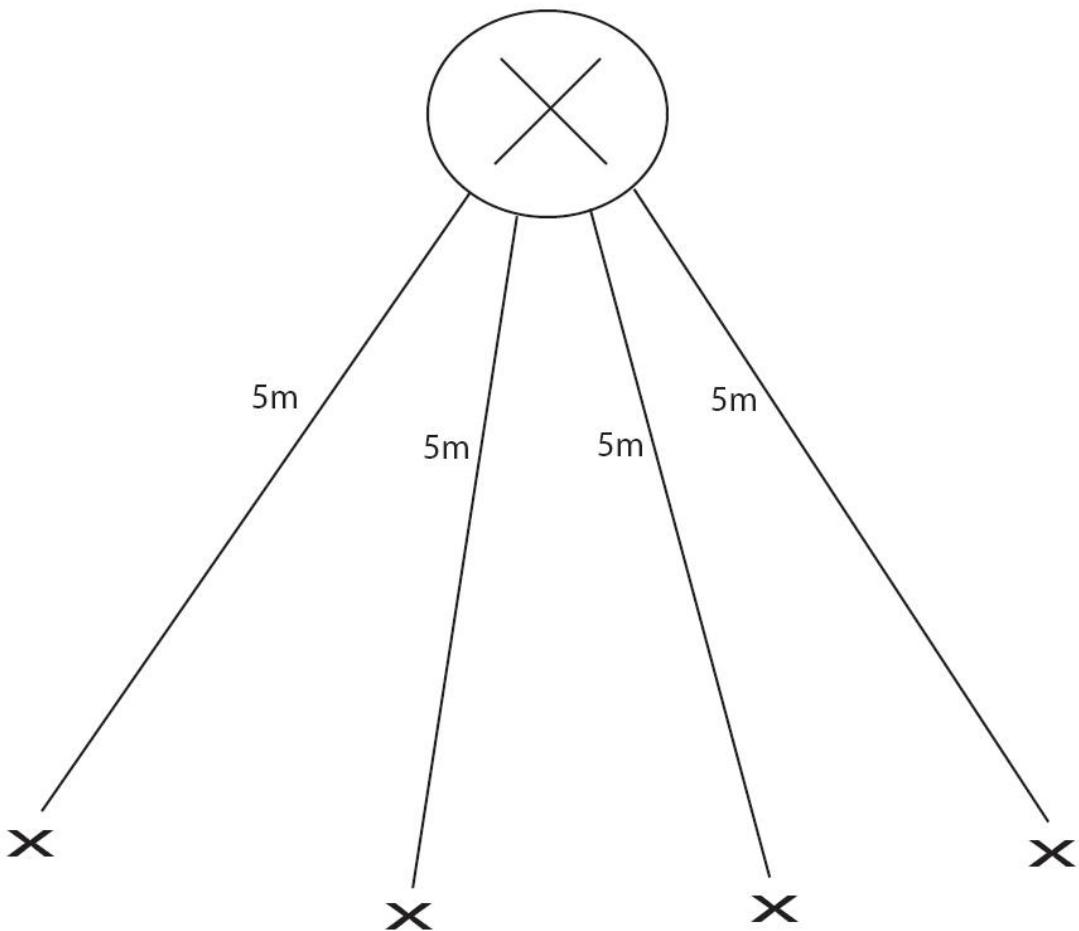
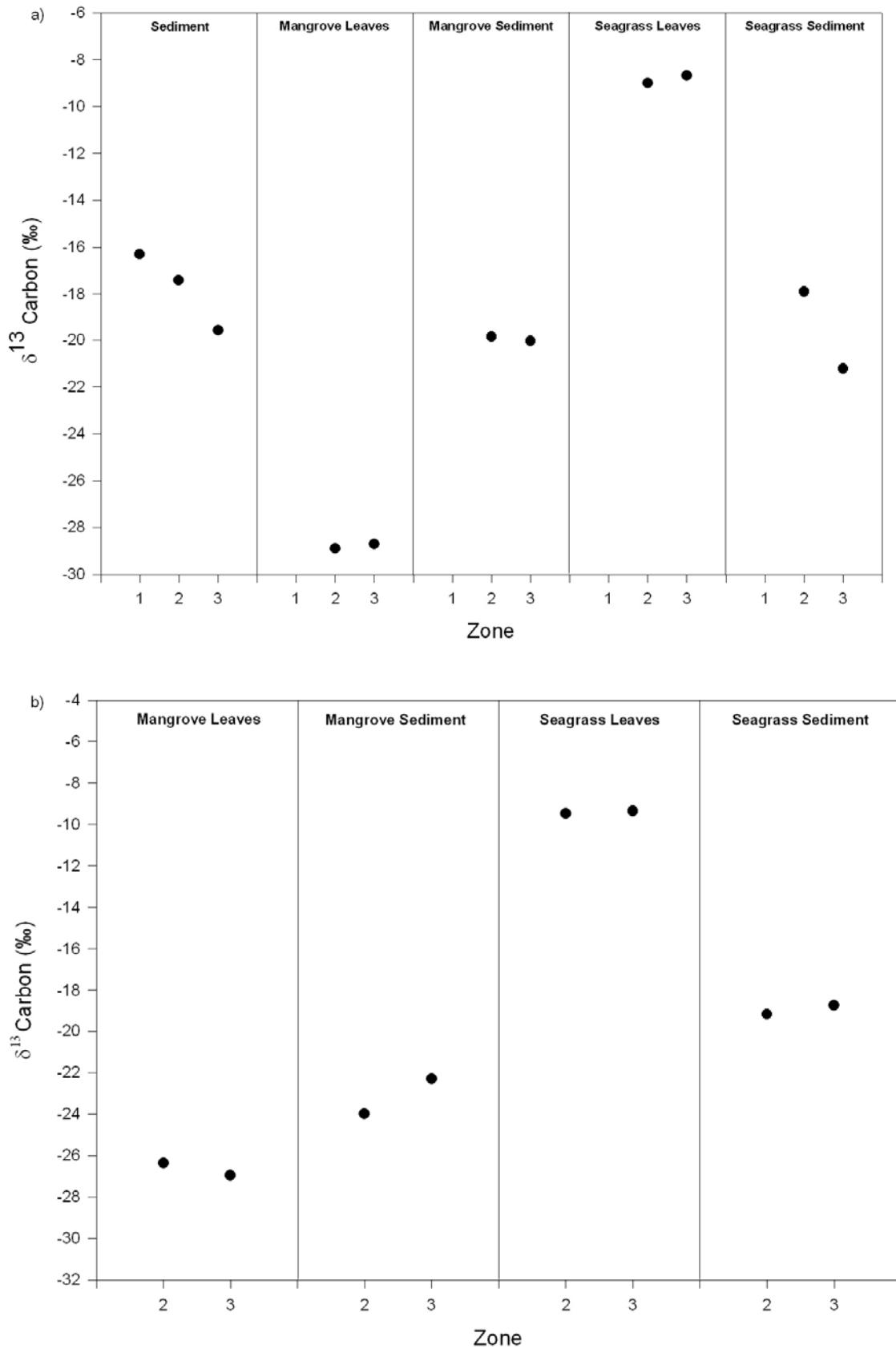


