ATOLL RESEARCH BULLETIN

NO. 387

DISTRIBUTIONAL CONTROL OF SEAGRASSES BY LIGHT AVAILABILITY,

TWIN CAYS, BELIZE, CENTRAL AMERICA

 $\mathbf{B}\mathbf{Y}$

J.A. CALEM AND J.W. PIERCE

ISSUED BY NATIONAL MUSEUM OF NATURAL HISTORY SMITHSONIAN INSTITUTION WASHINGTON, D.C., U.S.A. JANUARY 1993

INSTRIBUTIONAL CONTROL OF SEAGRASSES BY LIGHT AVAILABILITY,

TWIN CAYS, BELIZE, CENTRAL AMERICA

ΒY

J.A. CALEM¹ AND J.W. PIERCE²

ABSTRACT

Twin Cays are two mangrove islands in the lagoon behind the barrier reef of Belize, Central America with radically different aquatic environments in close juxtaposition. These environments range from open lagoon, with very clear water, to channels with high turbidity, and to creeks immediately adjacent to the mangrove swamps with reddish-brown water. Thirty-eight measurements of beam transmission of blue and green light were made at 11 stations in the channels and creeks of Twin Cays and a few at 2 stations in the open lagoon. Seagrasses, primarily <u>Thalassia testudinum</u>, occur only where blue wavelengths of light can penetrate to the bottom. Loss of blue light is due to either absorption by tannin or backscattering out of the water by suspended particles. Seagrasses are absent in the upper reaches of the tributary channels and creeks because the reddish-brown water, emanating from the mangrove swamps, effectively absorbs blue light. Such plants also are absent from areas that have high turbidity, resulting in scattering of the light and reflection back out of the water. This high turbidity is the result of high concentrations of suspended mineral particles, transported into the major channel between the islands by wind drift, after resuspension of bottom sediments by waves in the main lagoon. Elsewhere, seagrasses are common in Main Channel and lower reaches of the tributary channels.

INTRODUCTION

2

The type and density distribution of seagrasses in the subquatic environments of the Twin Cays area of Belize vary considerably from place to place. The factors controlling the distribution of this vegetation are not readily apparent in some of the areas. Four things are important and necessary for plant growth: energy from solar radiation, carbon in the form of CO_2 or HCO_3^- , mineral nutrients, and water (Kirk, 1983). Changes in salinity could exert some control on type and density of growth in small areas subjected to extreme runoff after heavy rains. It is doubtful that carbon or

 ¹Statistical Policy Branch, Environmental Protection Agency PM-223 401 M Street SW Washington, D.C. 20460
²Sedimentology Laboratory, Department of Paleobiology MS 125 Museum of Natural History, Smithsonian Institution Washington, D.C. 20560

Manuscript received 30 January 1992; revised 28 September 1992

mineral nutrients are limiting factors, considering the small size of the area and the efficient tidal mixing of the waters. This reconnaissance project is an attempt b determine if the lack of certain wavelengths of light might be a controlling factor for the distribution of some of the seagrasses in the channels and the reason for the deficiency.

Twin Cays is a remnant Pleistocene high (Shinn et al, 1982), lying in the lagoch between the barrier reef and the mainland of Belize, Central America (Fig. 1). Twin



Figure 1. Location map of Twin Cays and location of stations 1 and 2 in lagoon. Outlined area shown in detail in Figure 2.

Cays is approximately 2 km west of the barrier reef and 20 km east of the mainland. Twin Cays consists of two mangrove islands, East and West Islands, separated longitudinally by Main Channel, the major outlet from the mangrove swamps to the deeper lagoonal waters. (Fig. 2). The islands have a land area of 1.8 km². Maximum depth of Main Channel is about 2.5 m, with extensive shoals existing around the margins. Both islands are cut by a complex network of shallow channels draining standing ponds and the densely vegetated mangrove swamps.



Figure 2. Map of Twin Cays showing location of stations 3 through 13, named features in area, and bottom types.

The region has two seasons, a dry season from November through May and a wet season the remainder of the year with a few weeks transition between the two

3

(Rützler and Ferraris, 1982). Rain falls nearly every day during the wet season resulting in considerable fresh water runoff from the mangrove swamps.

