INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

ProQuest Information and Learning 300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA 800-521-0600



University of Alberta

Epiphyte growth and community structure on *Thalassia testudinum*: A case study from Grand Cayman

by

Hilary J. Corlett

C



Department of Earth and Atmospheric Sciences

Edmonton, Alberta Fall 2005



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: Our file Notre retérence ISBN:

NOTICE:

The author has granted a nonexclusive 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 noncommercial 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.

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.

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.



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.

University of Alberta

Library Release Form

| Name of Author: | Hilary J. Corlett |
|---------------------------|---|
| Title of Thesis: | Epiphyte growth and community structure on <i>Thalassia testudinum</i> : A case study from Grand Cayman |
| Degree: | Master of Science |
| Year This Degree Granted: | 2005 |

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly, or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Abstract

Thalassia testudinum, which is the most common seagrass found in lagoons around Grand Cayman, influences sedimentation by baffling currents, binding sediment on the seafloor, and providing substrates for a diverse epiphytic biota. The epiphytes, formed largely of organisms that are < 100 μ m long, include at least three species of red alga, 72 species of foraminifera, 61 species of diatoms, and a broad array of other, less common skeletal organisms. These epiphytes are organized in three communities, with the basal diatom community being overlain by the coralline alga community, which is then overlain by a community composed of a variety of taxa. The final layer is the most diverse of the three communities. The red algae community, which is the most extensive, typically covers ~75% of the leaf's surface. Few of these epiphytes are found in the sediment around the plants, suggesting that most were removed by current activity.

Acknowledgements

First of all I would like to thank Dr. Brian Jones for his patience and guidance over the past...ahem...three years. His writing and editorial skills are incredible. I hope to take away what I learned from him and apply it to future endeavors. Thanks also go to my committee, Dr. Brian Chatterton and Dr. Julia Foght, for their suggestions and challenging questions.

Thank you to the Government of the Cayman Islands, especially the Department of the Environment for their support of the project. I would also like to thank Hendrik van Genderen at the Water Authority for his help while we were in Cayman. The National Sciences and Engineering Research Council of Canada are thanked for the grant awarded to Brian Jones that provided financial support. I had a great time in Cayman with my field assistants, Sandy Bonny and Alex MacNeil, thank you both. Sandy, we now know how to crack open a coconut on the beach!

For helping with the analyses of my samples, I would like to thank George Braybrook for spending many hours on the SEM. George not only takes terrific pictures on the SEM, but makes the work fun and enjoyable! Also, thank you to the Thin Section Lab technicians, Mark Labbe and Don Resultay, for innovative and effective preparation of my samples.

During my time here at the University of Alberta, I have met some truly amazing people and made some really great friends. Thanks to everyone in the CSRG. Without the support of my friends I probably would have gone a little nuts at times. Thank you all for the wonderful memories and crazy nights!

Finally, I would like to thank my friends and family back home. I am lucky to still have many wonderful friends in Ontario that have continued to keep on touch and always keep my spirits high. My sister, brother, aunts and uncles are always there for me and I appreciate their support more than I can say. Thank you to my parents for always encouraging me to pursue anything and everything in life. Mom, I definitely could not have done it all without you. I love you very much.

Table of Contents

| Chapter 1 1.1 | Introduction Introduction | 1 1 |
|-------------------------|--|--------|
| 1.2 | T. testudinum and its role in sedimentation | 3 |
| 1.3 | Environmental controls on growth of <i>T</i> . <i>testudinum</i> | 6 |
| 1.4 | T. testudinum on Grand Cayman | 7 |
| 1.5 | Field methods | 13 |
| 1.6 | Sample preparation and analyses | 15 |
| 1.7 | Identification process | 16 |
| Chapter 2 | Results | 20 |
| 2.1 | Epiphytic biota | 20 |
| 2.2 | Dominant taxa | 62 |
| 2.2.1 | Coralline alga | 62 |
| 2.2.2 | Foraminifera | 62 |
| 2.2.3 | Diatoms | 63 |
| 2.2.4 | Other skeletal epiphytes | 63 |
| 2.3 | Lagoonal sediment | 64 |
| 2.4 | Synopsis | 66 |
| Chapter 3 | Epiphytic Community | 67 |
| 3.1 | Epiphytes identified in Grand Cayman vs. previous work | 67 |
| 3.2 | Other seagrass epiphytes | 71 |
| 3.3 | Community succession | 72 |
| 3.4 | Settlement/colonization of T. testudinum | 73 |

| 3.5 | Possible explanations for layered community | 76 |
|-----------|---|----|
| 3.6 | Exceptions in the order of colonization | 78 |
| Chapter 4 | Discussion and conclusion | 82 |
| 4.1 | Discussion | 82 |
| 4.2 | Conclusion | 89 |
| | | |

References

List of Tables

| Table 1.1 | List of previous studies done on contribution of <i>T</i> . <i>testudinum</i> epiphytes to sediment production | 2 |
|-----------|--|-------|
| Table 1.2 | Most recent estimates of <i>T. testudinum</i> growth in Grand Cayman lagoons | 9 |
| Table 2.1 | Coralline algae found on <i>Thalassia</i> in Grand Cayman lagoons | 20 |
| Table 2.2 | Foraminifera found on <i>Thalassia</i> in Grand Cayman lagoons | 21-22 |
| Table 2.3 | Diatoms found on Thalassia in Grand Cayman lagoons | 23-24 |
| Table 2.4 | Other epiphytes found on <i>Thalassia</i> in Grand Cayman lagoons | 25 |
| Table 2.5 | Epiphytes of <i>T. testudinum</i> that were found in sediment samples | 65 |
| Table 3.1 | Past studies of specific taxon of T. testudinum epiphytes | 69 |
| Table 3.2 | Epiphytes listed in studies that focus on how much sediment is generated by epiphytes on <i>T. testudinum</i> | 70 |

List of Figures

| Figure 1.1 | Morphology of Thalassia testudinum | 4 |
|------------------|---|-------|
| Figure 1.2 | Location of Study | 8 |
| Figure 1.3 | Thalassia testudinum in Pease Bay and Frank Sound | 11 |
| Figure 1.4 | Map of <i>Thalassia testudinum</i> in Grand Cayman lagoons | 12 |
| Figure 1.5 | Map of Grand Cayman indicating sample locations and density counts | 14 |
| Figure 1.6 | Diatom colonies | 18 |
| Figure 2.1-2.4 | Red Alga | 26-29 |
| Figure 2.5-2.16 | Foraminifera | 30-41 |
| Figure 2.17-2.27 | Diatoms | 42-52 |
| Figure 2.28 | Other Epiphytes | 53 |
| Figure 2.29 | Arthropods | 54 |
| Figure 2.30 | Sponges | 55 |
| Figure 2.31 | Coccoliths | 56 |
| Figure 2.32 | Dinoflagellates | 57 |
| Figure 2.33-2.34 | Borings | 58-59 |
| Figure 2.35-2.36 | Tubes | 60-61 |
| Figure 3.1 | Schematic diagram showing typical order of colonization of epiphytic material | 74 |
| Figure 3.2 | Diatoms on surface | 75 |
| Figure 3.3 | Diatoms Embedded in Red Alga | 79 |
| Figure 3.4 | <i>Thalassia testudinum</i> in South Sound and North Sound | 80 |

| Figure 4.1 | Sources of sediment in Grand Cayman lagoons | 83 |
|------------|---|----|
| Figure 4.2 | Thickness of coralline algae layers | 86 |

Chapter One - Introduction

1.1 Introduction

Seagrass has been a major influence on sedimentological processes since it first appeared in the Late Cretaceous (Nelsen and Ginsburg 1986). These angiosperms migrated from land into the Tethys Seaway during the breakup of Laurentia (Eva 1980). Little is known about the radiation of seagrass from that area into the temperate and tropical coastal areas it presently occupies all over the world. It is difficult to trace its history because examples of fossilized seagrasses are extremely rare (Ivany 1990). There are presently approximately 50 modern species of seagrasses documented. Each genus typically has a geographic location in which they are the dominant type of seagrass (Hemminga and Duarte 2000). The most common species of seagrass found in the Caribbean Sea is *Thalassia testudinum* Banks (ex König).

Previous studies (Land 1970; Patriquin 1972; Nelsen and Ginsburg 1986; Almasi *et al.* 1987; Bosence 1989; Frankovich and Zieman 1994; Koch 1999) have shown that *T. testudinum* affects sedimentation by (1) causing deposition of fine sediment that falls out of suspension when passing through the leaves of the plant, (2) stabilizing substrates with its complex root system, and (3) providing substrates suitable for epiphytes that, upon , death, become part of the sediment.

The contribution that epiphytic organisms make to sedimentation has not been fully defined. Results of past studies attempting to quantify this contribution have been highly variable (Table 1.1). The discrepancies in these results have been mainly attributed to differences in methodology and to a lesser degree, the environmental conditions between locations (Frankovich and Zieman 1994). There has been little effort to identify all of the

| Location | Epiphytic carbonate production (g CaCO ₃ m ⁻² yr ⁻¹) | Reference |
|-----------------|---|-----------------|
| Discovery Bay, | 40-180 | Land, 1970 |
| Jamaica | | |
| Barbados | 2 800 | Patriquin, 1972 |
| Florida Bay, | 30-303 | Nelsen, 1986 |
| Florida, U.S.A. | | |
| Florida Bay, | 81-482 | Bosence, 1989 |
| Florida, U.S.A. | | |
| Florida Bay, | 2-283 | Frankovich and |
| Florida, U.S.A. | | Zieman, 1994 |

| Table 1.1 - List of studies on contribution of T. testi | udinum |
|---|--------|
| epiphytes to sediment production. | |

skeletal epiphytes that are responsible for this generation of sediment. Without identification of the epiphytes present on blades of *T. testudinum*, it is impossible to fully comprehend how the environmental conditions of the lagoons affect the colonization of seagrass leaves and therefore, how much sediment could possibly be generated by epiphytes.

Using samples of *Thalassia testudinum* collected from various lagoons around Grand Cayman this study focuses on the epiphytes that live on their leaves with the specific aims of (1) identifying the constituent taxa, (2) determining their community structure, and (3) delineating their community succession. Potentially, these organisms can contribute a significant amount of sediment to the lagoons. The extent of this contribution is assessed by comparing the epiphytes found on the *T. testudinum* leaves with the skeletal components of the lagoonal sediment found around the plants as well as the bioclasts that have been reported by previous studies of lagoonal sediments from Grand Cayman (Li 1997; Li *et al.* 1997; Kalbfleisch and Jones 1998; Li *et al.* 1998; MacKinnon and Jones 2001; Beanish and Jones 2002).

1.2 Thalassia testudinum and its role in sedimentation

T. testudinum's morphology influences sedimentation. A *T. testudinum* shoot (Figure 1.1) will typically have 3-5 erect "grass-like" leaves that are 4-12 mm wide and up to 1 m long (cf. Patriquin 1972 his Fig. 1; Littler *et al.* 1989). The leaves rarely attain this length due to grazing animals such as sea urchins, herbivorous fishes, and green turtles (Ogden 1980; Hemminga and Duarte 2000). The leaves act to slow current speeds, which causes floating mud and silt sized particles to fall out of suspension and settle on the seafloor.



Figure 1.1 - Morphology of *T. testudinum*. A) *T. testudinum*, Frank Sound (note bite marks - arrows). B) Schematic *T. testudinum* showing morphology of the plant. Diagram modified from Patriquin (1972).

The shoots propagate from a system of roots and rhizomes that grow 5-10 cm beneath the sediment-water interface (Clinton 1981). The horizontal development of these rhizomes allows the grasses to expand into new areas with tough well-anchored runners (Littler *et al.* 1989). This network of rhizomes allows *T. testudinum* to stabilize shifting bottom sediments (Nelsen and Ginsburg 1986).

T. testudinum also influences sedimentation through its provision of habitat for various organisms that live on its leaves. Many of these epiphytes are calcareous, including coralline red algae, foraminifera, sponges, gastropods, bivalves, coccoliths, and ostracods. Non-calcareous epiphytes include diatoms, dinoflagellates, brown algae, annelid worms, and amphipods.

The epiphytes and the *T. testudinum* plants have a symbiotic relationship. The blades provide a substratum for biota to attach themselves to (Hemminga and Duarte 2000). Growth or attachment of organisms on the leaves usually starts at the tip and extends toward the base (Patriquin 1972). As this growth continues to expand toward the base of the plant, the density of the organisms at the tip is continually increasing. The 3-5 cm at the terminus of the leaf usually becomes completely encrusted with organisms and breaks off from the remaining younger part of the leaf that is still attached to the stem (Patriquin 1972).