Figure 3.1. Typical setup used to collect *T. testudinum* biomass cores *in-situ*. Small x's radiating out from the centre (delineated by a circle with X inside) were the sites of cores collected. Each radiating line measured approximately 5 m, and was taken at random angles from the centre.



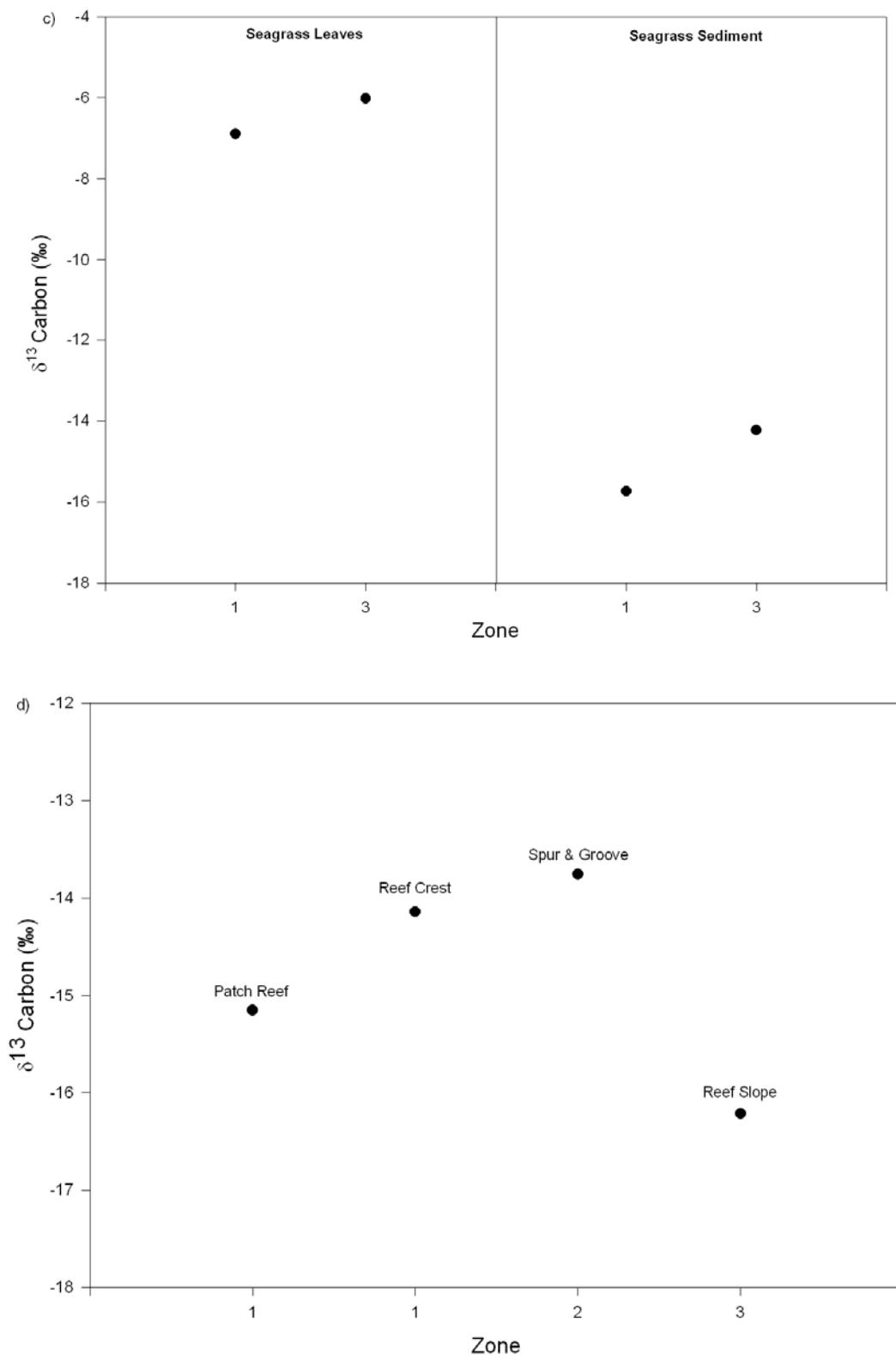


Figure 3.2.  $\delta^{13}\text{C}$  isotope values for varying sediments and leaves of three different zones and types of habitats within the seascape: a) bridge reefs; b) mangrove channels; c) seagrass beds; and d) natural reefs.