Dramatic changes in water color and type of material on the bottoms of the channels occur in the Twin Cays area. Water in Main Channel is milky, greenish-blue, often transparent enough to see to the channel bottom. The channel bottom consists of white carbonate sediments. Seagrasses (primarily <u>Thalassia testudinum</u>) grow in profusion over much of the channel bottom except at the north and south ends. Here, the channel floor is bare carbonate sand, sparsely littered with mangrove leaves. Currents associated with north winds carry fine carbonate sediments from shoals, just north of the channel mouth, into the north end of the channel. During these times, the water is highly turbid and it is impossible to see the bottom. A similar situation occurs at the south end of the channel with material swept off the shoals at the south end of East Island by either by refraction of waves around the point, during northerly winds, or as a result of waves generated by southerly winds.

In the creeks and narrow tributary channels, the color of the water changes to deep reddish-brown, colored by tannin leached from the mangrove swamps. The change is abrupt in Lair Channel, occurring over a horizontal distance of less than 2 m, whereas in Boston Bay the change is more gradual, occurring over a distance of 10 m or more. The bottoms of the tributary channels consist of a dark brown organic ooze. Seagrasses grow only in the shallowest parts of these channels, if they are present at all.

Tides, wind velocity and direction, and rainfall greatly affect the water quality in the channels of Twin Cays. Tidal currents scour the floor of the channels when water is funnelled into narrow, shallow channels and creeks. Although relatively well protected from direct winds, a strong current can set up in Main Channel, depending on the strength and direction of the wind. During the times of our sampling, very little resuspended carbonate was transported any great distance into the tributary channels.

Ebb tide moves tannin-charged water from the swamps into the tributary channels. At times of heavy rain there is considerable discharge of fresh water from the swamps such that the tributary channels contain mostly brown water. No brownish water was observed in Main Channel during our sampling, even though several heavy rainstorms occurred.

METHODS

We made trips to Belize in February, 1989 and March, 1990. Both times were during the supposedly "dry" season but in both cases the weather was unseasonably wet, cold, stormy and windy. This reduced the amount of time available for sampling as well as producing unexpected conditions of heavy runoff of fresh water from the mangrove swamps. Sampling was done at stations in Main Channel and tributaries thereto where water depth was sufficient to operate a small boat (Fig. 2). Two stations in the lagoon, about halfway between Twin Cays and Carrie Bow Cay were also occupied (Fig. 1). These two stations provided a base line of clear water against which the data from the stations in the Twin Cays area could be compared.

Stations were occupied in the morning and afternoon each day, weather permitting, to collect light transmission data and water samples. A Martektm transmissiometer was used to obtain light transmission values over a 1/4-meter horizontal path length; readings were made throughout the water column at 1/2- or 1/4-m intervals from near-surface to near-bottom at each station. Transmission data were converted to attenuation per meter (c/m) by:

c/m = 4[-ln(t)]

where t is the decimal fraction of light transmission per quarter-meter path length. The transmissometer was calibrated in air at 86.5% transmission. In 1989, a green filter (Wratten 61, peak transmission 520 nm) was used in the transmissometer. In 1990, we used the green filter early in the sampling but later installed a blue filter (Wratten 47B, peak transmission 430 nm). The transmissometer only allows insertion of one filter at a time so that the two filters could not be used concurrently. Transmission data from 1985, using different equipment, are also available.

Water samples were collected at near-surface and near-bottom depths at most stations every time the stations were occupied. In a few cases integrated samples of the entire water column were collected, primarily at very shallow stations or if the light transmission profile indicated an homogeneous water column. In 1989, replicate water samples were taken at each depth. The water samples were kept on ice until return to the base station, at which time they were filtered through pre-weighed $0.6\mu m$ (nominal pore diameter) Nucleoporetm filters. The filters were stored on ice until return to the laboratory in Washington for determination of concentrations of suspended particulates. Concentrations of total suspended material (TSM) were determined gravimetrically; concentrations of mineral suspended material (MSM) were determined by firing the filters at 1000°C, which destroys the filter in addition to the organic fraction, and weighing the remaining material. Concentrations of organic suspended material (OSM) were determined by the difference between TSM and MSM. No equipment was available for salinity measurement or for fluorescence to measure chlorophyll a concentration. We used a visual measure of water color as a rough indicator of dissolved tannin concentration in the water. We have no independent quantitative measure of dissolved tannin concentration. OSM, therefore, is an underestimation of the total concentration of organic compounds in the water, dissolved or particulate, at any station.

