PROCEEDINGS
OF THE
SIXTH SYMPOSIUM
ON THE
NATURAL HISTORY OF THE BAHAMAS

Edited by
Nancy B. Elliott
D. Craig Edwards
and
Paul J. Godfrey

with additional editorial assistance from
Linda A. Swift and Melinda M. Godfrey

Production Editors
Daniel R. Suchy
Nicole G. Suchy

Bahamian Field Station, Ltd.
San Salvador, Bahamas
1996

Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).

Back Cover Photo: Group photo of the 6th Symposium participants and speakers.

Photos by Paul Godfrey (Computer processed prints by Lanny Miller).

© Copyright 1996 by Bahamian Field Station, Ltd.

All Rights Reserved

No part of this publication may be reproduced or transmitted
in any form or by any means, electronic or mechanical,
including photocopy, recording, or any information storage and
retrieval system, without permission in written form.

Printed in USA by Don Heuer

ISBN 0-935909-60-5

A COMPARISON OF SUBTIDAL BENTHIC MACROPHYTE COMMUNITIES IN WAVE-EXPOSED AND WAVE-SHELTERED HABITATS OFF THE COASTS OF THREE CAYS NEAR ANDROS ISLAND, BAHAMAS

Dawn M. Ford and W. Hardy Eshbaugh
Miami University,
Oxford, OH 45056

ABSTRACT

Wave-exposed and wave-sheltered habitats near Pigeon, Calabash, and Saddleback Cays, Bahamas were sampled in order to compare macrophyte species composition, richness, diversity, and biomass. Relationships between community type and environmental variables were examined.

Wave-exposed sites were co-dominated by *Batophora oerstedi* and *Valoniopsis pachynema*; wave-sheltered sites were co-dominated by *Thalassia testudinum* and *Batophora oerstedi*. Wave-exposed sites exhibited at least 2.2 times greater species richness, 2.5 times greater species diversity, and supported greater aboveground biomass than wave-sheltered sites.

Differences in community composition and structure between sites appeared to result from sediment depth. Wave-exposed sites, exposed to strong wave action, generally exhibited hard substrata with areas of shallow sand. Wave-sheltered sites, exposed to weak current velocity, had relatively deep sediment accumulation.

INTRODUCTION

The composition and structure of terrestrial plant communities have been well studied. The knowledge gathered and the theory developed from such studies has permitted comparisons between terrestrial communities. In contrast, there have been relatively few studies of benthic subtidal macrophyte communities. Past studies have been qualitative due to the difficulties of sampling underwater (John et al. 1977). However, with the availability of underwater diving techniques (SCUBA), it is possible to acquire quantitative data similar to those attained for terrestrial communities.

In the Caribbean, the spatial heterogeneity of benthic macrophyte communities and the factors controlling their structure and composition are significant elements of the ecosystem that should be addressed (Hanisak 1993). Most studies examining causal factors for macrophyte distribution have focused mostly on depth with little regard for other environmental variables (Chapman 1986). Factors not depth-related such as cumulative water movement, nutrient availability (Hiscock 1983), and substrate type (Morrissey 1980) have been suggested as important variables to be studied. Hiscock (1983) stressed that these three factors are strongly interrelated. Total water movement, which is a summation of tidal streams, wave action, and residual currents affects nutrient transport and substratum type and thereby affects seabed habitats and organisms occurring there.

This study examines benthic macrophyte communities occurring in the lagoon created by the barrier reef off the coast of Andros Island, Bahamas. Generally in high energy, wave-exposed areas, patch reefs provide heterogeneous habitats for establishment of many species of seaweeds and as a result often support communities of high species richness and diversity (Kaplan 1982). In contrast, in low energy wave-sheltered areas, seagrass beds occur in which generally few seaweed species can establish. This results in communities of low species richness and diversity.

The objectives of this study were (1) to examine differences in species composition, richness, diversity, and biomass between wave-exposed and wave-sheltered sites, and (2) to relate these differences to nutrient availability (NO_3^-), sediment depth, and current velocity.

MATERIALS AND METHODS

Andros Island lies east of Key West, Florida and is the largest of the Bahamian Islands (Eshbaugh and Wilson 1990). The west coast of Andros is fringed by the Great Bahama Bank and the east coast is bordered by the third largest barrier reef in the world (Abbott 1984). Three cays off the northeastern coast of Andros Island were sampled during the summer of 1994: Pigeon Cay (24°53'05" N - 24°52'55" N latitude and 77° 53'45" W - 77°53'40" W longitude), Calabash Cay (24°54' N latitude and 77°55' W longitude), and Saddleback Cay (24°56'00" N - 24°55'55" N latitude and 77°55'20" W - 77°55'05" W longitude) (Figure 1). These cays are similar in size and easily accessed by boat from Forfar Field Station.