The seagrass benefits from initial colonization of the leaves because the epiphytes reduce the amount of light reaching the leaf, maintaining the optimal level of surface irradiance needed to grow. The organisms benefit from the reduced current conditions in seagrass beds and from the substrate provided by the blades that allows the epiphytes to filter feed. There is a thin cuticle that covers the surfaces of *T.testudinum* and aids in the

transfer of gases and solutes from the seagrass to its surrounding environment (Tomlinson 1980). If this is completely covered by epiphytic material, these essential exchanges may not take place. As the epiphyte coverage becomes thicker, sunlight may also be unable to penetrate though the epiphytic material and the rate of diffusion of CO_2 (and other nutrients) is reduced, causing the leaf to die (Borowitzka and Lethbridge 1989).

1.3 Environmental Controls on Growth of T. testudinum

Factors limiting the growth of *T. testudinum* are temperature, light, turbidity, wave action, salinity, and an adequate rooting substrate (Moore 1963).

T. testudinum thrives in water temperatures of 20-30 °C (Phillips 1960). The plant may survive outside of this range for a short time but temperatures above or well below may eventually cause leaf mortality. Its preference for warmer tropical climates makes it the dominant species of the Caribbean, although it may also be found in some temperate climates (Hemminga and Duarte 2000).

T. testudinum's optimal growth depth is directly related to the amount of light needed for it to photosynthesize. The light requirement for seagrass is calculated as a percentage of surface irradiance that needs to be received for the plant to grow. The range needed by seagrasses is 4-29% with an average of ~11% (Hemminga and Duarte 2000). Turbidity, which will influence light penetration, is also an important factor controlling the growth of seagrass. *T. testudinum* will not grow deeper than 11 meters (Moore 1963).

T. testudinum can survive a broad range of salinities with a definitive optimum of 30‰ (Hemminga and Duarte 2000). Minimum and maximum salinity tolerances have been established through various experiments and observations. The range of salinities that *T. testudinum* has been found to withstand in lagoons throughout the United States is 10‰-40‰ (Phillips 1960; Moore 1963). Similar to temperature limits, *T. testudinum* can

withstand changes in salinity for short periods of time. MacMillan and Moseley (1967) determined experimentally that *T. testudinum* could tolerate salinities on the order of 60‰ without any significant decrease in growth. These experiments also showed that *T. testudinum* seems to adjust better to higher salinities than to lower levels.

Seagrasses are rooted plants, which means that in order for a *T. testudinum* meadow to thrive there must be adequate thickness of sediment for rooting on the lagoon floor. *T. testudinum* depends, to some degree, on nutrients from the sediment (Ogden and Zieman 1977). Deposition of fine sediments will increase in a lagoon that is inhabited by *T. testudinum* (Land 1970; Patriquin 1972; Almasi *et al.* 1987; Bosence 1989; Frankovich and Zieman 1994), which means the plant can influence its own expansion.

1.4 T. testudinum on Grand Cayman

The Cayman Islands (Figure 1.2), which comprise Grand Cayman, Little Cayman, and Cayman Brac, are located south of Cuba and north-west of Jamaica between 19° and 20° N and 79° and 82° W (Davies and Brunt 1994). Grand Cayman, the largest of the three islands, is approximately 35 km long and 14 km wide. The island is bordered by a semi-continuous reef with the exception of the west coast, which is the leeward coast. The coastline of Grand Cayman is characterized by numerous lagoons, or sounds as they are known locally.

T. testudinum meadows are one of the dominant facies found in North Sound, East Sound, South Sound, Pease Bay, and Frank Sound (Table 1.2). It thrives in these lagoons because of optimal temperature (28°C), water clarity (10-20 m), and salinity (35-38‰)



Figure 1.2 - Location of study. A) Map of Grand Cayman. B) Map showing location of Grand Cayman in the Caribbean Sea.

 ∞

| Lagoon | % of lagoon covered by T. testudinum | Reference |
|--------------------|---|----------------------------|
| North Sound | ~ 60 | MacKinnon and Jones 2001 |
| South Sound | 51.2 | Beanish et al. 2002 |
| Pease Bay | 19.8 | Kalbfleisch and Jones 1998 |
| Frank Sound | 31.8 | Kalbfleisch and Jones 1998 |
| East Sound (South) | 38.3 | Tongpenyai and Jones 1991 |
| East Sound (North) | 14.9 | Tongpenyai and Jones 1991 |

 Table 1.2 – Most recent estimates of T. testudinum coverage in Grand Cayman lagoons.

conditions (Moore 1963; Kalbfleisch and Jones 1998). There is also adequate cover of sediment in the lagoons for *T. testudinum* to expand its rooting systems. Tongpenyai and Jones (1991) showed that in East Sound, Pease Bay, and South Sound, the extension of the *T. testudinum* meadows between 1971 and 1985 resulted in a decrease in the area of the Bare Sand Facies. This trend was shown to have continued in a study by Beanish and Jones (2002) that used digital image analysis of air photos to map the facies present in South Sound in 1971 and 1992. These two facies appear to have an inverse relationship. *T. testudinum* influences the sedimentation rates in the lagoon usually resulting in an increase in the amount of fine sediment generated and retained in the lagoon, therefore increasing the area covered by bare sand. This increase in sediment then allows for the expansion of *T. testudinum* meadows.

The *T. testudinum* communities are found lining the shoreward edge of each lagoon (Figure 1.3), with the exception of North Sound, where it is mainly found in the interior of the lagoon (Roberts 1994; MacKinnon and Jones 2001). The meadows can extend out as far as the zone located just behind the reef crest (Figure 1.3 and 1.4) referred to as the rubble or reef shoal zone (Kalbfleisch and Jones 1998; MacKinnon and Jones 2001; Beanish *et al.* 2002). Density of the *T. testudinum* shoots has been broken down into: very dense (>2000 shoots/m²), dense (500-2000 shoots m²), medium (250-500 shoots/m²), and sparse (<250 shoots/m²) (Beanish and Jones 2002).



Figure 1.3 - A) Pease Bay, note *Thalassia testudinum* meadows. B) Frank Sound, dense *T. testudinum* growth near shore.



Figure 1.4 - Map of *T. testudinum* in Grand Cayman lagoon. A) *T. testudinum* coverage in Pease Bay and Frank Sound. Modified from Kalbfleisch and Jones (1998). B) *T. testudinum* coverage in South Sound. Modified from Beanish and Jones (2002). C) *T. testudinum* coverage in East Sound. Modified from Rigby and Roberts (1976). D) *T. testudinum* coverage in North Sound. Modified from Rigby and Roberts (1976).

1.5 Field Methods

Seagrass was collected from South Sound, Pease Bay, Frank Sound, East Sound, and North Sound (Figure 1.4) in November 2003. The samples were taken at shallow (0.2-0.5 m) and deeper (1.1-2.5 m) intervals from all but North Sound, where only shallow samples were obtained. Access to North Sound was limited during the study and samples were taken from a shallow interval near the mangrove swamps that fringe the northwest corner of the lagoon. Dried samples of *T. testudinum* were also obtained from the beach in South Sound and Pease Bay.

At all sample locations, water depth and distance from shore was recorded and samples were placed in airtight sample bags with a few drops of seawater. Density counts were conducted in South Sound, Pease Bay, and Frank Sound (Figure 1.4). These were performed at the same shallow and deep intervals using a 0.5×0.5 m quadrat that was randomly positioned on the seafloor. Seagrass blades were clipped at the sediment-water interface and counted on shore.

Sediment samples were obtained from South Sound, Pease Bay, and Frank Sound. The sediment samples collected were ~ 0.5 kg. These samples were taken at the sediment water interface, in between the base of the *T. testudinum* plants at a depth of ~ 0.2 m.

The outer depth of *T. testudinum* growth in Grand Cayman (~2.5 m) allowed all field work to be conducted while snorkeling. Observations of associated flora and fauna were taken at each sample location.





1.6 Sample Preparation and Analyses:

Various methods of sample preparation were employed in this study. Each method was developed through trial and error with the intent of studying the epiphytes *in situ* wherever possible. Analyses of the samples was performed primarily with the JEOL 6301F (Field Emission Scanning Electron Microscope). Petrographic microscopes were also used when necessary.

The primary method used in preparation was to rinse the samples with distilled water under a compound microscope. The initial visual inspection of the sample under the compound microscope was needed to pick the specimens with epiphytes that had remained relatively intact and in place on the blade of grass. Most samples were rinsed with distilled water if there was sand from the sample bag stuck to the blades. Following this, samples would be left for approximately 24 hours to dry. The blades of grass, with epiphytic material still attached, were then cut into approximately 1 cm segments and mounted onto 1.25 cm diameter SEM stubs with carbon tape. In some cases, the epiphytic crust would lift up from the surface of the blade in which case, a silver paint was used to "glue" the crust back down. This method of sample preparation proved to be the most effective in viewing the epiphytic material *in situ* on the blade of grass.

To view cross sections of the *T. testudinum* with its epiphytic crust samples required mounting of the seagrass in epoxy. The epoxy slabs were sliced into thin sections cut length-wise along the blade. The thin slices were mounted onto a slide and viewed under a light microscope to pick out the slides that had the most intact epiphytes. These slides were mounted onto an SEM stub, sputtered with gold and examined on the SEM.

The bottom of the epiphytic crust and a "clean" surface of *T. testudinum* were also examined in this study. In this case, samples were placed in the freezer overnight and, when frozen, the epiphytic material was removed from the blade. The "clean" blades of *T. testudinum* are not completely free of epiphytic material as some organisms remain on the blade after removing the main epiphytic crust. The epiphytic material is extremely fragile and needs to be frozen if it is to be kept intact when scraping it off the seagrass blade. After removing the epiphytes, both the epiphytic crust and the "clean" blade were dried and then mounted on SEM stubs.

Eleven sediment samples were also examined on the SEM to see if the epiphytes identified on *T. testudinum* were visible in the sediment. Three samples; one from South Sound and two from Pease Bay were prepared before sieving to see whether any of the larger epiphytes (e.g. larger foraminifera, *Spirobis* worm tubes, red alga) were visible in the sediment. The remaining sediment was sieved to less than 109µm and then placed on SEM stubs for analysis. These eight samples consisted of two stubs from each sample collected from: South Sound, Frank Sound, and two locations in Pease Bay.

1.7 Identification Process

The epiphytes living on the *T. testudinum* leaves that have calcareous or siliceous skeletons include various species of coralline algae, foraminifera, diatoms and several other organisms, considered to be minor epiphytes. Coralline algae were identified using pre-existing literature on *T. testudinum* epiphytes (Humm 1964; Land 1970; Patriquin 1972; Nelsen and Ginsburg 1986; Bosence 1989; Frankovich and Zieman 1994; Perry and Beavington-Penney 2005). The foraminifera, diatom, and other minor epiphytes were

identified by comparison with taxa previously identified and described by d'Orbigny (1846), Heron-Allen and Earland (1915), Cushman (1924), Cushman (1931), Boltovskoy and Wright (1976), Hofker (1976), Buzas *et al.* (1977), McIntire and Moore (1977), Werner (1977), Cushman (1980), Guttinger (1986a; 1986b; 1986c; 1986d; 1986e; 1986f), Snoeijs (1993), Snoeijs and Vilbaste (1994), Snoeijs and Paotapova (1995), Snoeijs and Kasperoviciene (1996), Snoeijs and Balashova (1998), Wilson (1998), Stefano *et al.* (2000), Mann (2002), Javaux and Scott (2003), and Sar *et al.* (2003). Additional assistance in the identification process was provided by Dr. A. Wolfe (Earth and Atmospheric Sciences Department, University of Alberta) and Dr. F. Clark (Earth and Atmospheric Sciences Department, University of Alberta).

Approximately 15% of foraminifera and 15% of diatom species were not identified because (a) some were juvenile specimens (e.g. foraminifera – only proloculus and one or two chambers developed), (b) there was difficulty seeing all angles of specimens on the SEM, (c) some forms present in sample have not been previously described, (d) there was a lack of specimens, or (e) the quality of specimens was poor. Some diatoms exist on the *T. testudinum* in colonies and cannot be identified as their diagnostic features were not visible (Figure 1.6).

The relative abundance was estimated for each epiphytic specimen identified in this study. These are qualitative estimates that were performed using a four point scale (i.e. VC = very common, C = common, R = rare, VR = very rare). Fifty-three samples were prepared and examined on the SEM. The abundance estimates were based on how often a species was seen during approximately 100 hours of examination on the SEM and



Figure 1.6 - Diatom colonies. Note that only the girdles are visible.

imaged on 1383 photomicrographs from those samples. For example, a species identified as being very common (VC) would be seen on virtually every sample examined and would be seen more than once on an individual sample. In contrast, taxa classified as very rare (VR) were only seen once or twice throughout the entire study.

Chapter Two - Results

2.1 Epiphytic Biota

Epiphytes living on the *Thalassia testudinum* in the Grand Cayman lagoons are numerous and diverse. Overall, the epiphytes are dominated by coralline algae, foraminifera, and diatoms. This biota includes three species of crustose coralline algae (Table 2.1, Figures 2.1-2.4), 72 species of foraminifera (Table 2.2, Figures 2.5-2.16), and 61 species of diatoms (Table 2.3, Figures 17-27). Other, less abundant epiphytes include sponges, gastropods, ostracods, and coccoliths (Table 2.4, Figures 2.28-2.31). Overall, ~85% of the species have calcareous or siliceous skeletons (this includes coralline algae, with cell walls composed of CaCO₃). The remaining 15% non-skeletal organisms include dinoflagellates (Table 2.4, Figure 2.32), brown algae, worms (Table 4, Figure 2.28C-D), and several species of cyanobacteria.