6

RESULTS AND DISCUSSION

Concentrations of suspensates and light attenuation data by sampling station revealed that marked differences in these values occur over relatively short distances in the Twin Cays area (Table 1). Temporal changes also occurred on a relatively short time scale. For example, there were large differences between the open lagoon (stations 1 and 2) where concentrations of suspensates and light attenuation were consistently low, to Main Channel (stations 3, 4 and 6), where concentrations of mineral suspensates were quite high under certain wind conditions and light attenuation varied sympathetically with concentration. In the small creeks and secondary channels

	TABLE 1														
					BLUE	GRN				1994 - A. 1994 -		A	BLU	GRN	
STA.	YR	TSM	OSM	MSM	ATTN	ATTN		STA.	YR	TSM	OSM	MSM	ATT	ATT	
1	89	0.12	0.00	0.12		0.12		10S	90	0.57	0.32	0.25		0.70	
2	89	0.12	0.00	0.12		0.00		10B	90	2.99	0.64	2.35		0.72	
6S	89	0.62	0.16	0.46		0.47		5S	90	0.57	0.46	0.10		0.29	
6B	89	0.86	0.04	0.82		0.68		5B	90	0.40	0.22	0.19		0.08	
7	89	1.09	0.64	0.45		1.07		13	90	0.59	0.35	0.24		0.42	
9	89	1.14	0.67	0.47		1.58		3S	90	0.43	0.36	0.07	0.00		
13	89	0.18	0.00	0.18		0.75		3B	90	1.40	0.54	0.86	0.17		
38	89	1.04	0.73	0.31		1.26		4	90	0.71	0.25	0.46	0.17		
3B	89	2.08	0.84	1.24		1.60		12	90	2.36	1.39	0.96	0.88		
4	89	0.87	0.55	0.32		0.84		11 S	90	0.24	0.00	0.24	0.54		
35	89	0.99	0.23	0.76		0.51		11B	90	0.60	0.18	0.42	0.37		
3B	89	1.55	0.55	1.00		1.54		10S	90	1.83	1.80	0.03	3.70		
4	89	0.66	0.00	0.66		0.70		10B	90	1.31	1.31	0.00	1.59		
11S	89	0.57	0.16	0.41		1.10		7S	90	0.71	0.64	0.07	1.97		
11B	89	0.58	0.33	0.25		0.88		7B	90	1.59	0.85	0.74	1.24	•	
12	89	0.76	0.07	0.70		1.05		6S	90	0.42	0.07	0.35	0.95		
3S	90	0.97	0.41	0.55		0.65		6B	90	0.76	0.52	0.24	1.29		
3B	90	1.07	0.55	0.52		0.65		13	90	2.7	2.42	0.29	1.42		
11S	90	0.84	0.40	0.44		0.65		8S	9 0	1.24	0.99	0.25	1.94		
11B	90	0.79	0.25	0.54		0.75		8B	90	0.71	0.35	0.36	1.14		
									BLUE	GRN					
					TSM	OSM		MSM	ATT	ATT					
				AVE	0.96	0.51		0.47	1.16	0.76					
				STD	0.65	0.50		0.42	0.91	0.43					
				N	40	40		40	15	25					
				MAX	2.99	2.42		2.35	3.70	1.60					
				MIN	0.12	0.00		0.00	0.00	0.00					
					0.12	0.00		0.00	0.00	0.00					

Table 1. Concentrations of total, organic, and mineral suspensates (mg/l) in samples and blue and green attenuation values (c/m) for 1989 and 1990 readings. S and D after station numbers indicate near-surface (S) and near-bottom (D) samples.

of the mangrove swamps, high concentrations of organic material were found and blue light was more highly attenuated than green light.

Beam attenuation of selected wavelengths of light is dependent upon absorption by the water as well as upon absorption and scattering by constituents, either dissolved or suspended, in the water. Since scattering is generally not wavelength sensitive, except when highly colored particles are present (Jerlov, 1976), blue and green wavelengths should be equally affected by scattering. Absorption is wave length dependent. Therefore, we assume that, if the green and blue wave lengths were similarly affected under the same conditions, scattering predominated.