Field Methodology

Six 50 m transects were sampled off the coast of each cay, three on the windward side (wave-exposed) and three on the leeward side (wave-sheltered). The location of the first transect was chosen randomly and successive transects were placed 25 m apart. Beginning at the approximate low tide mark, transects were marked at 5 m intervals parallel to one another and perpendicular to the shoreline. Chaining pins and sharpened carriage screws were used as markers. In hard substrata, an air drill was used to set the markers. In soft substrata, the markers were driven in using a hammer. Sampling was done at each 5 m marker in a 0.25 m^2 quadrat. In water < 2 m deep, sampling was accomplished by snorkeling; in water > 2 m, sampling was done using SCUBA. Sampling techniques were similar to those used by Van der Velde and King (1984).

Sampling was generally performed at low tide and all layers of vegetation were sampled by separating individuals to expose lower layers. Macrophytes unable to be identified in the field were placed in numbered plastic bags with seawater and taken to the lab for microscopic examination. Taylor (1960) and Littler and Littler (1989) were the primary sources used for identification. For each species, cover was estimated using the following percent cover classes:

<1
1-5
6-10
11-20
21-40
41-70
71-100

At each quadrat, depth and temperature were recorded. Substrate was recorded as hard (rock or coral) or soft (sand or mud), and the approximate depth of the sediment was measured. Current velocity was measured three times along each transect (5, 25, 50 m) at one minute intervals using a weighted mechanical current meter. At the end of the field season, quadrats at the 25 and 50 m points along each transect were harvested for aboveground biomass. Fleshy individuals were cut above the holdfast/rhizome with a knife, and crustose species were removed by scraping. The plants were dried in an oven at 70°c for approximately twelve hours before weighing (De Wreede 1985).

Nearshore water samples (three replicates) were collected on each side of each cay for salinity measurements and nutrient analyses (soluble nitrates). Second-derivative analysis was used for NO_3^- determination; its detection limit = <5 ug NO_3- -N liter^{-1} (Crumpton et al. 1992).

Voucher specimens were dried or preserved in a 3:1 solution of seawater and formalin (Tsuda and Abbott 1985) and were deposited in the Willard Sherman Turrell Herbarium (MU). Assistance in identification of several specimens was given by Drs. Mark and Diane Littler of the Smithsonian Institution.

Data Analysis

Species diversity was calculated using the Shannon-Weaver index (1949). Species importances were expressed as the mean of relative values of cover and frequency. Results were expressed as species equivalents, exp H' = antilog [-sum p_i (log p_i)]. Differences in biotic and abiotic parameters between transects and sites were examined by t-tests (Sigma Plot). Regression analysis was used to examine relationships between environmental variables and species composition using