Table 2.1 – Coralline algae found on *Thalassia* in Grand Cayman lagoons. VC = very common, C = common, R = rare, VR = very rare

| Таха | Abundance | Figure |
|---|-----------|----------|
| Hydrolithon farinosum (Lamouroux) Penrose & | VC | 2.1, 2.4 |
| Chamberlain | | |
| Indeterminate R01 | С | 2.2 |
| Indeterminate R02 | R | 2.3 |

| Taxa | Abundance | Figure |
|---|-----------|--------------|
| Anomalina sp | C | <u> </u> |
| Raagina aff nhillinninenis Cushman | R | 2.JA 2.5R |
| Ragging sp. 1 | P | 2.50 |
| Bagging sp. 2 | R | 2.50 |
| Candeina sp. 2 | D N | 2.5D 2.5E |
| Cornuspira sp. | VP | 2.5E |
| Discorbis of chasteri Heron-Allen and Farland | P | 2.51 |
| Discorbis 2 chasteri Heron-Allen and Earland | C | 2.0A 2.6B |
| Discorbis granulosa Heron-Allen and Borland | C | 2.00 |
| Discorbis of murravi Heron-Allen and Farland | C | 2.0C 2.6D |
| Discorbis sn 1 | R | 2.0D 2.6F |
| Discorbis sp. 7 Discorbis sp. 2 | R | 2.0E |
| Discorbis sp. 2 Discorbis sp. 3 | R | 2.01 |
| Elnhidium sp. 1 | VR | 2.7R |
| Elphidium sp. 2 | VR | 2.70 |
| Elphidium sp. 2 Elphidium sp. 3 | VR | 2.70 |
| Globigering conglobata Cushman | C | 2.7E |
| Globigering dubig Cushman | C | 2.7E |
| Globigering sellii Borsetti | R | 2.8A |
| Globigering bulloides d'Orbigny | VR | 2.8B |
| <i>Globigerina</i> sp. 1 | R | 2.8C |
| <i>Globigerina</i> sp. 2 | R | 2.8D |
| Globigerina sp. 3 | R | 2.8E |
| Globigerina sp. 4 | VR | 2.8F |
| Globigerina sp. 5 | R | 2.9A |
| Globigerina sp. 6 | R | 2.9B |
| Globigerina sp. 7 | R | 2.9C |
| Globorotalia ? | VR | 2.9D |
| Lamarckina cf. haliotidea Heron-Allen and | VR | 2.9E |
| Earland | | |
| Lamarckina sp. 1 | VR | 2.9F |
| Lamarckina sp. 2 | VR | 2.10A |
| Lamarckina? 3 | VR | 2.10B |
| Miliammina circularis Heron-Allen and Earland | VR | 2.10C |
| <i>Miliolinella oblonga</i> Montago | R | 2.10D |
| Miliolinella sp. 1 | R | 2.10E |
| Miliolinella sp. 2 | R | 2.10F |
| Planispira?1 | VR | 2.11A |
| Planorbulina acervalis Brady | VR | 2.11B |
| Pyrgo ? | VR | 2.11C |
| Quinqueloculina costata d'Orbigny | С | 2.11D |
| <i>Ouinqueloculina laevigata</i> d'Orbigny | VR | 2.11E |

Table 2.2 – Foraminifera found on *Thalassia* in Grand Cayman lagoons. VC = very common, C = common, R = rare, VR = very rare

Table 2.2 – Foraminifera found on *Thalassia* in Grand Cayman lagoons VC = very common, C = common, R = rare, VR = very rare

| Taxa | Abundance | Figure |
|--|-----------|--------|
| Quinaueloculina longirostra d'Orbigny | VR | 2,11F |
| Quinqueloculing poevang d'Orbigny | C | 2.111 |
| Quinqueloculina? lamarckiana d'Orbigny | R | 2.12R |
| Quinqueloculina sp. 1 | VR | 2.120 |
| Quinqueloculina sp. 2 | R | 2.120 |
| Quinqueloculina ? 3 | R | 2.12E |
| Quinaueloculina? 4 | VR | 2.12E |
| Rosalina floridana Cushman | C | 2.13A |
| Rosalina sp. | R | 2.13B |
| Sphaeroidina bulloides d'Orbigny | R | 2.13C |
| Spirilling vivipara Ehrenberg | R | 2.13D |
| Spirillina sp. 1 | C | 2.13E |
| Spirillina sp. 2 | Č | 2.13F |
| Triloculina bermudezi Acosta | Ċ | 2.14A |
| Triloculina cf. subrotunda Montagu | R | 2.14B |
| Triloculina circularis Bornemann | R | 2.14C |
| <i>Triloculina</i> sp. | VR | 2.14D |
| Trochammina globigeriniformis Parker and | С | 2.14E |
| Jones | | |
| <i>Trochammina siphonifera</i> Cushman | VR | 2.14F |
| Valvulineria sp. | R | 2.15A |
| Indeterminate F01 | VR | 2.15B |
| Indeterminate F02 | VR | 2.15C |
| Indeterminate F03 | VR | 2.15D |
| Indeterminate F04 | VR | 2.15E |
| Indeterminate F05 | R | 2.15F |
| Indeterminate F06 | VR | 2.16A |
| Indeterminate F07 | VR | 2.16B |
| Indeterminate F08 | VR | 2.16C |
| Indeterminate F09 | VR | 2.16D |
| Indeterminate F10 | VR | 2.16E |
| Indeterminate F11 | VR | 2.16F |

| Taxa | Abundance | Figure |
|--|-----------|----------------|
| Achnanthes pericava Carter | R | 2.17A |
| Amphora sp. 1 | С | 2.17B |
| Amphora sp. 2 | С | 2.17C |
| Amphora sp. 3 | R | 2.17D |
| Amphora sp. 4 | VR | 2.17E |
| Amphora sp. 5 | VR | 2.17F |
| Amphora sp. 6 | VR | 2.18A |
| Amphora sp. 7 | VR | 2.18B |
| Biddulphia sp. | R | 2.18C |
| Campylodiscus sp. | R | 2.18D |
| Cocconeis placentula Ehrenberg | VC | 2.18E-F, 2.19A |
| Cocconeis convexa Giffen | R | 2.19B |
| Cocconeis scutellum Ehrenberg | С | 2.19C |
| Cocconeis sp. 1 | С | 2.19D |
| Cocconeis sp. 2 | R | 2.19E |
| Cocconeis sp. 3 | R | 2.19F |
| Cyclotella atomus Hustedt | R | 2.20A |
| Diploneis stroemii Hustedt | VR | 2.20B |
| Fragilaria sp. | R | 2.20C |
| Gomphonemopsis exigua var. platypus Østrop | R | 2.20D |
| Haslea ostrearia Gaillon ? | R | 2.20E |
| Mastogloia pusilla var. subcapitata Hustedt | С | 2.20F |
| Mastogloia erthrea Grunow | VC | 2.21A |
| Mastogloia aspera Peragallo | R | 2.21B |
| Mastogloia corsicana Grunow | VC | 2.21C |
| Mastogloia smithii Grunow | VC | 2.21D |
| Mastogloia fimbriata (Brightwell) Cleve | С | 2.21E |
| Mastogloia aff. fimbriata (Brightwell) Cleve | С | 2.21F, 2.22A |
| Mastogloia binotata (Grunow) Cleve | R | 2.22B |
| Mastogloia lacrimata Voigth | R | 2.22C |
| Mastogloia asperuloides Hustedt | R | 2.22D |
| Mastogloia cocconeiformis Grunow | С | 2.22E |
| Mastogloia sp. 1 | R | 2.22F |
| Mastogloia sp. 2 | С | 2.23A |
| Mastogloia sp. 3 | VR | 2.23B |
| Mastogloia sp. 4 | С | 2.23C |
| Mastogloia sp. 5 | С | 2.23D |
| Mastogloia sp. 6 | R | 2.23E |
| Mastogloia sp. 7 | R | 2.23F |
| Mastolgoia sp. 8 | R | 2.24A |
| Mastogloia sp. 9 | С | 2.24B |
| Mastogloia sp. 10 | С | 2.24C |

Table 2.3 – Diatoms found on *Thalassia* in Grand Cayman lagoons. VC = very common, C = common, R = rare, VR = very rare
| Taxa | Abundance | Figure |
|--|-----------|--------|
| Mastogloia sp. 11 | С | 2.24D |
| Navicula sp. | R | 2.24E |
| Nitzschia constricta Kützing | R | 2.24F |
| Nitzschia improvisa Simonsen | R | 2.25A |
| Rhoicosphenia sp. | R | 2.25B |
| Rhopaloidia gibberula (Smith) Krammer | С | 2.25C |
| Synedra sigma Kützing | С | 2.25D |
| Synedra tabulata var. acuminata Grunow | R | 2.25E |
| Synedra sp. | R | 2.25F |
| Indeterminate D01 | VR | 2.26A |
| Indeterminate D02 | R | 2.26B |
| Indeterminate D03 | R | 2.26C |
| Indeterminate D04 | VR | 2.26D |
| Indeterminate D05 | R | 2.26E |
| Indeterminate D06 | VR | 2.26F |
| Indeterminate D07 | VR | 2.27A |
| Indeterminate D08 | R | 2.27B |
| Indeterminate D09 | VR | 2.27C |
| Indeterminate D10 | VR | 2.27D |

Table 2.3 – Diatoms found on *Thalassia* in Grand Cayman lagoons. VC = very common, C = common, R = rare, VR = very rare

Table 2.4 – Other epiphytes found on *Thalassia* in Grand Cayman lagoons. VC = very common, C = common, R = rare, VR = very rare

| vc - very common, c - common, K - rare, vK - very rare | | | |
|--|-----------|-----------|--|
| Таха | Abundance | Figure | |
| Gastropods | R | 2.28A-B | |
| Serpulid worm tubes | С | 2.28C-D | |
| Ostracods | R | 2.29A-D | |
| Amphipod | R | 2.29E-F | |
| Sponge spicules | С | 2.30A-F | |
| Coccoliths | R | 2.31A-D | |
| Dinoflagellates | R | 2.32A-F | |
| Borings and tubes | С | 2.33-2.36 | |



FIGURE 2.1: Red Alga

- A) Hydrolithon farinosum (Lamouroux) Penrose & Chamberlain, on Thalassia (X), note conceptacles (Y), ~0.2 m depth Pease Bay
- B) *H. farinosum* (Lamouroux) Penrose & Chamberlain, ~0.2 m depth, South Sound C) 2 layers of *H. farinosum* (Lamouroux) Penrose & Chamberlain
- first layer to colonize the leaf (X), second layer (Y), ~0.2 m depth, South Sound D) 2 layers of *H. farinosum* (Lamouroux) Penrose & Chamberlain, ~0.2 m depth,
- South Sound E) Close up of conceptacle, ~0.2 m depth, Pease Bay
- F) Close-up of previous image, note HMC crystals that compose the cell walls



FIGURE 2.2: Red Alga

- A) Indeterminate (R01) and Hydrolithon farinosum (Lamouroux) Penrose & Chamberlain (Y), sample taken from beach, South Sound

- B) Indeterminate (R01), ~0.2 m depth, South Sound
 C) Two layers of Indeterminate (R01), ~0.2 m depth, Pease Bay
 D) Indeterminate (R01), sample taken from beach, South Sound
 E) Close-up on algae conceptacle, ~1.8 m depth, Frank Sound
 F) Close-up on algae conceptacles, ~1.8 m depth, Frank Sound



FIGURE 2.3: Red Alga

- A) Coralline algae (Indeterminate R02) on *Thalassia* (X), ~1.8 m depth, Frank Sound B) Indeterminate (R02), ~1.8 m depth, Frank Sound C) Indeterminate (R02), ~1.8 m depth, Frank Sound D) Indeterminate (R02), close up of surface, ~1.8 m depth, Frank Sound E) Indeterminate (R02), conceptacles, ~1.8 m depth, Frank Sound F) Indeterminate (R02), two layers, ~1.8 m depth, Frank Sound



FIGURE 2.4: Red Alga

- A) Cross-section through coralline alga (X) and seagrass leaf (Y), ~0.2 m depth, South Sound
- B) Close-up on previous image
- C) Cross-section through coralline alga and seagrass leaf, note algal encrusts both sides of the seagrass leaf, ~0.2 m depth, South Sound
- D) Cross section through two algae conceptacles, ~0.2 m depth, South Sound
- E) Cross section through algae 'hooked' around the tip of the seagrass leaf, ~0.2 m depth, South Sound
- F) Close-up on conceptacle in previous image, ~0.2 m depth, South Sound