Least squares regression analysis (outliers dropped) reveals that attenuation of green light is significantly correlated with TSM at the .999 confidence level (Fig. 3), as well as with the concentrations of MSM and OSM at the same confidence level. Attenuation of blue light, on the other hand, is correlated only with the concentration of OSM at a .997 confidence level (Fig. 4), and is not significantly correlated with either the concentration of TSM or MSM. This suggests that the dominant cause of blue light attenuation is absorption by organic material, not scattering. Dissolved organic



Figure 3. Plot of green attenuation (c/m) versus TSM concentration (mg/l). r=0.77. One outlier not included in plot.

material, giving rise to the reddish-brown coloration in the water, plays an important part in the absorption process by selectively absorbing the blue wavelengths of light. Interestingly, concentrations of organic and mineral suspensates are not significantly correlated with each other. This indicates that the organic and mineral phases of suspended particulates are derived from different sources; i.e., organic suspensates from the mangrove swamps and mineral suspensates from the Main Channel and fringing shoals. Interestingly, concentrations of organic and mineral suspensates are not significantly correlated with each other. This indicates that the organic and mineral phases of suspended particulates are derived from different sources; i.e., organic suspensates from the mangrove swamps and mineral suspensates from the Main Channel and fringing shoals.



Figure 4. Plot of blue attenuation (c/m) versus concentration of OSM. r=0.73. One outlier not included in plot.

A nonlinear regression model of green light attenuation and TSM results in a better fit than a linear relationship. We fit $c/m=b_1 \exp(-b_2/x)$ where c/m is the attenuation per meter path length, the b's are constants and x is TSM. R², the proportion of the variance of the dependent variable explained by this regression, is 0.88 (r=0.94) as opposed to 0.59 (r=0.77) for the linear regression. Such a model implies that there is a limiting value of TSM for green light attenuation; i.e., above this critical value of TSM, no further change occurs, to any great degree, in green attenuation.

Water in the open lagoon (stations 1 and 2) attenuated very little light of either wavelength. Blue and green attenuation for these stations were approximately equal (1985 data). Concentrations of OSM were below detection level and concentrations of MSM were the lowest recorded in the study area. These waters, within the limits of the Martek transmissometer and assuming very little particle scattering, are similar to extremely clear oceanic waters (Smith and Baker, 1981).

Concentrations of suspensates and beam attenuation in the enclosed waters of Twin Cays were quite variable. Concentrations of MSM were highest in Main Channel. Concentrations of OSM were highest in the tributary channels and creeks. MSM contributed only a negligible amount of material to the total suspended load at the stations in the channels and creeks.

Scattering predominated over absorption through most of Main Channel (stations 3 & 4). Blue attenuation was consistently low at these stations and slightly less than green attenuation. Differences in attenuation occurred at stations in the Main Channel but appear to be due to changes in the concentrations of MSM rather than changes in concentration of OSM. We found little evidence of absorption of blue light over green, indicating that scattering predominated.

When the wind was from the north, the water at the north end of Main Channel (Sta. 3) was milky green because of high concentrations of suspended carbonate particles. Sight distance into the water column was limited. Green light was highly attenuated at this time. When there was no wind, the water at the north end of the Channel was extremely clear. Attenuation of blue light at the north end of the channel under conditions of little to no wind was quite low.

Wind frequencies from the northwest and northeast are quite common in the Twin Cays area (Rützler and Ferraris, 1982). Hence, the northern end of Main Channel must be quite turbid a condiserable part of the time. <u>Thalassia</u> growth is extremely sparse in this area.

The water at the dock (Sta. 4) was relatively clear on all occasions we visited Twin Cays. Attenuation of blue light was less than that of green. Average concentrations of OSM was less than that of average concentrations of MSM. Values of attenuation and particulate concentrations at the dock were less than those at the north end of Main Channel. <u>Thalassia</u> is abundant in this area.

Waters in the southern part of Main Channel (Sta. 6) were more turbid than those at the dock at the time of our visits. Average blue attenuation was greater than average green attenuation, suggesting the presence of some dissolved tannin in the water. Concentrations of MSM were greater than those of OSM. Under conditions of a southeasterly or easterly wind, turbidity could become quite high in the southern part of Main Channel. <u>Thalassia</u> growth is sparse, which may be due to greater water depth, significant intermittent turbidity, presence of dissolved organic material, or a combination of factors.

Attenuation of blue light was double that of green in the tributary channels where reddish-brown water was present. The farther up these channels and closer to the influence of the mangrove swamps, the greater was the attenuation of the blue wavelengths. This is due to an increase in absorption of the shorter wavelengths by the brownish water. OSM concentrations were higher than MSM at these stations.

At Hidden Lake (Sta. 9), Hidden Creek (Sta. 8), and its opening into Boston Bay (Sta. 7), attenuation of blue light was greater than that of green. Absorption predominated over scattering. Attenuation of blue light was higher in the surface waters than the water near the bottom both times that we visited the area in 1990. The high values were due to fresher, tannin-charged waters emanating from the mangrove swamps during ebb tide, a situation similar to that noted by Mazda, et al. (1990).