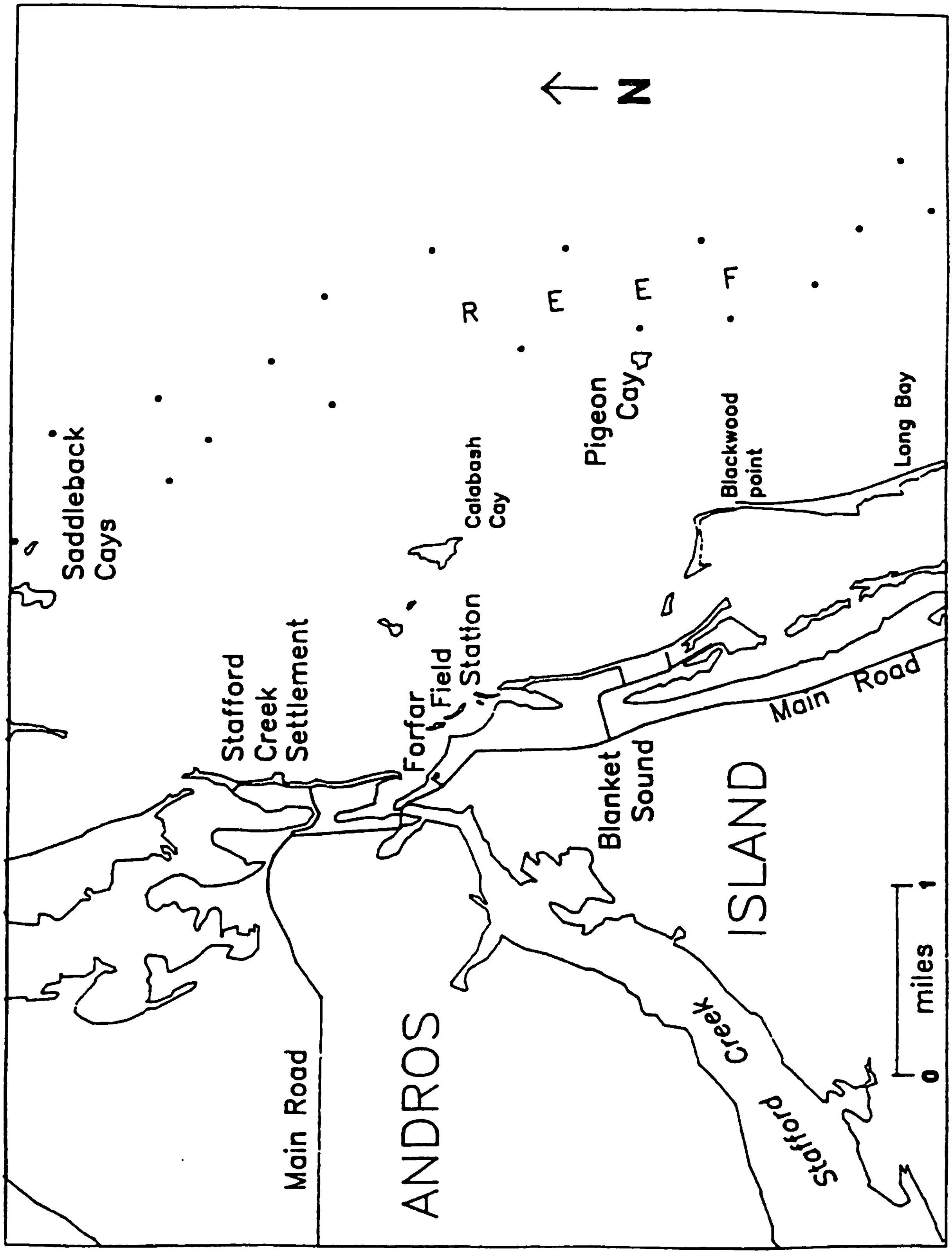

Figure 1. Map of Pigeon, Calabash, and Saddleback Cays, Bahamas

detrended correspondence analysis axes (Canoco). In all statistical analyses, alpha = .05.

RESULTS

Species Composition

Specimens of 100 species of macrophytes were sampled, 97 were identified (43 Chlorophyta, 17 Phaeophyta, 34 Rhodophyta, 3 Spermatophyta); three species remain unidentified and were named Unknowns 1, 2; and 3.

Floristic data for wave-exposed and wave-sheltered sites at Pigeon Cay, Calabash Cay, and Saddleback Cay are found in Table 1. Of the 100 species, eight were ubiquitous (occurred off each side of each cay): *Acetabularia crenulata*, *Batophora oerstedi*, *Dictyosphaeria cavernosa*, *Halimeda incrassata*, *Halimeda monile*, *Valoniopsis pachynema*, *Udotea flabellum*, and *Laurencia intricata*. Pigeon Cay samples had 67 species documented, 28 of which were found only there. Of the 47 species sampled at Calabash Cay, 8 were unique and of the 52 species collected at Saddleback Cay, 11 were found only there.

The dominant species based on relative importance percentages at the wave-exposed (windward) site of Pigeon Cay was *Valoniopsis pachynema* (Table 2). Subdominants included *Batophora oerstedi*, *Sargassum pteropleuron*, *Halimeda tuna*, *Microdictyon marinum*, and *Sargassum hystrix var. buxifolium*. The wave-sheltered (leeward) site was dominated by the angiosperm *Thalassia testudinum* and *Batophora oerstedi*, followed by *Valoniopsis pachynema*.

The wave-exposed site at Calabash Cay was co-dominated by *Batophora oerstedi* and *Valoniopsis pachynema*, followed by *Halimeda tuna*, *Acetabularia crenulata*, and *Laurencia intricata*. The wave-sheltered site was co-dominated by *Batophora oerstedi* and *Thalassia testudinum* followed by *Halimeda incrassata*, *H. monile*, and *H. tuna*.