FIGURE 2.5: Foraminifera A) Anomalina sp., note attachment (X), ~0.5 m depth, North Sound B) Baggina aff. phillippinenis Cushman, ~0.2 m depth, Pease Bay C) Baggina sp. 1, ~0.5 m depth, North Sound D) Baggina sp. 2, ~1.5 m depth, South Sound E) Candeina sp., ~1.5 m depth, South Sound F) Cornuspira sp., ~0.2 m depth, South Sound



FIGURE 2.6: Foraminifera

- A) Discorbis cf. chasteri Heron-Allen and Earland, ~1.8 m depth, Frank Sound
- B) Discorbis cf. chasteri Heron-Allen and Earland, ~0.5 m depth, North Sound
 C) Discorbis granulosa Heron-Allen and Borland, ~0.2 m depth, Pease Bay
 D) Discorbis cf. murrayi Heron-Allen and Earland, ~0.2 m depth Pease Bay
- E) Discorbis sp. 1, \sim 0.2 m depth, South Sound
- F) Discorbis sp. 2, sample taken from beach, Pease Bay



- A) Discorbis sp. 3, ~0.5 m depth, North Sound
 B) Elphidium sp. 1, ~0.2 m depth, Pease Bay
 C) Elphidium sp. 2, ~0.2 m depth, Pease Bay
 D) Elphidium sp. 3, ~2.1 m depth, South Sound
 E) Globigerina conglobata Cushman, ~0.2 m depth, Pease Bay
 F) Globigerina dubia Cushman, ~0.2 m depth, Pease Bay





- **FIGURE 2.9: Foraminifera** A) *Globigerina* sp. 5, ~0.2 m depth, Pease Bay

- B) Globigerina sp. 5, ~0.2 m depth, Fease Bay
 B) Globigerina sp. 6, ~0.2 m depth, South Sound
 C) Globigerina ? 7, ~0.2 m depth, Pease Bay
 D) Globigerina ? 8, ~1.5 m depth, South Sound
 E) Lamarckina cf. haliotidea Heron-Allen and Earland, ~0.2 m depth, Pease Bay
 F) Lamarckina sp. 1, ~2.1 m depth, South Sound



FIGURE 2.10: Foraminifera

- A) Lamarckina sp. 2, ~0.2 m depth, South Sound
- B) Lamarckina sp. 3, ~0.5 m depth, North Sound
- C) Miliammina circularis Heron-Allen and Earland, ~2.1 m depth, South Sound
- D) Miliolinella oblonga Montago, ~0.5 m depth, North Sound
 E) Miliolinella sp. 1, ~2.6 m depth, East Sound
 F) Miliolinella sp. 2, ~1.8 m depth, Frank Sound



- FIGURE 2.11: Foraminifera A) *Planispira* ?, ~0.2 m depth, Pease Bay B) *Planorbulina acervalis* Brady, ~2.1 m depth, South Sound C) *Pyrgo* ?, ~0.2 m depth, Pease Bay
- D) Quinqueloculina costata d'Orbigny, ~2.1 m depth, South Sound
 E) Quinqueloculina laevigata d'Orbigny, ~0.5 m depth, North Sound
- F) Quinqueloculina longirostra d'Orbigny, ~0.2 m depth, Pease Bay



FIGURE 2.12: Foraminifera

- A) Quinqueloculina poeyana d'Orbigny, ~2.1 m depth, South Sound
 B) Quinqueloculina cf. lamarckiana d'Orbigny, ~0.2 m depth, Pease Bay
- B) Quinqueloculina ci. tamarckiana d'Orolgity, ~0.2 ft
 C) Quinqueloculina sp. 1, ~2.1 m depth, South Sound
 D) Quinqueloculina sp. 2, ~0.2 m depth, Pease Bay
 E) Quinqueloculina ? 3, ~2.1 m depth, South Sound
 F) Quinqueloculina ? 4, ~0.2 m depth, South Sound



FIGURE 2.13: Foraminifera

- A) Rosalina floridana Cushman, ~1.8 m depth, Frank Sound B) Rosalina sp., ~0.2 m depth, South Sound
- C) Sphaeroidina bulloides d'Orbigny, ~0.2 m depth, Pease Bay
 D) Spirillina vivipara Ehrenberg, ~0.2 m depth, Pease Bay
 E) Spirillina sp. 1, ~0.2 m depth, South Sound
 F) Spirillina sp. 2, ~0.2 m depth, Pease Bay



FIGURE 2.14: Foraminifera

- A) Triloculina bermudezi Acosta, ~0.2 m depth, Pease Bay
- B) Triloculina cf. subrotunda Montagu, ~0.5 m depth, North Sound

- C) Triloculina circularis Bornemann, ~0.2 m depth, North Sound
 D) Triloculina sp., ~0.2 m depth, Pease Bay
 E) Trochammina globigeriniformis Parker and Jones, ~0.2 m depth, Pease Bay
- F) Trochammina siphonifera Cushman, ~0.2 m depth, Pease Bay



FIGURE 2.15: Foraminifera A) Valvulineria sp., ~2.6 m depth, East Sound B) Indeterminate (F01), ~ 0.2 m depth, Pease Bay C) Indeterminate (F02), ~ 0.2 m depth, South Sound D) Indeterminate (F03), ~ 0.2 m depth, South Sound E) Indeterminate (F04), ~ 0.2 m depth, Pease Sound F) Indeterminate (F05), ~ 0.2 m depth, Pease Sound

40



FIGURE 2.16: Foraminifera

- A) Indeterminate (F06), ~1.8 m depth, Frank Sound
- B) Indeterminate (F00), ~1.8 m depth, Frank Sound
 B) Indeterminate (F07), ~0.2 m depth, South Sound
 C) Indeterminate (F08), ~0.2 m depth, Pease Bay
 D) Indeterminate (F09), ~0.5 m depth, North Sound
 E) Indeterminate (F10), ~1.8 m depth, Frank Sound
 F) Indeterminate (F11), ~0.2 m depth, South Sound



FIGURE 2.17: Diatoms A) Achnanthes pericava Carter, ~ 0.2 m depth, Pease Bay B) Amphora sp. 1, ~0.2 m depth, South Sound C) Amphora sp. 2, ~1.8 m, depth, Frank Sound D) Amphora sp. 3,~0.5 m depth, North Sound E) Amphora sp. 4, ~1.5 m depth, Frank Sound F) Amphora sp. 5, ~0.2 m depth, South Sound



- FIGURE 2.18: Diatoms A) Amphora sp. 6, ~2.1 m depth, South Sound B) Amphora sp. 7, ~0.2 m depth, South Sound C) Biddulphia sp., ~0.5 m depth, North Sound D) Campylodiscus sp., ~0.2 m depth, East Sound E) Cocconeis placentula Ehrenberg, ~1.5 m depth, Pease Bay F) Cocconeis placentula Ehrenberg, ~0.2 m depth, South Sound



FIGURE 2.19: Diatoms

- A) Cocconeis placentula Ehrenberg, ~1.5 m depth, Pease Bay B) Cocconeis convexa Giffen, ~0.5 m depth, North Sound C) Cocconeis scutellum Ehrenberg, ~2.6 m depth East Sound D) Cocconeis sp. 1, ~1.8 m depth, Frank Sound E) Cocconeis sp. 2, ~1.8 m depth, Frank Sound F) Cocconeis sp. 3, ~1.5 m depth, Pease Bay

44



FIGURE 2.20: Diatoms

- A) Cyclotella atomus Hustedt, ~0.5 m depth, North Sound
 B) Diploneis stroemii Hustedt, ~2.1 m depth, South Sound
 C) Fragilaria sp., sample taken from beach, South Sound

- D) Gomphonemopsis exigua var. platypus Østrop, ~0.2 m depth, Pease Bay E) Haslea ostrearia Gaillon ? (X), ~0.2 m depth, South Sound
- F) Mastogloia pusilla var. subcapitata Hustedt, ~0.2 m depth, South Sound



FIGURE 2.21: Diatoms

- A) Mastogloia erthrea Grunow, ~0.2 m depth, Pease Bay B) Mastogloia aspera Peragallo, ~0.2 m depth, Pease Bay C) Mastogloia corsicana Grunow, ~1.8 m depth, Frank Sound D) Mastogloia smithii Grunow, ~0.2 m depth, Pease Bay E) Mastogloia fimbriata (Brightwell) Cleve, ~1.8 m depth, Frank Sound F) Mastogloia aff. fimbriata (Brightwell) Cleve, ~1.5 m depth, Pease Bay



- FIGURE 2.22: Diatoms A) Mastogloia aff. fimbriata (Brightwell) Cleve, ~1.8 m depth, Frank Sound B) Mastogloia binotata (Grunow) Cleve, ~1.5 m depth, Pease Bay

- C) Mastogloia binotata (Grunow) Cleve, ~1.5 in depth, Pease Bay
 C) Mastogloia lacrimata Voigth, ~1.8 m depth, Pease Bay
 D) Mastogloia asperuloides Hustedt, 1.8 m depth, Frank Sound
 E) Mastogloia cocconeiformis Grunow, ~2.1 m depth, South Sound
 F) Mastogloia sp. 1, ~0.2 m depth, Pease Bay



FIGURE 2.23: Diatoms

A) Mastogloia sp. 2, ~0.2 m depth, Pease Bay B) Mastogloia sp. 3, ~0.2 m depth, Pease Bay C) Mastogloia sp. 4, ~2.1 m depth, South Sound D) Mastogloia sp. 5, ~0.2 m depth, Pease Bay E) Mastogloia sp. 6, ~1.5 m depth, Pease Bay F) Mastogloia sp. 7, ~1.8 m depth, Frank Sound



- FIGURE 2.24: Diatoms A) Mastogloia sp. 8, ~0.2 m depth, South Sound B) Mastogloia sp. 9, ~0.3 m depth, Frank Sound C) Mastogloia sp. 10, ~0.2 m depth, Pease Bay D) Mastogloia sp. 11, ~1.8 m depth, Frank Sound E) Navicula sp., ~0.2 m depth, South Sound F) Nitzschia constricta Kützing, ~0.2 m depth, Pease Bay



- FIGURE 2.25: Diatoms A) Nitzschia improvisa Simonsen, ~2.1 m depth, South Sound B) Rhoicosphenia sp., ~0.2 m depth, Pease Bay
- C) Rhopaloidia gibberula (Smith) Krammer, ~2.1 m depth, South Sound
- D) Synedra sigma Kützing, ~0.2 m depth, South Sound
 E) Synedra tabulata var. acuminata Grunow, ~0.2 m depth, Pease Bay
- F) Synedra sp., ~0.2 m depth, Pease Bay



FIGURE 2.26: Diatoms

- A) Indeterminate (D01), ~0.3 m depth, Frank Sound
- B) Indeterminate (D01), ~0.5 m depth, Frank Sound
 B) Indeterminate (D02) (X), sample taken from beach, South Sound
 C) Indeterminate (D03), ~1.5 m depth, Pease Bay
 D) Indeterminate (D04), ~0.2 m depth, Pease Bay
 E) Indeterminate (D05), ~0.2 m depth, Pease Bay
 F) Indeterminate (D06), ~1.5 m depth, South Sound



FIGURE 2.27: Diatoms

- A) Indeterminate (D07), ~2.6 m depth, East Sound B) Indeterminate (D08), ~2.1 m depth, South Sound C) Indeterminate (D09), ~0.5 m depth, North Sound D) Indeterminate (D10), ~2.1 m depth, South Sound



FIGURE 2.28: Other Epiphytes

- A) Gastropods, ~0.2 m depth, South Sound
 B) Gastropods, ~1.8 m depth, Frank Sound
 C) Worm tube (*Spirobis* sp.), sample taken from beach, South Sound
 D) Worm tube (*Spirobis* sp.), sample taken from beach, South Sound



FIGURE 2.29: Athropods

- A) Ostracod, ~0.2 m depth, South Sound
 B) Ostracod, ~0.2 m depth, Pease Bay
 C) Ostracod, sample taken from beach, Pease Bay
 D) Ostracod, ~1.5 m depth, Pease Bay
 E) Amphipod, ~0.5 m depth, North Bay
 F) Amphipod, ~0.5 m depth, North Bay





- FIGURE 2.31: Coccoliths A) Emiliania huxleyi (Wallich) Schiller, distal view, ~2.6 m depth, East Sound B) Emiliania huxleyi (Wallich) Schiller, ~2.1 m depth, South Sound C) Indeterminate, ~0.2 m depth, South Sound

- D) Indeterminate, ~1.8 m depth, Frank Sound



FIGURE 2.32: Dinoflagellates

- A) Prorocentrum sp. 1, ~0.2 m depth, Pease Bay
 B) Prorocentrum sp. 2, ~0.2 m depth, Pease Bay
 C) Prorocentrum sp. 3, ~0.2 m depth, Pease Bay
 D) Close-up on previous image
 E) Alexandrium sp., ~2.1 m depth, South Sound
 F) Indeterminate, ~0.2 m depth, Pease Bay