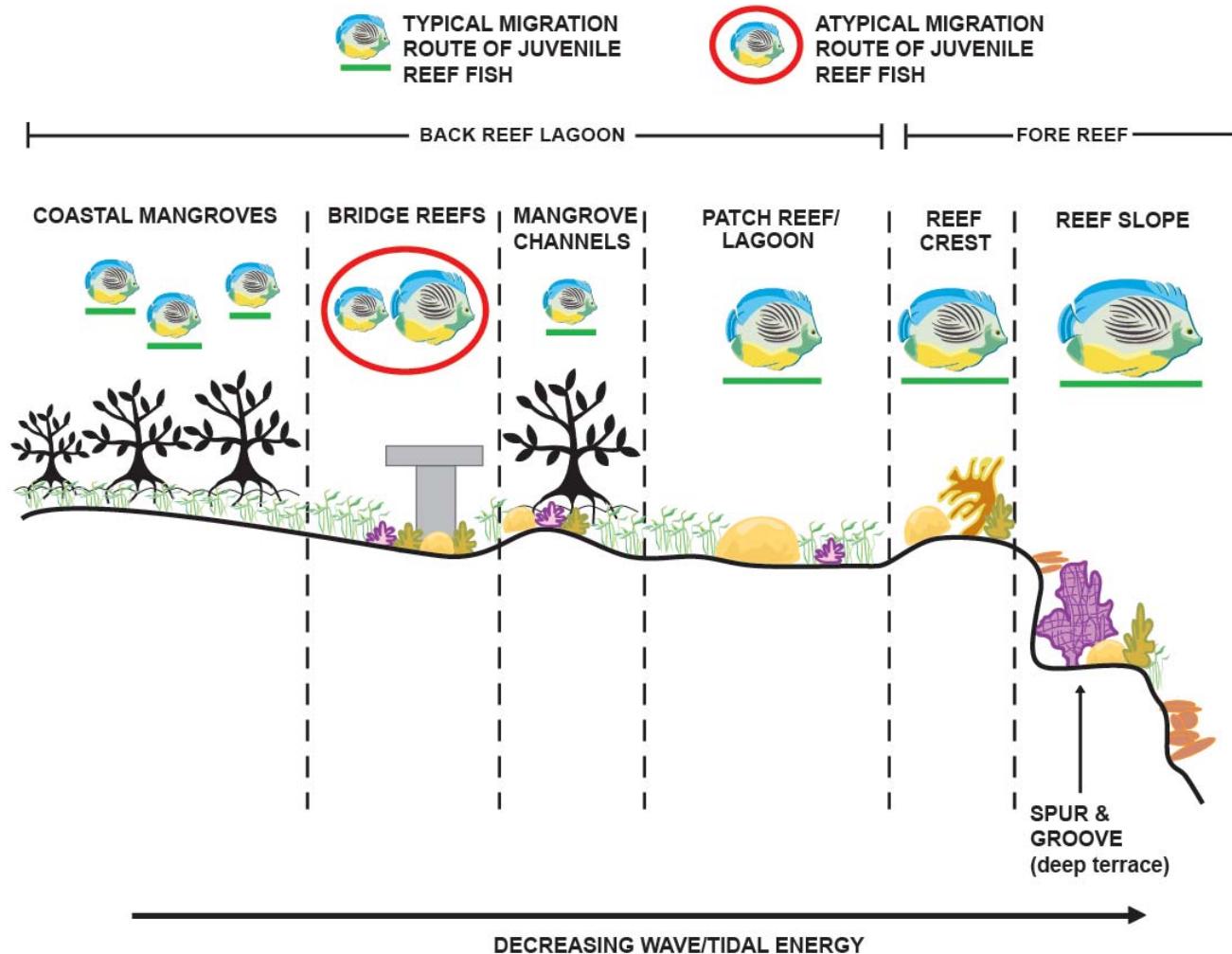


Figure 3.3. Cayo Coco-Guillermo seascape transect in seaward direction, indicating habitat types, typical species and route of juvenile reef fish. Size of reef fish indicates typical age of fish found in that particular habitat (i.e. small = juveniles, medium = intermediates, large = adults).

## **CHAPTER FOUR: Conclusion**

### **4.1 CONNECTIVITY WITHIN THE TROPICAL SEASCAPE**

This study has demonstrated that connectivity within the Cuban seascape is multi-dimensional, and ultimately responsible for the development of the bridge reefs. Through the flow of tidal currents linking the open ocean to the inter-island lagoons, coral larvae were successfully able to colonize the limestone rocks found underneath the bridges along the Cayo Coco - Cayo Guillermo coastal causeway. The seagrass patches and mangrove forests surrounding these bridges ultimately aided in the development of these reefs by improving water clarity from deposition of sediment in the complex root and leaf structures, increasing water depth throughout the lagoon, and by providing organic matter necessary for trophic dynamics to these sites.

Chapter 2 has shown that the BR2 site is most similar to the patch reef found in the back reef lagoon, due to similar coral species, physical habitat and benthic coverage. This bridge reef could also be considered a new type of patch reef, yet was formed completely by accident. BR2 is ultimately a ‘healthier’ reef than BR3, due to the existence of coral species not found in marginal habitats, with reproductive modes better suited for optimal reef environments. BR3 is considerably different from BR2, with only three coral species present, of which are typical of marginal habitats. Due to the many similarities with the mangrove channel reef sites, such as similar benthic composition and environmental characteristics, it can be assumed that BR3 is mimicking the mangrove channels, and receiving coral larvae from these sites. BR3 is surrounded by more mangrove forest than BR2, which explains this close similarity to the mangrove channels. The absence of coral in BR1 is likely due to the

extremely shallow water at high tide in the lagoon directly in front of the bridge, which limits dispersal of coral larvae, and negatively affects larvae from high temperatures, UV and sedimentation. Deeper water created by mangroves (as seen in Zones 2 and 3), can aid in coral larval dispersion, and improve water quality at the bridges. Throughout the seascape, depth is largely responsible for the types of species assemblages occurring, while water current speed and turbidity are also loosely responsible. By using multi-variate statistics, this study has shown how a new, unique habitat has become integrated into a Cuban seascape, and the importance of incorporating regional dynamics to explain ecology.