At Saddleback Cay, the wave-exposed site was dominated by *Batophora oerstedi*, *Sargassum pteropleuron*, and *Valoniopsis pachynema*, and subdominants were *Acetabularia crenulata*, *Dictyosphaeria cavernosa*, *Halimeda tuna*, and *Microdictyon marinum*. The wave-sheltered site was dominated by *Batophora oerstedi* and *Thalassia testudinum*. Others included *Halimeda incrassata*, *Acetabularia crenulata*, and *Halodule beaudettei*.

Species Richness and Diversity

Of the wave-exposed areas, Pigeon Cay had the greatest species richness followed by Calabash and Saddleback (Table 3). Of the wave-sheltered areas, the greatest number of species occurred with Pigeon Cay, followed by Saddleback, and Calabash. For all cays, species diversity was at least 2.5 times higher at the wave-exposed site (Table 4). Pigeon Cay exhibited the highest species diversity, and Calabash and Saddleback had nearly identical values.

Biomass

At all cays, the aboveground biomass was greater at wave-exposed sites than wave-sheltered sites; there were statistically-significant differences between the sides of Calabash and Saddleback (Table 5).

Environmental Factors

The depth gradient ranged from 0.3 to 1.8 m. Salinity values ranged between 35.9 and 37.1 (ppt); there were no statistically-significant differences between sides of a cay or between cays. There were no statistically significant differences between cays or sides of a cay for the level of soluble nitrate; the overall mean was 31.25 ug/l NO_3.

The substrate was generally coral and limestone rock with expanses of 1 to 2 cm of sand on wave-exposed sides of cays, while on wave-sheltered sides, sediments were 2-60 cm or deeper. There were statistically-significant differences between the sides of each cay.

There were statistically-significant differences of current velocity between sides of Calabash, but not at the other sites.

Temperatures (°C) ranged from 28 in the deepest areas to 33 in the shallowest areas. There were no statistically-significant differences between sides of a cay; however, Calabash Cay exhibited statistically-

Table 1. Floristic data for Pigeon Cay, Calabash Cay, and Saddleback Cay.

		Leeward Sites			Windward Sites		
CHLOROPHYTA	*	PIG	CAL	SAD	PIG	CAL	SAD
Acetabularia crenulata		X	X	X	X	X	X
Anadyomene saldanhae							X
Anadyomene stellata		X					
Avrainvillea levis		X					
Avrainvillea longicaulis					X		
Avrainvillea nigricans					X		
Avrainvillea rawsonii			X				
Batophora oerstedi		X	X	X	X	X	X
Caulerpa cupressoides		X		X			
Caulerpa lanuginosa		X	X	X			
Caulerpa mexicana		X		X			
Caulerpa prolifera		X	X	X			
Caulerpa racemosa		X					
Caulerpa sertularioides					X		
Caulerpa verticilllata		X					X
Cladocephalus luteofuscus		X					
Cladophoropsis membranacea				X			
Derbesia vaucheriaeformis			X				X
Dictyosphaeria cavernosa		X	X	X	X	X	X
Dictyosphaeria ocellata		X		X			X
Halimeda discoidea				X			
Halimeda incrassata		X	X	X	X	X	X
Halimeda lacrimosa var. lacrimosa		X					
Halimeda monile		X	X	X	X	X	X
Halimeda tuna		X	X	X	X	X	
Microdictyon marinum		X	X	X	X		
Neomeris annulata		X		X			
Penicillus capitatus		X	X		X	X	X
Penicillus lamourouxii			X				X
Polyphysa polyphysoides		X	X	X			
Rhipilia tomentosa				X			
Rhipocephalus oblongus			X	X			X
Rhipocephalus phoenix		X	X	X	X		
Udotea cyathiformis		X	X	X	X	X	
Udotea flabellum		X	X	X	X	X	X
Udotea occidentalis				X			
Udotea spinulosa							
Udotea wilsoni			X	X			
Valonia aegogropila							
Valonia macrophysa		X	X	X	X		
Valoniopsis pachynema		X	X	X	X	X	X
Ventricaria ventricosa		X		X			
PHAEOPHYTA							
Cystoseira myrica		X					
Dictyota bartayresii		X					

	PIG	CAL	SAD	PIG	CAL	SAD
Dictyota cervicornis	X	X	X		X	
Dictyota linearis	X	X	X			
Dictyota pfaffi	X					
Dilophus guineensis	X	X				
Lobophora variegata	X					
Padina jamaicensis	X					
Padina sanctae-crucis	X			X		
Rosenvingea intricata						X
Sargassum cymosum			X			X
Sargassum hystrix var. buxifolium	X	X				
Sargassum natans		X				
Sargassum platycarpum		X				
Sargassum pteropleuron	X	X	X			
Sargassum sp.		X				
Turbinaria turbinata	X					