FIGURE 2.33: Borings

- A) Borings in underside of coralline algae, sample taken from beach, South Sound
- B) Close-up of previous image, note branching patternC) Close-up of previous image showing mucus lining the borings
- D) Close-up of previous image
 E) Borings in underside of coralline algae, sample taken from beach, Pease Bay
 F) Close-up of previous image, note the mucus lining is partially missing



- FIGURE 2.34: Borings A) Large boring in coralline algae with several smaller branching borrows, depth ~1.5 m, Pease Bay
- B) Close-up of previous, note mucus lining
 C) Boring in coralline algae, depth ~1.5 m, Pease Bay
 D) Boring in coralline algae, depth ~1.5 m, Pease Bay
- E) Fungal borings in coralline algae, depth ~1.5 m, South Sound
- F) Close-up of previous


FIGURE 2.35: Tubes A) Tube network, depth ~0.2 m, Pease Bay B) Close-up of previous image C) Tube network within coralline algae, depth ~1.8 m, Frank Sound

D) Close-up of previous image

- E) Various tubes on and coming out of coralline algae, depth ~1.8 m, Frank Sound
- F) Close-up of previous image (X)



FIGURE 2.36: Tubes A) Raised aragonitic tube on coralline algae, depth ~1.8 m, Frank Sound B) Close-up of previous image C) Tube network, depth ~0.2 m, Pease Bay D) Close-up of previous image E) Tube network, depth ~0.2 m, Pease Bay F) Close-up of previous image (X)

2.2 Dominant Taxa

2.2.1 Coralline Alga

The two most common epiphytes, in terms of surface area coverage, are *Hydrolithon farinosum* (Lamouroux) Penrose & Chamberlain and an indeterminate coralline alga (Indeterminate R01). These two species form a light pink 'crust' across the entire surface of the blade of *T. testudinum* (Figures 2.1 and 2.2). The algae also 'hook' around the tip of the seagrass blade and grow on the underside of the seagrass (Figure 2.4). These algal crusts were ubiquitous on samples collected from South Sound, Pease Bay, Frank Sound, and East Sound. The samples from North Sound do not always have this algal crust present. Only one of four samples from North Sound has coralline alga present and, when present, the alga does not cover the entire blade but rather, grows in patches on the blade's surface.

2.2.2 Foraminifera

The foraminifera might be considered to be the most dominant epiphyte on the seagrass because of the large number (72) of species identified in the study. Their presence, however, was not as widespread as the coralline algae or the diatoms. No species of foraminifera was rated as very common on the leaves and only 13 were considered common (Table 2.2). Many species of foraminifera were only seen on a single sample. No species was considered to be dominant on the leaves. The epiphytic foraminifera do not appear to live on the seagrass in species- or genera-specific colonies.

There is no colonization pattern present among the epiphytic foraminifera. It is difficult to determine if there is a species of epiphytic foraminifera that prefers one

lagoon to another, or a specific water depth. It is possible that an epiphyte observed only once in this study is present in all the lagoons, but was not seen on the samples obtained. There are also some genera of foraminifera present that are motile, and therefore may travel between the sediment water interface and the seagrass. Based strictly on observations from the samples obtained in this study, colonization of the leaves by epiphytic foraminifera appears to be random.

2.2.3 Diatoms

Sixty-one species of diatoms were found on the leaves with several being found on every blade, commonly in monospecific colonies attached to each other by their girdles (Figure 1.5), or in colonies of several detached species of a single genus. Four taxa were rated as very common and 16 as common. *Cocconeis* and *Mastogloia* were found on virtually every sample. Various species of these two genera commonly live together; thus it is not unusual that they are found grouped in dense populations on the seagrass. Colonies of *Cocconeis* are mostly found directly on the seagrass surface whereas colonies of *Mastogloia* are found on the layer of coralline algae that covers the seagrass. One species of epiphytic diatoms, *Mastogloia frimbriata* (Brightwell) Cleve, was only found in the deep (1.8-2.5 m) seagrass samples.

2.2.4 Other skeletal epiphytes

The 'other' epiphytes (Table 2.4, Figures 2.28-2.31) found on *T. testudinum* are not common on every blade and therefore do not contribute much sediment to the lagoon. The gastropods, ostracods, and coccoliths are calcareous. The sponge spicules found on

the leaves, however, were derived from calcareous and siliceous sponges. The calcareous sponges were observed during field work, encrusting a few blades of *T. testudinum*. These encrusting sponges were the source of the scattered calcareous spicules seen on the leaves. The siliceous spicules probably came from sponges near the reef crest that were transported back into the lagoon, and deposited onto the seagrass. The gastropods and ostracods are not permanent residents of *T. testudinum*, but rather, use the leaves for collecting food (other epiphytes) and for egg deposition (Borowitzka and Lethbridge 1989). The coccoliths are not complete specimens. There were just a few plates of coccoliths that were deposited on the leaves, through the baffling action of the leaves. There are traces left on the leaves from past inhabitants. The worm tubes (Figure 2.28 C and D) are left by the worm *Spirobis* sp. (Land 1970). These tubes were commonly seen on the leaves. The other traces left on *T. testudinum* were borings and tubes left by unknown organisms (Figure 2.33-2.36). There are some borings, with ~ 1µm diameters, that appear to be fungal in origin.

2.3 Lagoon Sediment

Relative to the numerous epiphytes identified on the leaves, there were not many epiphytes seen in the sediment samples examined in this study. Of the dominant epiphytic taxa identified on the leaves, there were five species of diatoms, 14 species of foraminifera, and one species of red algae that were found in the sediment (Table 2.5). Ostracods and *Spirobis* worm tubes were also seen in the sediment. There

| Epiphytes in Sediment | # Specimens | Location | Figure |
|--------------------------|-------------|--------------|-----------|
| | | | |
| Diatoms | | | |
| Achnanthes pericava | l | PB | 2.17 A |
| Amphora sp. | 2 | PB, FS | 2.17 C |
| Navicula sp. | 1 | SS | 2.24 E |
| <i>Rhoicosphenia</i> sp. | 2 | PB | 2.25 B |
| Indeterminate (D05) | 1 | SS | 2.26 E |
| Foraminifera | | | |
| <i>Elphidium</i> sp. | 2 | SS, PB | 2.7 D |
| Elphidium sp. | 5 | SS | 2.7 B |
| Miliolinella oblonga | 1 | FS | 2.10 D |
| Miliolinella sp. | 1 | SS | 2.10 E |
| Planorbulina acervalis | 1 | PB | 2.11 B |
| Ouinaueloculina costata | 4 | SS. PB | 2.11 D |
| Ouniqueloculina | 1 | SS | 2.11 E |
| longirostra | - | 50 | 2 |
| Quniqueloculina poeyana | 8 | SS, PB | 2.12 A |
| Quinqueloculina sp. | 1 | FS | 2.12 D |
| Quinqueloculina? | 2 | SS, FS | 2.12 E |
| Quinqueloculina ? | 1 | SS | 2.12 F |
| <i>Rosalina</i> sp. | 3 | SS | 2.13 B |
| Textularia sp. | 2 | SS, PB | |
| Valvulineria sp. | 2 | FS | 2.15 A |
| Red Alga | | | |
| Coralline algae (no | 1 | SS | n/a |
| conceptacle) | • | 55 | 10 4 |
| Indeterminate (R01) | 2 | SS PR | 22E E |
| (conceptacles) | - | 55,15 | 2.2 13, 1 |
| Other | | | |
| Ostracod | 3 | 99 92 | 2 20 4 |
| Snivebig worm tube | 2 | 55, FD DD | 2.27 A |
| Spiroois worm tube | <u> </u> | r D | 2.20 C, D |

 Table 2.5 – Epiphytes of T. testudinum that were found in sediment samples.

1 - SS = South Sound, PB = Pease Bay, FS = Frank Sound

were other species of foraminifera and diatoms (few) in the sediment samples; however, they do not correspond with the epiphytes identified on *T. testudinum*.

2.4 Synopsis

Numerous epiphytes were identified on *T. testudinum* in Grand Cayman lagoons. The dominant epiphytic taxa are the coralline algae, the diatoms (61 species), and the foraminifera (72 species). There are only three species of coralline algae but they cover most of the leaf's surface in almost every sample. The diatoms were present on every sample, and there were more diatoms present on the leaves than foraminifera, even though there were more species of foraminifera identified in the study. Other, less abundant epiphytes identified on the leaves include ostracods, *Spirobis* worm tubes, gastropods, dinoflagellates, and coccolith fragments. Relatively few epiphytes were found in the sediment samples.

Chapter Three – Epiphytic Community

3.1 Epiphytes identified in Grand Cayman vs. previous work

Upon comparison of the community of epiphytes in Grand Cayman with previous studies on Thalassia testudinum's epiphytes (Humm 1964; Land 1970; Reyes-Vasquez 1970; Buzas et al. 1977; Nelsen and Ginsburg 1986; Bosence 1989; Frankovich and Zieman 1994; Wilson 1998), it seems that the full range of skeletal epiphytes associated with seagrass is not yet known. The focus of previous studies was either on one taxon that inhabits the leaves or on how much sediment is generated in a lagoon, in which case only a few of the easily visible epiphytes are mentioned. Thus, one aim of this study was to identify all of the skeletal epiphytes living on T. testudinum in Grand Cayman. The results of this study show that there is a diverse community of epiphytes on the leaves. There are several studies that only focused on one particular group of epiphytes (Humm 1964; Reyes-Vasquez 1970; Ballantine and Humm 1975; Buzas et al. 1977; Wilson 1998). These studies show that there are numerous organisms that inhabit T. testudinum (Table 3.1), but do not document a diverse community of epiphytes. Humm (1964) documented 113 algal macrophytes found on *T. testudinum*; however there is no mention of epiphytic foraminifera or diatoms, which are commonly found on T. testudinum in Grand Cayman lagoons.

Other studies that focused on how much sediment can be generated in a lagoon by epiphytes (Land 1970; Patriquin 1972; Nelsen and Ginsburg 1986; Bosence 1989; Frankovich and Zieman 1994), mention two species of coralline algae and a few types of other organisms (Table 3.2). The coralline algae, worm tubes, and single bivalve mentioned by Land (1970), Nelsen and Ginsburg (1986), and Frankovich and Zieman (1994) are all visible without the use of a microscope. Other epiphytes may have been present on the seagrass, but were not listed (Land 1970; Nelsen and Ginsburg 1986; Frankovich and Zieman 1994) because they would have only been visible under a microscope or on an SEM. Patriquin (1972) mentioned red alga and several genera of epiphytic foraminifera. Two of the six genera of foraminifera described by Patriquin (1972) were found on the *T. testudinum* leaves on Grand Cayman; however, a total of 21 genera of epiphytic foraminifera were identified from the Grand Cayman samples. There may, therefore, be a lower diversity of epiphytes living in Barbados lagoons (Patriquin 1972) than in Grand Cayman or the samples may have been recovered in such a way that the foraminifera were detached from the leaves.

Only one of the studies focusing on sedimentation by epiphytes mentions the presence of diatoms (Bosence 1989). In contrast, there are 56 species of epiphytic diatoms identified in Grand Cayman lagoons and there were several species (~20) considered to be common on the leaves. Other studies (Land 1970; Patriquin 1972; Nelsen and Ginsburg 1986; Bosence 1989; Frankovich and Zieman 1994) may not have documented these epiphytes because they were measuring the amount of calcium carbonate generated by seagrass epiphytes. The high abundance of diatoms seen in Cayman would suggest that silica may also be added to lagoonal sediments.

| Author and Location | # macroalgal* epiphytes identified | # epiphytic diatoms identified | # cpiphytic foraminifera identified | # of other skeletal epiphytes |
|---|--|--------------------------------------|---|-------------------------------------|
| Humm (1964) Biscayne Bay, Florida | 113 | 0 | 0 | 0 |
| Reyes-Vasquez (1970) Biscayne Bay, Florida | 0 | 42 | 0 | 0 |
| Ballantine and Humm (1975), Florida (west coast) | 68 | 2 | 0 | 0 |
| Buzas <i>et al</i> . 1977, Jamaica | 0 | 0 | 58 | 0 |
| Wilson (1998) | 0 | 0 | 11 | 00 |

 Table 3.1 – Past studies of specific taxa of T. testudinum epiphytes.