The results from this thesis have provided a greater understanding of marginal habitats and where corals can establish. With increasing levels of reef degradation and increased sea surface temperatures, survival in less-than optimal conditions may become crucial for coral reefs. For example, anomalously high temperatures in 2005 caused mass coral bleaching and mortality throughout the Caribbean (Donner et al. 2007), while sedimentation from runoff and hydrodynamic changes causing extreme salinity levels are occurring globally (Brown 1997). Artificial reefs are becoming an essential tool in maintaining reefs, and it is important to know the environmental limitations of coral species. Coral from marginal habitats may be the ideal coral species to plant and seed new artificial reefs, as these species will have greater chances of survival during periods of global change, due to their ability to withstand less-than-optimal conditions.

Chapter 3 looked at seascape connectivity from a different perspective by determining the coastal vegetation productivity contributions at both the bridge reef sites and the surrounding habitats. Seagrasses and mangroves proved to be extremely important to the productivity of the region, with mangroves influencing some sites more than others, such as

the BR3 site and the reef slope in Zone 3. The main producers and export of organic matter were also influenced by the physical environment, as areas with high salinity had less seagrass productivity, while zones with strong current and wave energy had overall less mangrove export and more influence from surrounding seagrass beds.

Marine ecology research often focuses on one aspect of the seascape, for example coral, fish or coastal vegetation. This thesis attempts to combine many aspects to provide a multi-organism approach of connectivity within the seascape. While mangroves are considered important for juvenile fish habitat or burial and export of organic matter, they are also integral to the viability of coral reefs. Not only do they and seagrass beds trap suspended particulate matter, they may also contribute to food webs within the reef, by exporting some mangrove organic matter to coral reefs, as seen in this study.

## 4.2 FUTURE DIRECTIONS

Although many environmental factors were measured in this study, as they were believed to be important in successful habitat establishment and development, one major factor was missed due to time and logistical constraints. In order to fully understand seascape connectivity, it is crucial to understand the directional patterns and rates of flow of the major currents influencing this region. Small scale current speed was measured at each individual site, yet the direction and variability of currents connecting all sites was overlooked. To capture this level, a combination of tidal and oceanic gauges would need to be deployed at various locations throughout the seascape (Smith 2004), and possibly use oceanic models or acoustic Doppler current profiles to map long-term current speeds and

directions, in addition to coral larvae dispersal at mass spawning times (Storlazzi et al. 2006, Treml et al. 2008).

The use of population genetics may also aid in determining which parental colonies the bridge reef corals developed from within the Cayo Coco-Guillermo seascape. To determine the genetics of parental colonies however, may prove time consuming due to the difficulty in extracting mitochondrial DNA variation in corals, and a lack of variable single-copy nuclear markers. Some studies though have been able to determine which colonies donated egg and sperm, with *Acropora palmata* being the first species within the Caribbean (Baums et al. 2005). Research has advanced, and it is now becoming commonplace to use these molecular techniques to not only map genetic variability and parent colonies, but also in creating viable Marine Protected Areas (Ridgway et al. 2008).

As marine ecosystems are made of dynamic populations and environments, it is essential to capture this variability when making conclusions based on observations. A long-term monitoring program is suggested for the Cayo Coco-Guillermo region, especially to observe changes in the physical environment and determine if continued success can occur. Of specific interest will be the salinity levels of the region, as the values are currently higher than normal and could continue to rise to lethal levels for most of the coral species present. If mass mortality occurs, we will need to monitor major phase-shifts from coral to macroalgae, and may need to use management techniques – such as addition of herbivorous fish (Conklin and Stimson 2004) or biocontrol agents (Conklin and Smith 2005) to control the spread of algae.

Although only briefly mentioned in Chapter 3, many reef fish species were seen residing or visiting all three bridge reefs. A future study, which could have economic

benefits, may be to determine if these bridge reefs enhance the number of commercially important fish species, due to increased food sources and decreased risk of predation from the structural complexity of the bridges. Many juvenile fish congregate in mangroves for both these reasons (Thayer et al. 1987, Laegdsgaard and Johnson 2001, Nagelkerken et al. 2001, Nagelkerken and van der Velde 2002, de la Moriniere et al. 2004), which implies the bridge reefs are mimicking mangrove habitats. The large abundance of adult fish present however, may indicate these sites are more of an intermediate staging area, until they are large enough to make it to the reef. By tagging fish at the bridge reefs, we could monitor their movements and determine if the bridge reefs are ultimately improving fish stock in the natural reefs.

Tracing organic material through carbon isotope analysis proved to be a useful technique in determining organic matter sources throughout the seascape. In addition to mangroves and seagrasses though, phytoplankton and algae samples may also be useful in identifying all organic matter at the bridge reefs and natural reefs. Mangrove forests had the greatest influence in coastal productivity throughout the regions; as such it would also be useful to determine the net import and export of mangrove carbon, through litter-fall and sediment trap experiments, and confirm the isotope analyses completed in this thesis.

Net primary productivity is an important part of the trophic structure of an area. All organisms visiting reefs or found throughout the seascape rely either directly or indirectly on coastal vegetation organic matter contributions for growth and development. To determine which source is most important for the energy supply of the region, isotopes could be used to trace food web structure through gut content analysis of fish, molluscs and other

invertebrates present, providing a more encompassing overview of the seascape trophic dynamics.