RHODOPHYTA

Amphiroa fragilissima	X			X		
Amphiroa rigida var. antillana	X					
Anotrichium tenue	X					
Callithamnion cordatum			X			
Ceramium rubrum	X	X				
Chondria curvilineata			X			
Chondria tenuissima		X	X			
Coelothrix irregularis	X		X			
Digenia simplex	X					
Tricleocarpa oblongata	X		X			
Gelidiella acerosa	X					
Gelidiella setacea	X	X				
Graciliaria damaecornis			X			
Heterosiphonia gibbesii						
Hydrolithon boergesenii	X	X	X			
Hypnea cervicornis	X					
Hypnea sp.	X					
Jania adherens	X	X				
Laurencia cervicornis	X					
Laurencia corallopsis	X					
Laurencia intricata	X	X	X	X	X	X
Laurencia microcladia						
Laurencia poitei	X					
Liagora farinosa						
Liagora pinnata	X	X				
Mesophyllum mesmorphum	X					
Neogoniolithon spectabile	X			X	X	
Neogoniolithon strictum	X		X	X		
Peyssonnelia sp.		X	X	X		
Spyridia complanata		X				
Spyridia filamentosa		X				
Titanoderma bermudense	X		X			
Trichogloea requienii	X					
Wrangelia argus			X			

	PIG	CAL	SAD	PIG	CAL	SAD
SPERMATOPHYTA						
Halodule beaudettei					X	X
Syringodium filiforme						X
Thalssia testudinum		X		X	X	X
UNKNOWNS						
Unknown 1	X					
Unknown 2			X			
Unknown 3	X	X		X		

* PIG = Pigeon Cay
CAL = Calabash Cay
SAD = Saddleback Cay

X = present

Table 2. Mean importance percentages for major species at each site.

	Pigeon		Calabash		Saddleback	
	W	L	W	L	W	L
Chlorophyta						
Acetabularia crenulata	1.6	1.4	6.1	4.2	8.0	7.1
Batophora oerstedi	8.9	24.4	26.4	34.5	17.8	30
Dictyosphaeria cavernosa	2.7	2.5	2.6	0.9	6.5	0.6
Halimeda incrassata	2.8	2.5	1.0	6.6	1.1	8.5
Halimeda monile	1.3	4.0	1.4	5.7	0.5	1.8
Halimeda tuna	7.7	4.6	8.8	5.0	6.2	0.0
Microdictyon marinum	7.6	4.6	2.2	0.0	5.6	0.0
Valoniopsis pachynema	13.2	6.9	15.3	2.5	13.8	0.6
Phaeophyta						
Sargassum hystrix	5.2	0.0	1.2	0.0	0.0	0.0
Sargassum pteropleuron	7.9	0.0	0.0	0.0	13.7	0.0
Rhodophyta						
Laurencia intricata	0.0	1.8	5.6	0.5	0.0	0.5
Spermophyta						
Halodule beaudettei	0.0	0.0	0.0	0.8	0.0	5.0
Thalassia testudinum	0.0	29.1	2.9	34.4	0.0	35.8

W = Windward
L = Leeward

Table 3. Species richness for each transect and each side.

Pigeon		Calabash		Saddleback	
Windward					
ABC	65	GHI	45	MNO	43
A	33	G	26	M	28
B	46	H	35	N	24
C	46	I	25	O	31
Leeward					
DEF	24	JKL	15	PQR	20
D	16	J	11	P	14
E	18	K	10	Q	13
F	13	L	5	R	10

Table 4. Species diversity (Shannon's index, exp H') for each transect and each side in species equivalents.

Pigeon		Calabash		Saddleback	
Windward					
ABC	27.2	GHI	17.7	MNO	17.0
A	20.6	G	13.3	M	14.4
B	23.3	H	16.4	N	13.2
C	28.1	I	13.0	O	16.0
Leeward					
DEF	10.9	JKL	6.2	PQR	6.5
D	10.5	J	6.7	P	6.4
E	9.6	K	5.6	Q	5.3
F	6.2	L	3.4	R	6.0

Table 5. Depth range, mean salinity, soluble nitrate, sediment depth, temperature, current velocity and aboveground biomass at each site.