* This includes Rhodophyta, Phaeophyta, Chlorophyta, and Cyanobacteria.

| Table 3.2 – Epiphytes listed in | studies that focus on how | v much sediment is generated by |
|---------------------------------|---------------------------|---------------------------------|
| epiphytes on T. testudinum. | | |

| Location | Epiphytes | Reference |
|---------------------------------|--|------------------|
| Discovery Bay, Jamaica | Coralline alga Melobesia membranacea, Fosliella farinosa Serpulid worm tubes Spirobis sp. | Land, 1970 |
| Bath, Barbados | Coralline alga Meobesia membranacea, Fosliella farinosa Articulated red alga Jania sp. Foraminifera Rotorbinella sp., Puteolina sp., Orbitolites sp., Planorbulina sp., Quinqueoculina sp., Bolivina sp. | Patriquin, 1972 |
| Florida Bay, Florida, U.S.A. | Coralline alga Melobesia membranacea, Fosliella farinosa Serpulid worm tubes Spirobis sp. | Nelsen, 1986 |
| Florida Bay, Florida, U.S.A. | Coralline alga Bivalves Worms Foraminifera Diatoms | Bosence, 1989 |
| Florida Bay, Florida, U.S.A. | Coralline alga Bivalve <i>Pinctada</i> sp. | Frankovich, 1994 |

3.2 Other Seagrass Epiphytes

Other species of seagrasses and their epiphytes have been studied from all over the world (Taylor and Lewis 1970; Harlin 1980; Willcocks 1982; Jacobs *et al.* 1983; Pinckney and Micheli 1998; Stefano *et al.* 2000; Gacia *et al.* 2003; Perry and Beavington-Penney 2005). The species of seagrass that has received the most attention is *Zostera marina* (Duarte 1999), which is common in temperate climates such as the North Atlantic, the Mediterranean, and the West and East Pacific. Many of the seagrasses found in coastal areas of Australia have been studied in great detail. There are several species of seagrasses present within each meadow and the climate varies across the continent making it easy to study ecological limitations (Larkum *et al.* 1989).

Research on other seagrass epiphytes has tended to focus either on identifying one group of epiphytes (Taylor and Lewis 1970; Harlin 1980; Willcocks 1982; Pinckney and Micheli 1998; Stefano *et al.* 2000) or on how the epiphytes affect sedimentation (Gacia *et al.* 2003; Perry and Beavington-Penney 2005). The studies that identify specific organisms on the leaves almost all exclusively identify macro and micro algal epiphytes. Perry and Beavington-Penney (2005) documented an epiphytic community similar to *T. testudinum*. One species of coralline red algae, found on the seagrass *Thalassia ciliatum* (Forsskål) den Hartog, covered most of the leaves on each plant examined. A few specific foraminifera and some *Spirobis* worm tubes were identified on top of the algal layer, and diatoms were also mentioned as part of the epiphytic community on the leaves (Perry and Beavington-Penney 2005).

3.3 Community Succession

Patterns in epiphytic colonization of seagrasses have been noted in previous studies (Ballantine 1979; Bulthius and Woelkering 1983; Jacobs et al. 1983; Bramwell and Woelkering 1984). Based on those studies, Borowitzka and Lethbridge (1989) suggested that the number and diversity of epiphytes on seagrasses increase toward the leaf tip and on the outmost, oldest leaf of the plant. There may be several reasons for this colonization pattern. Epiphytes that rely on photosynthesis are exposed to more sunlight and possibly a higher nutrient supply at the leaf's terminus (Borowitzka and Lethbridge 1989). Filter feeding epiphytes (e.g. sponges) live on the leaf tip where the leaves travel through more water as they sway back and forth and food passing by would also not be blocked by other leaves as it would at the base of the plant where the leaves are close together. Studies by Harrison (1982) and Harrison and Durance (1985) on epiphytes of the seagrass Zostera marina suggested there are less phenolic acids (compounds that are released by most terrestrial plants that can inhibit epiphyte settlement and growth) produced at the leaf tip. In a study where plastic strips were used to imitate seagrass habitats, however, the epiphytes colonized the 'seagrass' in the same pattern as on real seagrass (Horner 1987). The phenolic acids might not, therefore, be relevant to the epiphytes colonizing the terminus of the leaves first and more heavily. For some sea grass, the epiphytes prefer a specific side of the leaves and the number and diversity of species may be greater on the outer (upper) or the inner surface of the blade (Borowitzka and Lethbridge 1989). This preference may be due the life span of the particular species of seagrass because the epiphytes would have more time to colonize both surfaces of a leaf with a life span of 120 days, than one with a life span of 40 days (Heijs 1985). The

shape of the leaves may also affect this pattern of colonization. The different shape and orientation of seagrass leaves control immediate water circulation patterns, which may make one surface more hospitable than the other (Borowitzka and Lethbridge 1989).

3.4 Settlement/Colonization of T. testudinum

There are few studies that focus on the settlement stages of epiphytes on seagrasses. Both red algae and diatoms have been named as 'pioneer plants' that colonized seagrass and thereby made the leaf surfaces more hospitable for other epiphytes (Humm 1964; Ballantine 1979; Willcocks 1982). On *T. testudinum* from Grand Cayman, there is a structured community with a distinct succession of epiphytic communities (Figure 3.1). The level of biological diversity in the community increased with each layer.

Cocconeis, found directly on the leaf surface (Figure 3.2), are considered to be the basal epiphytic layer. This phenomenon has been seen elsewhere. In Australia, for example, *Cocconeis pediculus, C. placentula, C. placentula* var. *euglypta,* and *C. scutellum* form the '*Cocconeis-Typus*' community on the seagrass *Zostera marina* (Eddsbagge 1968). Similarly, several species of *Cocconeis* initially colonized a clean surface of *T. testudinum* in Texas, followed by a population of naviculoid diatoms that were intermixed with filamentous or encrusting red algae (Kitting 1984). The basal diatom community was found in nearly every sample examined from Grand Cayman. In some cases, however, this layer was completely covered by the middle and upper epiphyte layers.



Figure 3.1 - Schematic diagram showing typical order of colonization of epiphytic material.



FIGURE 3.2: Diatoms on Surface

A) Various species of Cocconeis on seagrass surface, ~ 0.2 m depth, South Sound

- B) Close-up of previous image
- C) Cocconeis, Rhoicosphenia, and Haslea on surface, ~ 0.2 m depth, South Sound
- D) Various species of *Cocconeis* on seagrass surface, ~1.5 m depth, Pease Bay
 E) Various species of *Cocconeis* on seagrass surface, ~0.5 m depth, North Sound
- F) Cocconeis scutellum Ehrenberg on seagrass surface, ~ 0.6 depth, East Sound

The coralline algae community (10-30 μ m thick, conceptacles up to ~200 μ m thick), formed mainly of *Hydrolithon farinosum* (Lamouroux) Penrose & Chamberlain, grew on top of the diatom community. The leaf is usually covered by these epiphytes on both sides of the blade in equal abundance (Figure 2.4A, C and E). These algal epiphytes were found on most of the samples examined from Grand Cayman. Some samples collected from the northwest corner of North Sound, however, lacked this community of epiphytes. Instead, the leaves at that locality were coated with brown algae. The encrusting red algae community, where present, covers almost the entire *Thalassia* blade, up until approximately the basal 5 cm by the root.

The uppermost epiphytic layer typically contains many different types of epiphytes. The upper layer of epiphytes is the most taxonomically diverse of all the layers, regardless of the sample location. Some of these epiphytes, including the foraminifera, gastropods, bivalves, and coccoliths, are calcareous. Several genera of diatoms, including *Mastogloia, Amphora, Rhopaloidia,* and *Synedra*, are found in this layer. Spicules (calcareous and siliceous) were also present in this layer. The calcareous spicules came from sponges that encrusted the leaves of *T. testudinum*, and the siliceous spicules were likely deposited on the blades from water passing through the plants. Most of the organisms in the upper layer are seen at both shallow (0.2-0.5 m) and deep (1.8-2.5 m) intervals in the lagoon.

3.5 **Possible Explanations for Layered Community**

There are a few possible explanations for the order of epiphyte colonization on *T*. *testudinum*. The phenolic acids mentioned by Harrison (1982) and Harrison and Durance

(1985) that are produced by seagrasses could be one reason why the diatoms colonize the surface first. They could be immune to the affects of the acids, and therefore able to attach themselves directly to the leaf's surface. The red algae, however, may be unable to colonize the grass where this acid is produced (Harrison 1982; Harrison and Durance 1985). Horner (1987), in his study of epiphyte colonization, documented the same epiphytic coverage on fake seagrass (plastic strips) as on real seagrass. The use of the plastic strips proved that the phenolic acids did not seem to affect patterns of colonization lengthwise along the blade from root to tip; however there was no mention of which organisms were the first to attach onto the leaves. The encrusting algae are still in contact with the leaf given that the diatoms do not usually cover the entire surface; therefore it is unlikely that the phenolic acid is the reason for the diatoms to be the pioneer colonizers.

Another possibility is that certain epiphytes, such as coralline red algae, cannot directly attach themselves to the surface of the leaf due to the cuticle covering *T*. *testudinum* leaves. The cuticle covers the entire blade and contains small perforations that are used in photosynthetic processes (Tomlinson 1980; Hemminga and Duarte 2000). The surface may be colonized more easily by diatoms because these microalgae have a smaller surface area and it is easier for them to stay attached at the seagrass-water interface (Borowitzka and Lethbridge 1989). Many diatoms produce extracellular polysaccharides in thread form, mucus pads, or tubes (Darly 1977; McIntire and Moore 1977). These excretions may also make it easier for the diatoms to attach and the leaf surface more hospitable for encrusting coralline algae.

The order that these epiphytes settle on the leaves may be essential in the epiphytic colonization of *T. testudinum*. Without the initial colonization of the leaves by the

diatoms, perhaps the algae (the most ubiquitous epiphyte) would not inhabit the leaf's surface. Of the few explanations as to the reason for this colonization pattern, the most probable one is due to the presence of the waxy surface, or cuticle, covering the *T. testudinum* leaves. The algae, when it is encrusting a surface, mimics whatever surface it is colonizing. The surface of the *T. testudinum* is flat and so the underside of the algae will also be flat. Two flat surfaces, one of which is covered in a waxy cuticle, would not attach very successfully. Once the smooth 'slippery' surface of the leaf is scattered with diatoms, topography increases, which may aid the encrusting algae to colonize the leaf and remain there. The algae may be using the diatoms as strongholds to grow around, in order to anchor itself to the leaves. There are imprints of diatoms in the underside of the diatom that has not dissolved, remains imbedded in the algae and cements fill in the pore space left by the concave valve. From these imprints, it is clear that the algae grew around the diatoms.

3.6 Exceptions in the order of colonization

Samples obtained from North Sound lack the middle epiphytic layer of coralline alga. The middle layer in these samples was replaced with brown algae (Figure 3.4). This difference can be observed at both a macroscopic and microscopic level. The samples obtained at this location were all from shallow water (0.2-0.5 m) and were situated adjacent to mangroves that line the shoreline of this northwest section of North Sound. The water clarity in this section of North Sound in much lower than in all of the other lagoons sampled, which suggests a high level of nutrients present in the water at this



- **FIGURE 3.3: Diatoms Embedded in Red Alga** A) Underside of coralline algae with diatoms embedded inside, ~ 2.6 m depth, East Sound
- B) Close-up of previous image, note the diatom valve is being filled with cement
- C) Underside of coralline algae with diatom embedded inside, ~ 2.6 m depth,
- East Sound
- D) Close-up of previous image



Figure 3.4 - A) *T. testudinum* in South Sound, note white crust on leaves (coralline alga). B) *T. testudinum* in North Sound, note growth of brown algae on leaves.

station. Macroalgal epiphytes in *T. testudinum* meadows have been found to have the highest growth rates, at low nutrient levels (Biber *et al.* 2003).

Chapter Four – Discussion and Conclusion

4.1 Discussion

Sediment in lagoons is derived from a variety of sources (Figure 4.1). Storms and hurricanes are a major influence on the composition of lagoon sediments. The degree to which these forces contribute to sedimentation depends on where the lagoon is located and whether it is an area that is prone to these events. The sediment that is produced inside the lagoon by various organisms is important to sediment buildup, however, a hurricane can transport all of these sediments out of the lagoon (Kalbfleisch and Jones 1998). Inorganic precipitation of calcium carbonate occurs more often in areas that are inhospitable to organisms. Lagoons are usually a perfect habitat for numerous organisms given that they are bathed in sunlight and are protected by some form of barrier. If a lagoon is completely cut off from open marine waters and becomes hyper saline, inorganic precipitation of calcium carbonate would likely increase and become a more important source of sediment.

Sediment that is produced inside a lagoon is almost completely generated by the biota that lives there. Epibenthic organisms that live on the lagoon floor such as green algae, mollusks, and foraminifera can be dominant sources of sediment (Neumann and Land 1975; Chevillon 1996; Gischler and Zingeler 2002). A study that examined sediments from a few lagoons in New Caledonia (Chevillon 1996) found that most of the sediment was formed of mollusks, foraminifera and *Halimeda* plates. Two of the lagoons in that study (Chevillon 1996) were located in atolls. These lagoons are completely surrounded by reefs; however, corals and coralline algae were minor constituents in the sediment samples. In contrast, a study by Adjas *et al.* (1990) found a great deal of coral-generated



Figure 4.1 - Sources of sediment in Grand Cayman lagoons.

sediment in the lagoons of two French Polynesian atolls (Mataiva and Takapoto). This sediment was primarily generated by boring sponges and lithophagid mollusks. Bioerosion can generate a great deal of sediment in lagoons through fish grazing on corals or by the internal bioerosion of corals and other large, hard substrates in the lagoon by sponges and worms (Acker and Risk 1985; Sammarco *et al.* 1987; Young and Nelson 1988; Adjas *et al.* 1990). The rate of bioerosion can, in some cases, keep up with the growth of the reef (Scoffin *et al.* 1980).