#### 4.3 REFERENCES

- Baums, I. B., C. R. Hughes, and M. E. Hellberg. 2005. Mendelian microsatellite loci for the Caribbean coral *Acropora palmata*. *Marine Ecology-Progress Series* **288**:115-127.
- Bouillon, S., T. Moens, and F. Dehairs. 2004. Carbon sources supporting benthic mineralization in mangrove and adjacent seagrass sediments (Gazi Bay, Kenya). *Biogeosciences* **1**:71-78.
- Brown, B. E. 1997. Disturbances to reefs in recent times. Pages 354-379 in C. Birkeland, editor. *Life and Death of Coral Reefs*. Chapman & Hall, Toronto.
- Conklin, E. J., and J. E. Smith. 2005. Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe Bay, Hawai'i and an experimental assessment of management options. *Biological Invasions* **7**:1029-1039.
- Conklin, E. J., and J. Stimson. 2004. An attempt to increase numbers of herbivorous fishes as a means of controlling populations of fleshy macroalgae on coral reefs in Kane'ohe Bay, Hawai'i. *Pacific Science* **58**:189-200.
- de la Moriniere, E. C., I. Nagelkerken, H. van der Meij, and G. van der Velde. 2004. What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Marine Biology* **144**:139-145.
- Donner, S. D., T. R. Knutson, and M. Oppenheimer. 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. *Proceedings of the National Academy of Sciences of the United States of America* **104**:5483-5488.
- Hemminga, M. A., and M. A. Mateo. 1996. Stable carbon isotopes in seagrasses: Variability in ratios and use in ecological studies. *Marine Ecology-Progress Series* **140**:285-298.

- Hemminga, M. A., F. J. Slim, J. Kazungu, G. M. Ganssen, J. Nieuwenhuize, and N. M. Kruyt. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology-Progress Series* **106**:291-301.
- Laegdsgaard, P., and C. Johnson. 2001. Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* **257**:229-253.
- Nagelkerken, I., S. Kleijnen, T. Klop, R. van den Brand, E. C. de la Moriniere, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology-Progress Series* **214**:225-235.
- Nagelkerken, I., and G. van der Velde. 2002. Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curacao (Netherlands Antilles)? *Marine Ecology-Progress Series* **245**:191-204.
- Ridgway, T., C. Riginos, J. Davis, and O. Hoegh-Guldberg. 2008. Genetic connectivity patterns of *Pocillopora verrucosa* in southern African Marine Protected Areas. *Marine Ecology-Progress Series* **354**:161-168.
- Smith, N. P. 2004. Transport processes linking shelf and back reef ecosystems in the Exuma Cays, Bahamas. *Bulletin of Marine Science* **75**:269-279.
- Storlazzi, C. D., E. K. Brown, and M. E. Field. 2006. The application of acoustic Doppler current profilers to measure the timing and patterns of coral larval dispersal. *Coral Reefs* **25**:369-381.
- Thayer, G. W., D. R. Colby, and W. F. Hettler. 1987. Utilization of the red mangrove prop root habitat by fishes in South Florida. *Marine Ecology-Progress Series* **35**:25-38.

- Treml, E. A., P. N. Halpin, D. L. Urban, and L. F. Pratson. 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology* **23**:19-36.
- Xu, Y., R. N. Mead, and R. Jaffé. 2006. A molecular marker-based assessment of sedimentary organic matter sources and distributions in Florida Bay. *Hydrobiologia* **569**:179-192.

**APPENDIX A:****Dynamics of salt, nutrients and organic matter in three bridges of Cayo Guillermo causeway**

by

**Roberto Gonzalez-de Zayas****Abstract**

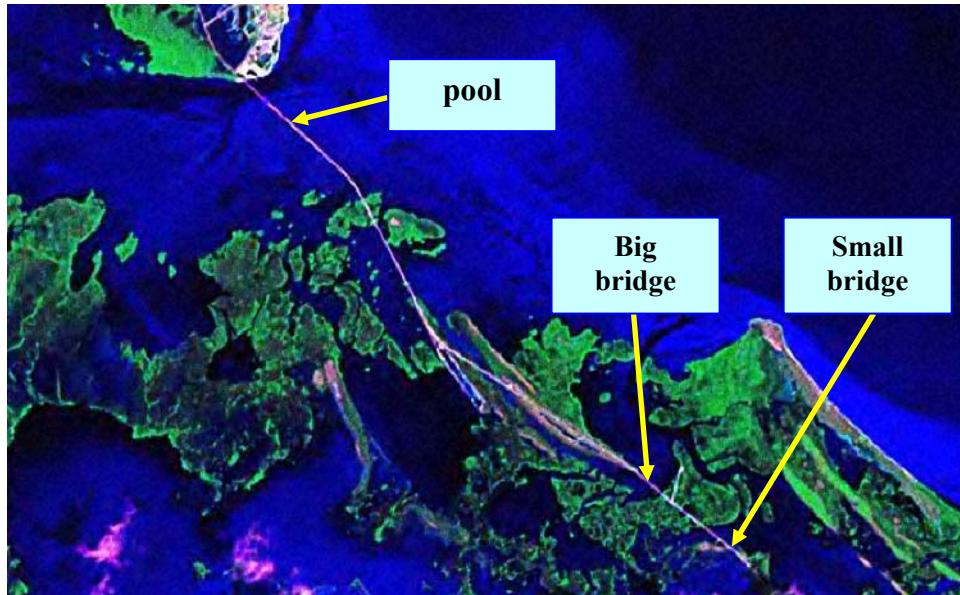
The objective of this study is to know how tides contribute to the exchange of water, salt, nutrients and organic matter. The main area of work was three bridges over the causeway from Cayo Coco to Cayo Guillermo; the sampling took one tidal cycle (one flow and ebb) every two hours. The results show the good water quality of this region, coinciding with other authors that are working at adjacent coastal waters.

**Methodology**

The study area, three bridges over causeway to Cayo Guillermo (Figure 1), was located in the western zone of Cayo Coco. They were identified according to their dynamic and ecological characteristics (pool or lagoon, big and small bridges). At each bridge, one point was sampled, with a frequency of two hours in flow and ebb tides (three sampling at each tide cycle). The samples were collected at surface in plastic bottles of 1.5 L. The sampling day was sunny with some periods of calm and there had been rain two days before.