	Depth Range m	Salinity ppt	Nitrate ug/l NO3-N	Sediment cm	Temp. c	Current cm/s	Biomass g/m2
Pigeon							
Windward	1.0-2.2	35.9	32.3	*1.0	29.2	32.6	242.1
Leeward	0.8-1.0	36.9	29.2	18.0	29.4	24.7	**224.4
Calabash							
Windward	0.3-1.4	35.6	30.7	*2.3	**31.8	*23.6	*378.6
Leeward	0.3-0.9	35.7	35.3	23.3	**32.5	15.3	39.8
Saddleback							
Windward	0.9-1.8	37.1	32.4	*1.1	29.8	18.6	*366.4
Leeward	0.8-1.2	36.7	27.7	36.1	29.3	23.3	75.2

* = statistically significantly different from leeward side

** = statistically significantly different from corresponding side of other cays

significantly higher temperatures than the other cays.

Vegetation-Environment Relationships

The results of the regression analysis of sediment depth and axis 1 and 2 values exhibited a statistically-significant relationship with p values less than .05 (p=.0001 and .001 respectively). The axis 1 r^2 was 61.7%; the axis 2 r^2 was 5.6%.

DISCUSSION

Species Composition

The species occurring off windward coasts were generally a combination of macrophytes excluding seagrasses. The algae that occurred in these habitats included fleshy seaweeds such as *Sargassum spp.*, *Dictyota spp.*, and most red algal species which have holdfasts that easily attach to rock or coral; erect calcareous species such as *Halimeda* and *Rhipocephalus spp.* which are able to root in the few centimeters of sand present in some areas; and encrusting calcareous species such as *Peyssonnelia sp.* and *Hydrolithon boergesenii* which creep along hard substrata.

The species assemblages found in wave-sheltered sites were very similar to those documented by Thorhaug (1977) for a subtropical lagoon in Biscayne Bay, Florida including *Thalassia testudinum*, *Laurencia spp.*, *Penicillus capitatus*, *Halimeda incrassata*, *Acetabularia crenulata*, *Rhipcephalus phoenix*, *Udotea flabellum*, *Batophora oerstedi*, and *Caulerpa sertularoides*. It was anticipated that these particular species would establish themselves in such habitats because the calcareous greens (*P. capitatus*, *H. incrassata*, *R. phoenix*, *U. flabellum*, and *C. sertularoides*) possess a mass of rhizoids allowing establishment in soft substrates (Neumann and Land 1975); the grass species possess extensive mats of "underground" rhizomes. The small fleshy species (*Laurencia spp.*, *A. crenulata*, and *B. oerstedi*) are able to attach to occasional shell or small rock fragments within the sediment by holdfasts. Shells and small rocks are relatively unstable compared to subtidal rock, and large perennial species of *Sargassum*, for example, cannot establish (Sears and Wilce 1975).

Thalassia testudinum was by far the dominant seagrass species. The two other seagrass species, *Syringodium filiforme* and *Halodule beaudettei* were only encountered at 1 or 2 sites, respectively. These grass species have been characterized as pioneer species that colonize disturbed habitats and cannot compete with the thick-bladed *T. testudinum* because of shading and competition for nutrients (Williams 1990).

Of the eight species occurring at all sites, *Batophora oerstedi* and *Valoniopsis pachynema* were the most ubiquitous and co-dominated all wave-exposed sites. *Halimeda spp.* also frequently dominated the areas sampled. These species are often referred to as the most important seaweed species of tropical reef systems (Kaplan 1982). The sand beaches of Andros Island and associated cays are largely comprised of the calcium carbonate skeletons of Chlorophyte algae, and *Halimeda spp.* are a major contributor (Littler and Littler 1989).

Species Richness and Diversity

As hypothesized, there was greater species richness and diversity of macrophyte communities at wave-exposed sites compared to wave-sheltered sites. Littler and Littler (1985) emphasized that the shallow rocky subtidal ecosystem supports more macroalgal species than any other marine habitat. This is partly due to the variety of substrates available for establishment of species. The leeward sides of the cays were relatively homogenous habitats with little topographic complexity and a single dominant substrate type, while the windward sides exhibited many microhabitats with extensive rock, sand, and coral substrate types which can support more species (Levinton 1982). Seaweeds are not effective in colonizing sedimentary substrata; seagrasses usually displace macroalgae as the dominant vegetation of sediments (Barnes and Hughes 1982).

Biomass

The greater aboveground biomass at wave-exposed sites compared to wave-sheltered sites was expected because the rocky subtidal has been documented to support greater biomass than any other marine habitat (Littler and Littler 1985). Moreover, the average biomass of a seaweed is approximately 25% greater than the biomass of a single marine vascular plant (Barnes and Hughes 1982).