In Grand Cayman the lagoons are dominated by storms; however, during inter-storm periods, much of the sediment is generated within the lagoon by the breakdown of biota, bioerosion, and *T. testudinum* colonization (Kalbfleisch and Jones 1998; Beanish and Jones 2002). In South Sound, most of the sediment is generated by mollusks, green algae and foraminifera and these sediments are broken down further through micritization processes, rather than physical abrasion (Beanish and Jones 2002). In South Sound, Frank Sound and Pease Bay, the *T. testudinum* causes preferential deposition of sediment, which creates banks of sand within the seagrass meadows (Kalbfleisch and Jones 1998; Beanish and Jones 2002).

Seagrasses are important to sedimentological processes in lagoons. Seagrass leaves baffle currents, causing fine sediment to fall out of suspension (Almasi *et al.* 1987). The roots of seagrasses bind the sediment, which creates banks of carbonate sand and silt in the lagoons. The epiphytes are also thought to contribute to sedimentation (Table 1.1), and there has been a study by Nelsen and Ginsburg (1986) that suggested all of the mudsized aragonite and high magnesium calcite in Florida Bay is generated by seagrass epiphytes. Estimates of sediment generated by epiphytes in other studies on *T. testudinum*

do not account for all the sediment in the lagoon (Land 1970; Patriquin 1972; Bosence 1989; Frankovich and Zieman 1994) and the estimates in each study are quite different (Table 1.1). Nevertheless, all of these studies concluded that epiphytic carbonate production is important in the generation of lagoonal sediment.

In this study of epiphytes living on *T.testudinum* in Grand Cayman lagoons, numerous skeletal epiphytes (siliceous and calcareous) were identified. The dominant taxa were three species of coralline algae that were ubiquitous on almost all samples. Past studies that mentioned the presence of coralline algae on *T. testudinum* (Humm 1964; Land 1970; Patriquin 1972; Nelsen and Ginsburg 1986) stated that these algal epiphytes were contributing to the sediment in the lagoons. The sediments, collected from seagrass meadows in Grand Cayman, only contained three fragments of coralline algae (Table 2.5). The species of coralline alga found on *T. testudinum* were also not present in any of the detailed facies analyses done on Grand Cayman lagoonal sediments (Kalbfleisch and Jones 1998; Beanish and Jones 2002).

There is a possibility that the alga does not remain in the sediment once it is detached from the seagrass blade. Coralline alga grows on the seagrass in thin crusts (10-30 μ m) and in small domal masses called conceptacles (Figure 4.2). It is likely that the crusts would not remain intact for very long in the sediment, even though the conditions in *T*. *testudinum* beds are normally very quiet. The crusts may also simply dissolve shortly after they are deposited. The conceptacles are larger (up to ~200 μ m thick) than the crust (Figure 4.2), but despite their size there were only two conceptacles observed in the sediment from Grand Cayman.



Figure 4.2 - Thickness of coralline algae layers

Comparison of the epiphytes in Grand Cayman with a study that focused on the foraminifera found in the sediments on the lagoon floors in Grand Cayman (Li et al. 1997; Li et al. 1998), lends to another interesting result. Li (1997), Li et al. (1997), and Li et al. (1998) identified 136 species of foraminifera in the sands. Seventy-two species of foraminifera were found to live on T. testudinum in Grand Cayman (Table 2.2). Only 9 of the epiphytic species living on the *T. testudinum* matched the species of foraminifera listed by Li (1997). This discrepancy could be attributed to the distribution of the epiphytic foraminifera in the lagoon sediments or to the different sizes of foraminifera examined in these studies. Only for a larger than 0.125 mm were examined by Li (1997), Li et al. (1997), and Li et al. (1998). Of the 72 species of foraminifera found on the *T. testudinum* leaves, 43 were smaller than 0.125 mm. It is possible, therefore, that the epiphytic foraminifera are in the lagoonal sediment, but were too small to be included in the studies by Li (1997), Li et al. (1997), and Li et al. (1998). This problem was explored further by examining the sediment samples obtained in this study. The sediments were sieved to < 0.109 mm to see if more epiphytic foraminifera were in the sediment. In these samples there were 12 species of foraminifera that matched the 72 foraminifera identified as epiphytes on T. testudinum (Table 2.5). None of these 12 foraminifera were abundant in the sediment. The foraminifera that were in the sediment were very well preserved so it is unlikely that the remainder of the epiphytic foraminifera would have dissolved.

In the examination of foraminiferal assemblages and sediment transport in Grand Cayman lagoons by Li *et al.* (1997) and Li *et al.* (1998) there were several foraminifera that are associated with a fore-reef environment, found in the lagoonal sediments. These foraminifera were probably transported in to the lagoons by storm events that brought coarse sediment over the reef crest and deposited in the lagoon (Li *et al.* 1998). In Li *et al.* (1997) the smaller tests, associated with lagoonal facies, were found in the fore-reef. This indicated that the water that drains out of the lagoon after a storm must have transported much of the finer sediment that was in suspension, out to the fore-reef area (Li *et al.* 1997).

Most of the diatoms identified on *T. testudinum* were not found in the sediment. The influence of storms may explain why there were only five species of epiphytic diatoms identified in the sediment samples. The diatoms were the second most abundant epiphyte on *T. testudinum*, after the coralline algae. The surface of the seagrass is colonized by the diatoms and there are still more diatoms present on the surface of the coralline algae. The diatoms that were found in the sediment samples were always found attached to another grain. Perhaps the epiphytic diatoms are small enough that they are carried away by the everyday currents present in the lagoon directly after detaching from the seagrass, unless they manage to attach onto another surface. Many of the diatoms that were seen in the sediment were broken, so it is also possible that these microalga breakup and dissolve after detachment.

All of the studies involving sediment assemblages in Grand Cayman lagoons (Li *et al.* 1997; Kalbfleisch and Jones 1998; Li *et al.* 1998; Beanish and Jones 2002) have concluded these lagoons are dominated by storms and hurricanes. There is some evidence of fair-weather conditions in the lagoons; however, the storms carry away much of the sediment generated by these processes (Kalbfleisch and Jones 1998). Being that the epiphytes on *T.testudinum* are so small, it is likely that any trace of the sediment produced by their skeletons, is suspended in storm currents and carried away.

Past research on the production of sediment by epiphytes living on *T. testudinum* (Land 1970; Patriquin 1972; Nelsen and Ginsburg 1986; Bosence 1989; Frankovich and Zieman 1994) may still be accurate. In this particular study, the sediment produced by the skeletal epiphytes might just be carried away by the storms that dominate Grand Cayman lagoons. If, however, the epiphytes are dissolving shortly after they reach the sediment water interface, sedimentologists may have to reevaluate how much seagrass epiphytes contribute to sedimentation.

4.2 Conclusions

Thalassia testudinum is abundant in Grand Cayman and affects the inter-storm deposition of sediment in the lagoons. The conclusions of this study are:

- There were numerous epiphytes identified on *T. testudinum*. The dominant taxa were three species of coralline red alga, 72 species of foraminifera, and 61 species of diatoms.
- Other minor skeletal epiphytes were found on the leaves such as ostracods, gastropods, and coccolith fragments. A number of traces were also left behind however most were not identified with the exception of the *Spirobis* worm tubes.
- There is a layered community succession on the leaves. The seagrass surface is colonized by *Cocconeis* diatoms. The diatom covered leaf is then covered by coralline red algae. The uppermost layer, which is the most diverse, is comprised of diatoms, foraminifera, worms, gastropods, ostracods, and ampihpods.
- It is likely that the diatoms make it possible for the coralline algae to colonize *T*. *testudinum*.

- Only a few pieces of algae, the most abundant epiphyte, were found in the sediment samples that were collected from the seagrass beds. Only 12 of the 72 species of epiphytic foraminifera and 5 of the epiphytic diatoms were found in the sediment samples.
- The epiphytic community on the seagrass is very diverse; however, it appears that the epiphytes may not significantly contribute to lagoonal sedimentation.
- The epiphytes are most likely transported out of the lagoon, which would further support the theory that lagoons in Grand Cayman are dominated by storm processes.

References

- ACKER, K.L., and RISK, M.J., 1985, Substrate destruction and sediment production by the boring sponge *Cliona caribbaea* on Grand Cayman island: Journal of Sedimentary Petrology, v. 55, p. 705-711.
- ADJAS, A., MASSE, J., and MONATAGGIONI, L.F., 1990, Fine-grained carbonates in nearly closed reef environments: Mataiva and Takapoto atolls, Central Paicific Ocean: Sedimentary Geology, v. 67, p. 115-132.
- ALMASI, M.N., HOSKIN, C.M., REED, J.K., and MILO, J., 1987, Effects of natural and artificial Thalassia on rates of sedimentation: Journal of Sedimentary Petrology, v. 57, p. 901 -906.
- BALLANTINE, D.L., 1979, The distribution of algal epiphytes on macrophyte hosts offshore from La Paruera, Puerto Rico: Botanica Marina, v. 22, p. 107-111.
- BALLANTINE, D.L., and HUMM, H.J., 1975, Benthic algae of the Anclote estuary. I. Epiphytes of seagrass leaves: Florida Science, v. 38, p. 144-149.
- BEANISH, J., and JONES, B., 2002, Dynamic carbonate sedimentation in a shallow coastal lagoon: Case study of South Sound, Grand Cayman, British West Indies: Journal of Coastal Research, v. 18, p. 254-266.
- BEANISH, J., SANCHEZ-AZOFEIFA, A., and JONES, B., 2002, Application of image analysis for mapping of sedimentary facies in a shallow lagoon: case study, south sound, Grand Cayman, British West Indies: International Journal of Remote Sensing, v. 23, p. 2877-2890.
- BIBER, P.D., HARWELL, M.A., and CROPPER JR., W.P., 2003, Modeling the dynamics of three functional groups of macroalgae in tropical seagrass habitats: Ecological Modelling, v. 175, p. 25-54.
- BOLTOVSKOY, E., and WRIGHT, R., 1976, Recent Foraminifera, Dr. W. Junk b.v. -Publishers - The Hague 515 p.
- BOROWITZKA, M.A., and LETHBRIDGE, R.C., 1989, Seagrass Epiphytes, *in* Larkum, A.W.D., McComb, A.J., and Shepard, S.A., eds., Biology of Seagrasses: Aquatic Plant Studies: New York, Elsevier Science Publishing Company Inc., p. 458-499.

- BOSENCE, D., 1989, Biogenic carbonate production in Florida Bay: Bulletin on Marine Science, v. 44, p. 419-433.
- BRAMWELL, M.D., and WOELKERING, W.J., 1984, Studies on the distribution of *Pheophyllum-Fosliella* plants (Corallinaceae, Rhodophyta) on leaves of the seagrass *Amphibolis antarctica* (Cymodoceaceae): Austrailian Journal of Botany, v. 32, p. 131-137.
- BULTHIUS, D.A., and WOELKERING, W.J., 1983, Seasonal variation in standing crop, density and leaf growth rate of seagrass, *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Austrailia: Journal of Experimental Biology and Ecology, v. 67, p. 91-103.
- BUZAS, M.A., SMITH, R.K., and KENNETH A, B., 1977, Ecology and Systematics of Foraminifera in Two *Thalassia* Habitats, Jamaica, West Indies: Smithsonian Contributions to Paleobiology, v. 31, p. 1-139.
- CHEVILLON, C., 1996, Skeletal composition of modern lagoon sediments in New Caledonia: coral, a minor consituent: Coral Reefs, v. 15, p. 199-207.
- CLINTON, D.J., 1981, Thalassia, Marine Botany: New York, New York Wiley, p. 266-267.
- CUSHMAN, J.A., 1924, The Foraminifera of the Atlantic Ocean, part 5: Chilostomellidae and Globigerinidae: Bulletin of the United States National Museum, Washington, Government Printing Office, 104 1-55 p.
- CUSHMAN, J.A., 1931, The foraminifera of the Atlantic Ocean, part 8, Rotaliidae, Amphisteginidae, Calcarinidae, Cymbaloporettidae, Globorotaliidae, Anomalinidae, Planorbulinidae, Rupertiidae and Homotremidae: Bulletin of the United States National Museum, Washington, United States Government Printing Office, 104 1-179 p.
- CUSHMAN, J.A., 1980, Foraminfera, London, Harvard University Press 605 p.
- DARLY, W.M., 1977, Biochemical Composition, *in* Werner, D., ed., The Biology of Diatoms: Botanical Monographs: London, Blackwell Scientific Publications, p. 198-224.