Salinity was determined *in situ* with a handrefractometer ATAGO with precision of 1 psu; dissolved oxygen was determined at the lab through Winkler method after fixing dissolved oxygen in the field with manganese sulphate in alkaline medium. For nutrients, all samples were carried to the lab and analyzed after one day at -20 °C. Ammonium, nitrites and reactive phosphorus were analyzed through procedures described by

Strickland and Parsons (1972); nitrates according to Kempers and Van-der-Velde (1992) and organic matter was measured as COD with the procedure described by Perigó and Montalvo (2000).



**Figure 1.** Study area at causeway from Cayo Coco to Cayo Guillermo.

## Results and discussion

### *Salinity*

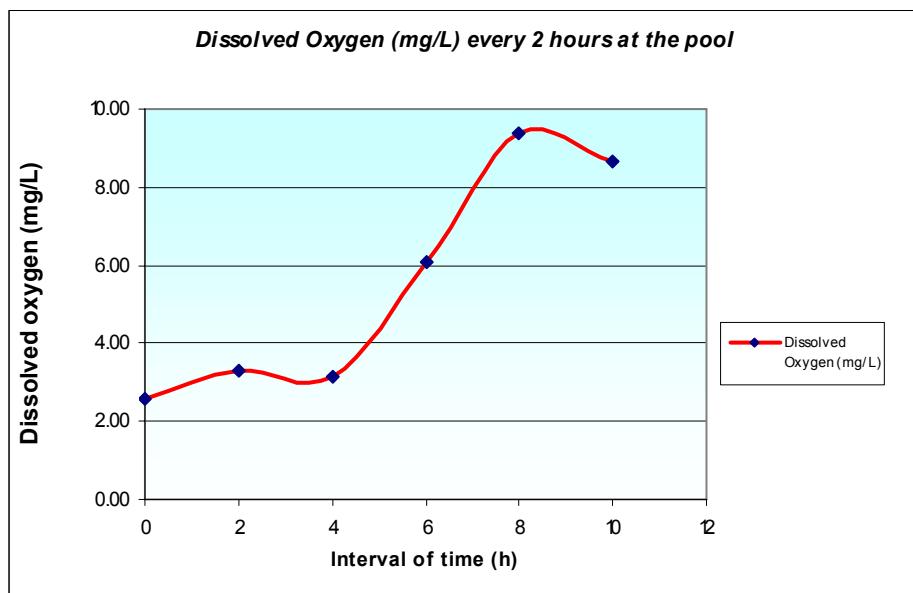
Salinity was in a range of 31 – 36 psu, the lowest salinities were in ebb tide at small bridge (31 psu) and the highest at the pool (36 psu). These values are consequence of the dynamics of these sites; the first is the most restricted shallow area with predominance of mangrove, the two days before rainfall was accumulated as freshwater south and northeast in existing natural reservoirs and was transported through tidal channels. At the pool, salinities were higher (36 psu) because this site has a good exchange with the sea and is only restricted during very low tides. This range of salinities is normal for the

development of aquatic species and mangrove and may be normal during the rainy season.

#### *Dissolved oxygen*

Dissolved oxygen contents at the three sites were between 2.57 and 9.39 mg/L, with the lowest contents in all sites in the first sampling of the day (beginning at 7.00 a.m). The low concentrations of dissolved oxygen at early morning are normal for the aquatic systems, at night all biological communities are “respiring”, this process is occurring with consumption of oxygen to oxidize organic matter. The highest amounts of oxygen (6 – 9 mg/L) were during the flow, coinciding with the day time with increasing photosynthetic activity by primary producers.

Figures 2, 3 and 4 show the dissolved oxygen curve at every two hours in three sites.



**Figure 2. Dissolved Oxygen curve every two hours at pool.**

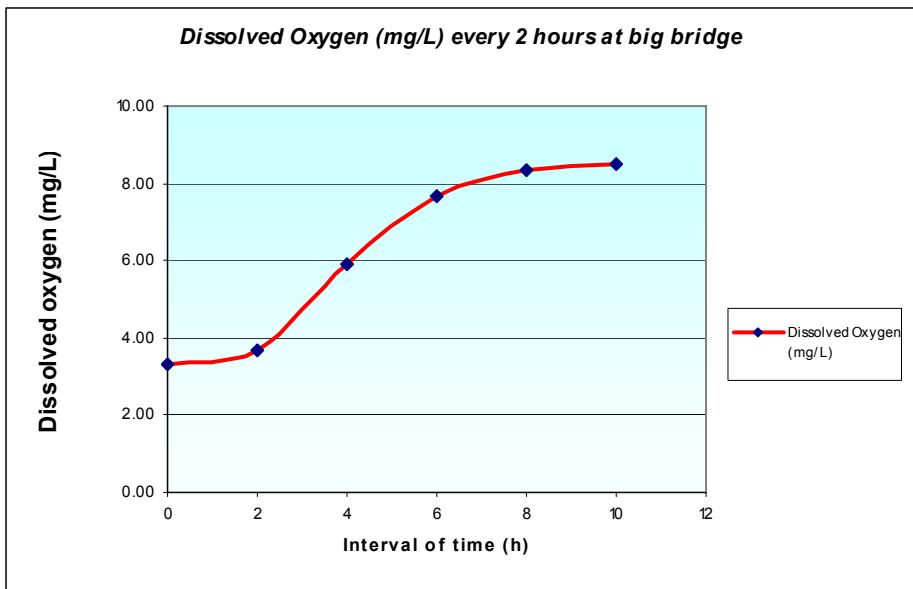


Figure 3. Dissolved Oxygen curve every two hours at Big Brigde.