The high biomass documented on the leeward side of Pigeon Cay may be due to the cay's small size and proximity to the main reef. Even on the leeward side, current velocity would be expected to be relatively high, although not proven in this study. This would result in less sediment accumulation and establishment of small coral heads increasing topographical complexity, allowing for greater macrophyte biomass.

The aboveground biomass for seagrass beds was extremely low compared to the 800 g m^{-2} (dry wt) value given by Barnes and Hughes for a similar tropical site (1982). In this study, the lowest values are exhibited at Calabash (wave-sheltered) where sand mounds caused by burrowing invertebrates, were present, probably the result of a shrimp species. Seagrasses cannot establish in these areas resulting in an extremely patchy community (Mark Boardman, pers. comm.).

Environmental Factors

Salinity.

Salinity values were within the range expected for the open ocean, which typically varies between 33 and 38 ppt (Levinton 1982). The absence of statistically-significant differences between cays or between sides of a cay was unexpected. Salinity tends to increase in water that has restricted circulation, so a greater salt concentration was expected on leeward sides compared to windward sides.

Nutrients.

The amount of macroalgal growth is largely regulated by the availability of nutrients in the water column (Knoppers 1994). Surface values of nitrate range between 1 and 120 ug/l NO_3-N, with highest values in the winter and lowest in the summer (Tait 1981). The values measured in this study are near the lower end of this range. Levels of nitrate were expected to be significantly higher at wave-exposed sites because strong water movement can increase the quantity of nutrients (Hiscock 1983); however, no differences were found.

Substrate.

The types of materials that form the sea floor are a result of several conditions including the speed of the bottom current, depth, proximity to shore and features of the coastline, and types of suspended matter in the water column. Substrate type (sediment depth), which is a result of intensity of water movement, was the only abiotic factor found to be consistently different between wave-exposed and wave-sheltered sites. It appears that what particular substrate is available determines which macrophyte species can establish. Those species that possess rhizomes or rhizoids are able to colonize sediments. For grass species, the sediment not only serves as a site of attachment, but serves as a nutrient source much like soil for terrestrial vascular plants. Some algal species that are able to establish in sand plains do not have rhizoids, but holdfasts that require shell, rock, or coral fragments in the sand (Hay 1981). Most seaweed species with holdfasts, especially large species, as well as encrusting coralline red algae require solid substrata to grow to maturity (Sears and Wilce 1975).

Current Velocity.

The greater flow rates anticipated for wave-exposed sites compared to wave-sheltered sites were determined for only one cay, Calabash. Personal observation suggests that current velocities were much greater at all wave-exposed sites. This discrepancy may be the outcome of ineffective methods for measuring water velocity. Littler and Littler (1985) emphasized that a measurement of water motion is a complex task; perhaps a more modern electromagnetic device would have been more accurate.

Temperature.

In low latitudes, the surface water of marine systems is usually between 26 and 30°C; however in shallow areas or partially enclosed ones, the temperature may reach 35°C (Tait 1981). The mean temperature of waters surrounding Pigeon and Saddleback fell within the normal range; Calabash exhibited statistically-significantly warmer temperatures likely the result of extremely shallow waters on both sides of the cay.

CONCLUSIONS

The wave-exposed and wave-sheltered habitats of Pigeon, Calabash, and Saddleback Cays supported benthic macrophyte communities that were different in species composition, richness, diversity, and biomass. Of the environmental factors examined in this study, only sediment depth was consistently different between habitats.

The type of substrate available is a result of wave action; the stronger the cumulative water movement, the less sediment that can accumulate. The wave-exposed areas, typically characterized by patch reef and limestone rock substrata with shallow sediment, maintained the most diverse assemblages of seaweeds including erect calcareous greens, upright filamentous species, creeping crustose reds, and large perennial browns. In contrast, wave-sheltered areas of seagrass meadows and mangroves were dominated by angiosperms, most frequently *Thalassia testudinum*, with few macroalgal species. The most dominant species at all sites were *Batophora oerstedi*, *Valoniopsis pachynema*, and *Thalassia testudinum*. These species all exhibit a mat-like growth form and can establish in many types of environments.

These differences in species

composition between the two habitat types reflect differences in means of attachment by macrophytes to substrates. Species with holdfasts are only able to establish on hard substrata, whether it be solid rock or small rock or shell fragments within sediment. Species with rhizoids or rhizomes can grow only in accumulated sediment.