- DAVIES, J.E., and BRUNT, M.A., 1994, Scientific Studies in the Cayman Islands, *in* Brunt,
 M.A., and Davies, J.E., eds., The Cayman Islands: Natural History and
 Biogeography, Kluwer Academic Publishers, p. 1.-12.
- D'ORBIGNY, A., 1846, Foraminifères Fossiles du Bassin Tertiaire de Vienne: Die Fossilen Foraminiferen des Tertiaeren beckens von Wien, Paris, Verlagsbuchhandlung von Gide et comp.,5 1-303 p.
- DUARTE, C.M., 1999, Seagrass ecology at the turn of the millenium: challanges for the new century: Aquatic Botany, v. 65, p. 7-20.
- EDDSBAGGE, H., 1968, Some problems in the relationship between diatoms and seaweeds: Botanica Marina, v. 11, p. 64-67.
- Eva, A.N., 1980, Pre-Miocene seagrass communities in the Caribbean: Paleontology, v. 23, p. 231-236.
- FRANKOVICH, T.A., and ZIEMAN, J.C., 1994, Total epiphyte and epiphytic carbonate production on Thalassia testudinum across Florida Bay: Bulletin on Marine Science, v. 54, p. 679-695.
- GACIA, E., DUARTE, C.M., MARBA, N., TERRADOS, J., KENNEDY, H., FORTES, M.D., and TRI, N.H., 2003, Sediment deposition and production in SE-Asia seagrass meadows: Estuarine Coastal and Shelf Science, v. 56, p. 909-919.
- GISCHLER, E., and ZINGELER, D., 2002, The origin of carbonate mud in isolated carbonate platforms of Belize, Central America: International Journal of Earth Sciences, v. 91, p. 1054-1070.
- GUTTINGER, W., 1986a, Collection of SEM Micrographs of Diatoms, CH-6984 Pura, 1.
- GUTTINGER, W., 1986b, Collection of SEM Micrographs of Diatoms, CH-6984,2.
- GUTTINGER, W., 1986c, Collection of SEM Micrographs of Diatoms, CH-6984 Pura,3.
- GUTTINGER, W., 1986d, Collection of SEM Micrographs of Diatoms, CH-6984 Pura,4.
- GUTTINGER, W., 1986e, Collection of SEM Micrographs of Diatoms, CH-6984 Pura, 5.
- GUTTINGER, W., 1986f, Collection of SEM Micrographs of Diatoms, CH-6984 Pura,6.
- HARLIN, M.M., 1980, Seagrass epiphytes, *in* Phillips, R.C., and McRoy, C.P., eds.,Handbook of Seagrass Biology: An Ecosystem Perspective: New York, GarlandSTPM Press, p. 117-153.

- HARRISON, P.G., 1982, Control of microbial growth and of amphipod grazing by watersoluable compounds from leaves of *Zostera marina*: Marine Biology, v. 67, p. 225-230.
- HARRISON, P.G., and DURANCE, C.D., 1985, Reductions in photosynthetic carbon uptake in epiphytic diatoms by water-soluble extracts of leaves of *Zostera marina*: Marine Biology, v. 90, p. 117-119.
- HEUS, F.M.L., 1985, The seasonal distribution and community structure of the epiphytic algae on *Thalassia hemprichii* (Ehrenb.) Aschers. from Papau New Guinea: Aquatic Botany, v. 21, p. 295-324.
- HEMMINGA, M.A., and DUARTE, C.M., 2000, Seagrass Ecology, Cambridge, Cambridge University Press 310 p.
- HERON-ALLEN, E., and EARLAND, A., 1915, The Foraminifera of the Kerimba Archipelago (Portugese East Africa), part II: Transactions of the Zoological Society of London, p. 543-794.
- HOFKER, J., 1976, Further studies on Caribbean foraminifera, *in* Hummelinck, P.W., and Van der Steen, L.J., eds., Studies on the Fauna of Curaçao and other Caribbean Islands, Foundation for Scientific Research in Surinam and the Netherlands Antilles, p. 256.
- HORNER, S.M.J., 1987, Similarity of epiphytic biomass distribution on *Posidonia* and artificial seagrass leaves: Aquatic Botany, v. 27, p. 159-67.
- HUMM, H.J., 1964, Epiphytes of the seagrass, *Thalassia testudinum*, in Florida: Bulletin of Marine Science of the Gulf and Caribbean, v. 14, p. 306-341.
- IVANY, 1990, Animal-plant relationships and paleobiogeography of an Eocene seagrass community from Florida: Palios, v. 5, p. 244-258.
- JACOBS, R.P.W.M., HERMELINK, P.M., and VAN GEEL, G., 1983, Epiphytic algae on eelgrass at Roscoff, France: Aquatic Botany, v. 15, p. 157-173.
- JAVAUX, E.J., and SCOTT, D.B., 2003, Illustration of modern benthic foraminifera from Bermuda and remarks on distribution in other subtropical/tropical areas: Palaeontologia Electronica, v. 6, p. 1-29.

- KALBFLEISCH, W.B.C., and JONES, B., 1998, Sedimentology of shallow, hurricaneaffected lagoons: Grand Cayman, British West Indies: Journal of Coastal Research, v. 14, p. 140-160.
- KITTING, C., 1984, Selectivity by dense dense populations of small invertebrates foraging maong seagrass blade surfaces: Estuaries, v. 7, p. 276-288.
- KOCH, E.W., 1999, Sediment resuspension in a shallow *Thalassia testudinum* banks ex König bed: Aquatic Botany, v. 65, p. 269-280.
- LAND, L.S., 1970, Carbonate mud: production by epibiont growth on *Thalassia testudinum*: Journal of Sedimentary Petrology, v. 40, p. 1361-1363.
- LARKUM, A.W.D., MCCOMB, A.J., and SHEPARD, S.A., 1989, Biology of Seagrasses: Introduction, Aquatic Plant Series Two: New York, Elsevier, p. 1-5.
- LI, C., 1997, Foraminifera as sediment tracers, Grand Cayman [unpublished Ph.D. thesis]: University of Alberta, Edmonton, 200 p.
- LI, C., JONES, B., and BLACHON, P., 1997, Lagoon-shelf sediment exchange by storms -Evidence from Foraminiferal Assemblages, East Coast of Grand Cayman, British West Indies: Journal of Sedimentary Research, v. 67, p. 17-25.
- LI, C., JONES, B., and KALBFLEISCH, W.B.C., 1998, Carbonate sediment transport pathways based on foraminifera: case study from Frank Sound, Grand Cayman, British West Indies: Sedimentology, v. 45, p. 109-120.
- LITTLER, D.S., LITTLER, M.M., BUCHER, K.E., and NORRIS, J.N., 1989, Marine plants of the Caribbean: A field guide from Florida to Brazil, Washington, D.C., Smithsonian Institution Press 272 p.
- MACKINNON, L., and JONES, B., 2001, Sedimentological evolution of North Sounds, Grand Cayman - A freshwater to marine carbonate succession driven by Holocene sea-level rise: Journal of sedimentary Research, v. 71, p. 568-580.
- MACMILLAN, C., and MOSELEY, F.N., 1967, Salinity tolerance of five marine spermatophytes of Redfish Bay, Texas: Ecology, v. 48, p. 329-342.
- MANN, D.G., 2002, Diatoms: Organism and Image, *in* Buf, H.d., and Bayer, M.M., eds., Automatic Diatom Identification: Singapore, World Scientific Publishing Co. Pte. Ltd., p. 9-40.
- MCINTIRE, C.D., and MOORE, W.W., 1977, Marine Littoral Diatoms-Ecological Considerations, *in* Werner, D., ed., The Biology of Diatoms: London, Blackwell Scientific Publications, p. 333-372.
- MOORE, D.R., 1963, Distribution of the seagrasses, *Thalassia*, in the United States: Bulletin of Marine Science of the Gulf and Caribbean, v. 18, p. 329-342.
- NELSEN, J.E., and GINSBURG, R.N., 1986, Calcium carbonate production by epibionts on Thalassia in Florida Bay: Journal of Sedimentary Petrology, v. 56, p. 622-628.
- NEUMANN, A.C., and LAND, L.S., 1975, Lime mud deposition and calcareous algae in the Bight of Abaco, Bahamas: A budget: Journal of Sedimentary Petrology, v. 45, p. 763-786.
- OGDEN, J.C., 1980, Faunal relationships in Caribbean seagrass beds, *in* Phillips, R.C., and McRoy, C.P., eds., Handbook of Seagrass Biology: An Ecosystem Perspective: New York, Garland STPM Press, p. 173-198.
- OGDEN, J.C., and ZIEMAN, J.C., 1977, Ecological aspects of coral reef-seagrass bed contacts in the Caribbean: Third International Coral Reef Symposium, p. 377-389.
- PATRIQUIN, D.G., 1972, Carbonate mud production by epibionts on *Thalassia:* An estimate based on leaf growth rate data: Journal of Sedimentary Petrology, v. 42, p. 687-689.
- PERRY, C.T., and BEAVINGTON-PENNEY, S.J., 2005, Epiphytic calcium carbonate production and facies development within sub-tropical seagrass beds, Inhaca Island, Mozambique: Sedimentary Geology, v. In press.
- PHILLIPS, R.C., 1960, Observations on the ecology and distribution of the Florida seagrasses: Florida State Board of Conservation Professional Papers Series, v. 2, p. 1-72.
- PINCKNEY, J.L., and MICHELI, F., 1998, Microalgae on seagrass mimics; Does epiphyte community structure differ from live seagrasses: Journal of Experimental Biology and Ecology, v. 221, p. 59-70.
- REYES-VASQUEZ, G., 1970, Studies on the Diatom flora living on *Thalassia testudinum* König in Biscayne Bay, Florida: Bulletin of Marine Science, v. 20, p. 105-134.

96

- ROBERTS, H.H., 1994, Reefs and lagoons of Grand Cayman, *in* Davies, M.A.B.a.J.E., ed., The Cayman Islands: Natural History and Biogeography, Kluwer Academic Publishers, p. 75-104.
- SAMMARCO, P.W., RISK, M.J., and ROSE, C., 1987, Effects of grazing and damselfish territoriality on internal bioerosion of dead corals: indirect effects: Journal of Experimental Biology and Ecology, v. 112, p. 185-199.
- SAR, E.A., ROMERO, O., and SUNESEN, I., 2003, Cocconeis Ehrenberg and Psammococconeis Garcia (Bacillariophyta) from the Gulf of San Matías, Patagonia Argentina: Diatom Research, v. 18, p. 79-106.
- SCOFFIN, T.P., STEARN, C.W., BOUCHER, D., FRYDL, P., HAWKINS, C.M., HUNTER, I.G., and MACGEACHY, J.K., 1980, Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II - erosion, sediments and internal structure: Bulletin of Marine Science, v. 30, p. 475-508.
- SNOEIJS, P., 1993, Intercalibration and distribution of diatom species in the Baltic Sea, Uppsala, Opulus Press, 1 130 p.
- SNOEIJS, P., and BALASHOVA, N., 1998, Intercalibration and distribution of diatom species in the Baltic Sea, Uppsala, Opulus Press, 5 144 p.
- SNOEIJS, P., and KASPEROVICIENE, J., 1996, Intercalibration and distribution of diatom species in the Baltic Sea, Uppsala, Opulus Press, 4 125 p.
- SNOEIJS, P., and PAOTAPOVA, M., 1995, Intercalibration and distribution of diatom species in the Baltic Sea, Uppsala, Opulus Press, 3 125 p.
- SNOEIJS, P., and VILBASTE, S., 1994, Intercalibration and distribution of diatom species in the Baltic Sea, Uppsala, Opulus Press, 2 125 p.
- STEFANO, M.D., MARINO, D., and MAZZELLA, L., 2000, Marine taxa of *Cocconeis* on leaves of *Posidonia oceanica*, including a new species and two new varieties: European Journal of Phycology, v. 35, p. 225-242.
- TAYLOR, J.D., and LEWIS, M.S., 1970, The flora, fauna, and sediments of the marine grass beds of Mahe, Seychelles: Journal of Natural History, v. 4, p. 199-220.

- TOMLINSON, P.B., 1980, Leaf Morphology and Anatomy in Seagrasses, *in* Phillips, R.C., and McRoy, C.P., eds., Handbook of Seagrass Biology: An Ecosystem Perspective: New York, Garland STPM Press, p. 7-28.
- TONGPENYAI, B., and JONES, B., 1991, Application of image analysis for delineating modern carbonate facies changes through time: Grand Cayman, western Caribbean Sea: Marine Geology, v. 96, p. 85-101.
- WERNER, D., 1977, The Biology of Diatoms: Botanical Monographs, London, Blackwell Scientific Publications, v. 13 498 p.
- WILLCOCKS, P.A., 1982, Colonization and Distribution of the red algal epiphytes Melobesia mediocris and Smithora naiadum on the seagrass Phyllospadix torreyi: Aquatic Botany, v. 12, p. 365-373.
- WILSON, B., 1998, Epiphytal foraminiferal assemblages on the leaves of the seagrasses
 Thalassia testudinum and *Syringodium filiforme*: Caribbean Journal of Science, v. 34,
 p. 131-132.
- YOUNG, H.R., and NELSON, C.S., 1988, Endolithic biodegradation of cool-water skeletal carbonates on Scott shelf, northwestern Vancouver Island, Canada: Sedimentary Geology, v. 60, p. 251-267.