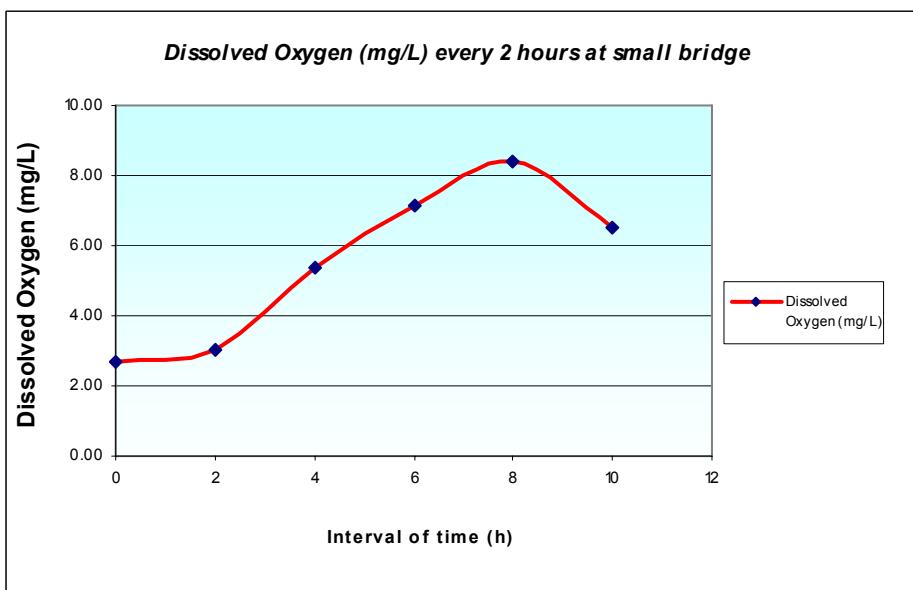


Figure 4. Dissolved Oxygen curve every two hours at Small Brigde.

The curves show a normal behaviour in an aquatic system, with low dissolved oxygen at prime hours of day and increasing to maximum concentration from 2:00 to 4:00 p. m. The obtained results are coincident with other studies at the area (CIEC, 1997).

*Nutrients*

The contents of all nutrients (ammonium, nitrates, nitrites and reactive phosphates) were normal for these coastal waters (Tables 1, 2 and 3). Some authors reported similar concentrations of nutrients at places near the study area (CERC, 1997; 2004; GEF/PNUD Report, 2000). The absence of anthropogenic sources is the main cause of seawater quality in this area, which only has as a source of nutrients the natural process of organic matter mineralization. The presence of green algae fixing nitrogen is normal in coastal waters because nitrogen is the limiting nutrient in these waters. The dynamics of nutrient with ebb and flow tide does not show any correlation between the concentrations and tidal cycles.

**Table 1. Physicochemical Parameters at the pool.**

Time	Tide	Salinity (ups)	Dissolved Oxygen (mg/L)	N-NH <sub>4</sub> <sup>*</sup> ( $\mu$ M/L)	N-NO <sub>3</sub> <sup>*</sup> ( $\mu$ M/L)	N-NO <sub>2</sub> ( $\mu$ M/L)*	P-PO <sub>4</sub> ( $\mu$ M/L)*	COD (mg O <sub>2</sub> ) <sub>L</sub> **
7:34 a.m	low (S-N)	35	2,57	14,89		Indect	Indect	1,10
9:41 a.m	low (S-N)	36	3,32	15,79		Indect	Indect	1,10
11:38 a.m	low (S-N)	35	3,14	23,51		Indect	Indect	0,87
1:10 p.m	high (N-S)	36	6,08	25,49		0,032	0,029	1,32
3:47 p.m	high (N-S)	36	9,39	11,48		Indect	Indect	1,10
5:17 p.m	high (N-S)	36	8,65	5,55		Indect	Indect	1,10

N-NO<sub>2</sub> - indet.<0.001  $\mu$ M/LP-PO<sub>4</sub> - indet.<0.004  $\mu$ M/L**Table 2. Physicochemical Parameters at the big bridge.**

Time	Tide	Salinity (ups)	Dissolved Oxygen (mg/L)	N-NH <sub>4</sub> <sup>*</sup> ( $\mu$ M/L)	N-NO <sub>3</sub> <sup>*</sup> ( $\mu$ M/L)	N-NO <sub>2</sub> ( $\mu$ M/L)*	P-PO <sub>4</sub> ( $\mu$ M/L)*	COD (mg O <sub>2</sub> ) <sub>L</sub> **
7.22 a.m	low (S-N)	33	3,32	13,27		0,007	Indect	1,77
9:25 a.m	low (S-N)	33	3,7	10,22		0,037	0,009	0,87
11:24 a.m	low (S-N)	33	5,91	13,27		0,044	Indect	1,77
1:23 p.m	high (N-S)	35	7,69	13,09		0,021	Indect	1,55
3.31 p.m	high (N-S)	32	8,35	15,61		0,01	Indect	1,77
5:28 p.m	high (N-S)	33	8,52	13,45		0,001	0,004	1,99

P-PO<sub>4</sub> - indet.<0.004  $\mu$ M/L**Table 3. Physicochemical Parameters at the small bridge.**

Time	Tide	Salinity (ups)	Dissolved Oxygen (mg/L)	N-NH <sub>4</sub> <sup>*</sup> ( $\mu$ g/L)	N-NO <sub>3</sub> <sup>*</sup> ( $\mu$ g/L)	N-NO <sub>2</sub> ( $\mu$ g/L)*	P-PO <sub>4</sub> ( $\mu$ g/L)*	COD mg O <sub>2</sub> ) <sub>L</sub> **
7:15 a.m	low (S-N)	34	2,7	12,91		0,014	0,004	1,32
9:15 a.m	low (S-N)	31	3,03	12,37		0,033	0,024	1,55
11:15 a.m	low (S-N)	31	5,4	9,68		0,005	0,019	1,10
1:32 p.m	high (N-S)	32	7,13	19,38		0,024	Indect	1,77
3:19 p.m	high (N-S)	32	8,38	20,64		0,055	Indect	2,22
5:37 p.m	high (N-S)	33	6,51	12,02		0,046	Indect	2,22

P-PO<sub>4</sub> - indet.<0.004  $\mu$ M/L

### Chemical Oxygen Demand

The measurement of organic matter at seawater as COD is used in most studies of seawater quality. The range of COD obtained (0.87 – 2.22 mg O<sub>2</sub>/L) was coincident with the amounts of COD determined for open water at adjacent sea (González - de Zayas *et al*, 2004). Sometimes these concentrations can increase due to contribution of mangrove

or others sources; the contribution of terrestrial sources is scarce at this region, because these sources are far away.