ACKNOWLEDGMENTS

We extend our appreciation to International Field Studies for allowing us to accomplish this project. Logistical support for our research was provided by Ms. Erica Dryden and the staff of Forfar Field Station. Financial support was contributed by an Academic Challenge Grant (Botany Department, MU) and a Willard Sherman Turrell Herbarium Fund Grant (MU).

LITERATURE CITED

Abbott, K.S. 1984. The marine algal flora of three blue holes off Andros Island, Bahamas. Master's Thesis, Duke University

Barnes, R.S.K. and R.N. Hughes. 1982. An Introduction to Marine Ecology. Blackwell, London.

Chapman, A.R.O. 1986. Population and community ecology of seaweeds. *In* Advances in Marine Biology, vol. 23. Blaxter, J.H.S. and A.J. Southward, eds. pp. 1-163.

Crumpton, W.G., T.M. Isenhart, and P.D. Mitchell. 1992. Nitrate and organic N analyses with second-derivative spectrosopy. Limnology and Oceanography 37(4): 907-913.

De Wreede, R.E. 1985. Destructive (harvest) sampling. *In* Handbook of Phycological Methods, Ecological Field Methods: Macroalgae. Littler, M.M. and D.S. Littler, eds. pp. 147-160. Cambridge University Press, London.

Eshbaugh, W.H. and T.K. Wilson. 1990. The tropical flora of Andros Island, Bahamas: Observations and notes. *In* Proceedings of the 3rd Symposium on the Botany of the Bahamas. Smith, R.R., ed. pp. 17-23. Bahamian Field Station, San Salvador, Bahamas.

Hanisak, M.D. 1993. Shallow macroalgae communities associated with seagrass beds on Exuma Bank, Bahamas. Journal of Phycology 29 (supplement): 21.

Hay, M.E. 1981. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. The American Naturalist 118(4): 520-539.

Hiscock, K. 1983. Water movement. *In* Sublittoral Ecology. The Ecology of the Shallow Sublittoral Benthos. Earll, R. and D.G. Erwin, eds. 58-96. Clarendon Press, Oxford.

John, D.M., D. Lieberman, and M. Leiberman. 1977. A quantitative study of the structure and dynamics of benthic subtidal algal vegetation in Ghana (Tropical West Africa). Journal of Ecology 65: 497-521.

Kaplan, E.H. 1982. A Field Guide to Coral Reefs of the Caribbean and Florida. Houghton Mifflin, Boston.

Knoppers, B. 1994. Aquatic primary production in coastal lagoons. *In* Coastal Lagoon Processes. Kjerve, B., ed. pp. 243-286. Elsevier, Amsterdam.

Levinton, J.S. 1982. Marine Ecology. Prentice-Hall, New Jersey.

Littler, D.S. and M.M. Littler. 1985. Phycological Methods: Macroalgae. Smithsonian Institute.

Littler, D.S., M.M. Littler, K.E. Bucher, and J.N. Norris. 1989. Marine Plants of the Caribbean:A Field Guide from Florida to Brazil. Smithsonian Institution Press, Washington D.C.

Neumann, A.C. and L.S. Land. 1975. Lime mud deposition and calcareous algae in the bight of Abaco, Bahamas: A budget. Journal of Sedimentary Petrology 45: 763-786.

Morrissey J. 1980. Community structure and zonation of macroalgae and hermatypic corals on a fringing reef flat of Magnetic Island (Queensland, Australia). Aquatic Botany 8(2): 91-139.

Sears, J.R. and R.T. Wilce. 1975. Sublittoral, benthic marine algae of southern Cape Cod and adjacent islands: seasonal periodicity, associations, diversity, and floristic composition. Tait, Ecological Monographs 45: 337-365.

Tait, R.V. 1981. Elements of Marine Ecology. Butterworths, London.

Taylor, William Randolph. 1960. Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas. The University of Michigan Press, Ann Arbor.

Thorhaug, A. and M.A. Roessler. 1977. Seagrass community dynamics in a subtropical estuarine lagoon. Aquaculture 12: 253-277.

Tsuda, R.T. and I.A. Abbott. 1985. Collection, handling, preservation, and logistics. *In* Handbook of Phycological Methods, Ecological Field Methods: Macroalgae. Littler, M.M. and D.S. Littler, eds. pp. 67-86. Cambridge University Press, London.

Van Der Velde, J.T. and R.J. King. 1984. The subtidal seaweed communities of Bare Island, Botany Bay. Wetlands (Australia) 4: 7-22.

Williams, S.L. 1990. Experimental studies of Caribbean seagrass bed development. Ecological Monographs 60(4): 449-469.