## **Conclusions**

- Salinity range is normal for coastal systems with a tidal exchange with the open sea, even with the presence of shallow zone limited by causeway.
- Dissolved oxygen is in low amounts at first hours, but after noon increases due to photosynthetic activity and the influence of tides.
- Nutrient contents are normal of coastal aquatic systems.
- Concentrations of organic matter chemically degradable are similar to those of open sea, ranging from 0.87 to 2.22 mg O<sub>2</sub>/L.
- Water quality in the study area is good for aquatic life and for the development of organisms like corals.

## **References**

- Coastal Ecosystem Research Center (CERC). 1997. Environmental Impact Assessment to construction of dolphin aquarium at Canal de los Perros.
- Coastal Ecosystem Research Center (CERC). 2004. Environmental Impact Assessment to construction of dolphin aquarium at Natural Park “El Baga”.
- GEF/PNUD Project Report. CUB/98/G32. 2000. Protecting biodiversity and establishing sustainable development in the Sabana – Camagüey Ecosystem. 110 pp.
- González – de Zayas, R., L. Hernández – Roque, and Y. Alvarez – Rivera. 2004. Physicochemical monitoring of seawater and bays north of Ciego de Avila Province. 19 pp.
- Kempers, A. J. y G. Van-der-Velde. 1992. Determination of nitrate in eutrophic coastal sea-water by reduction to nitrite with hydrazine. *Int. J. Environ. Anal. Chem.* 47 (1): 1-6
- Perigó and Montalvo (2000). Manual for analysis of seawater. Institute of Oceanology. 100 pp.
- Strickland and Parsons. 1972. A Practical Handbook of Seawater Analysis. Fisheries Research Board of Canada. Ottawa. 310 pp.

## APPENDIX B

Table 1. Fish presence/absence throughout the bridge reefs, based on fish surveys conducted in February 2005.

<b>Common Name</b>	<b>Scientific Name</b>	<b>BR1</b>	<b>BR2</b>	<b>BR3</b>
Anchovies	<i>Engraulidae (Family)</i>		x	x
Bandtail puffer	<i>Sphoeroides spengleri</i>	x		x
Bar jack	<i>Caranx ruber</i>		x	
Beaugregory	<i>Stegastes leucostictus</i>	x	x	x
Bicolour Damselfish	<i>Stegastes partitus</i>	x		
Black grouper	<i>Mycteroperca bonaci</i>		x	x
Black-ear wrasse	<i>Halichoeres poeyi</i>		x	
Blue tang	<i>Acanthurus coeruleus</i>	x	x	
Blue-head Wrasse	<i>Thalassoma bifasciatum</i>	x		
Blue-striped grunt	<i>Haemulon sciurus</i>	x	x	x
Calamus sp. (porgy)	<i>Calamus sp.</i>			
Clown wrasse	<i>Halichoeres maculipinna</i>		x	
Cocoa damselfish	<i>Stegastes variabilis</i>		x	
Coryphopterus sp. (goby)	<i>Coryphopterus sp.</i>	x	x	x
Doctorfish	<i>Acanthurus chirurgus</i>	x	x	x
Dog Snapper	<i>Lutjanus jocu</i>	x		
Flagfin mojarra	<i>Eucinostomus melanopterus</i>	x		x
Flat Needlefish	<i>Ablennes hians</i>	x	x	x
Four-eye butterflyfish	<i>Chaetodon capistratus</i>		x	x
French angelfish	<i>Pomacanthus paru</i>	x	x	x
French grunt	<i>Haemulon flavolineatum</i>			x
Gambusia sp. (minnow)	<i>Gambusia sp.</i>		x	
Gray snapper	<i>Lutjanus griseus</i>	x	x	x
Great barracuda	<i>Sphyraena barracuda</i>	x	x	x
Hogfish	<i>Lachnolaimus maximus</i>		x	x
Juvenile grunt	<i>Haemulon sp.</i>			x
Manjúas	<i>Anchoa hepsetus</i>			x
Mugil sp. (mullet)	<i>Mugil sp.</i>	x		
Night sergeant	<i>Abudefduf taurus</i>		x	
Porcupine-fish	<i>Diodon hystrix</i>		x	
Pork-fish	<i>Anisotremus virginicus</i>		x	
Princess parrotfish	<i>Scarus taeniopterus</i>		x	
Puddingwife	<i>Halichoeres radiatus</i>		x	
Queen angelfish	<i>Holacanthus ciliaris</i>		x	
Red-band parrotfish	<i>Sparisoma aurofrenatum</i>	x		x
Saddled blenny	<i>Malacoctenus triangulatus</i>		x	
Sailors choice	<i>Haemulon parra</i>	x	x	x
Sand diver	<i>Synodus intermedius</i>		x	

Schoolmaster	<i>Lutjanus apodus</i>	x	x	x
Sergeant major	<i>Abudefduf saxatilis</i>	x	x	x
Silversides	<i>Atherinidae (Family)</i>	x		
Slippery dick	<i>Halichoeres bivittatus</i>	x		x
Spot-fin butterfly-fish	<i>Chaetodon ocellatus</i>		x	
Squirlselfish	<i>Holocentrus adscensionis</i>		x	
Stoplight parrotfish	<i>Sparisoma viride</i>	x	x	x
Striped parrotfish	<i>Scarus iserti</i>	x	x	x
White grunt	<i>Haemulon plumieri</i>		x	x
Yellow-fin mojarra	<i>Gerres cinereus</i>	x	x	x
Yellowtail parrotfish	<i>Sparisoma rubripinne</i>	x	x	x
<b>Species Richness per site</b>		<b>25</b>	<b>36</b>	<b>27</b>