OSM concentrations were greater than MSM in these reddish-brown waters in the Hidden Creek area. The bottom was composed of a thick brown organic ooze. No <u>Thalassia</u> growth was present. Suspensate concentrations (TSM) were higher in nearbottom waters in one instance and in near-surface waters in the other when we sampled in this area. In the former case, sampling occurred at mid-ebb tide (highest current velocity) and the high suspensate concentration is attributed to resuspension of bottom sediments by tidal currents. In the latter case, sampling occurred near low tide or very early flood tide when would expect the surface water to consist primarily of fresher water from the swamps with any suspensate material that was present originating in the swamps.

The transition from the greenish-blue water of Main Channel to the reddish-brown water flowing from Hidden Creek appeared to be gradual across Boston Bay, suggesting efficient mixing of the two water types. Attenuation of green light was less in Boston Bay (Sta. 5) than at either the southern end of Main Channel (Sta. 6) or at Hidden Creek (Stations 7 and 8). Concentrations of TSM were generally quite low. The low concentration of MSM at the center of Boston Bay would indicate that most of the suspended mineral matter at the southern end of the Main Channel rapidly settled out of the water column in the quieter waters of Boston Bay. The low concentration of OSM here would indicate that the organic-rich waters of Hidden Creek were effectively diluted by mixing with the greater volume of clearer water in the more open Boston Bay. No blue light transmission values were taken in this area. <u>Thalassia</u> grows in patches in this area, the density of growth declining toward Hidden Creek.

A distinct front between brown and green water masses existed in Lair Channel at the times of sampling. The change in appearance of the water color across the front was dramatic. Up channel, the water was reddish-brown; down channel, a milky green. The front moved up and down channel in response to tidal stage. Seagrass growth was dense down channel whereas it rapidly disappeared up channel and by the Lair (Sta. 10), no seagrasses were present. There was no difference in attenuation of green light in the two types of water in 1989. Attenuation of green light in the reddishbrown water in 1990 was similar to that of 1989. We expected that there would be a marked difference in attenuation of blue light in the different water masses revealing a difference in tannin enrichment across the front, i.e., the brown water having higher blue attenuation values than the green water. In fact, higher blue attenuation occurred down channel in the green water than up channel in the brown. Offsetting the possible greater absorption by the brown water, concentrations of suspensates (TSM) were nearly an order of magnitude higher in surface waters on the green water side of the front at the time of sampling. Substantial scattering of blue light may account for the high value of blue light attenuation. Toward the Lair (Sta. 10), which dead-ends at the mangrove prop roots, the attenuation of blue light increased to where less than 8% of the incident light was transmitted over a distance of one meter.

Grouper Gardens (Sta. 13) presents an interesting case. Although this small inlet is surrounded by mangrove swamps, the water appears to be relatively clear and has a greenish brown coloration. The bottom is covered with the green alga, <u>Avrainvillea sp.</u> No seagrass is present in this inlet although the water clarity would suggest that such plant growth could be supported. Attenuation of the blue wave lengths of light was greater than that of the green wave lengths, indicating a considerable amount of tannin in the water. The apparent clarity of the water may have been deceptive because of a relatively shallow depth of this inlet. The exclusion of <u>Thalassia</u> from this area may be accounted for by a lack of blue light or intense grazing pressure in these dense stands. <u>Avrainvillea sp.</u> produces secondary metabolites, which are not palatable to grazing fish, thus reducing herbivory (J. Norris, pers. comm.).

Large aggregates, primarily of organic material with included carbonate particles, often appear in the water column in Lair Channel and Grouper Gardens. These aggregates apparently have become detached from the bottom by the positive buoyancy imparted by bubbles within the aggregates. They were most common on bright sunny days in the afternoon and it is assumed that the bubbles were oxygen generated by algae on the bottom. The aggregates, although accounting for a large proportion of the mass of the suspensates and important for mass balance and export studies, had little effect on light transmission. Therefore, they were deliberately excluded from the water samples taken for concentration data. The aggregates broke apart when attempts were made to obtain samples and display a fragility similar to that reported for marine "snow" (Hammer et al., 1975).

CONCLUSIONS

Transmission of light controls the distribution of seagrasses in the Twin Cays area of the Belize lagoon. The absence of <u>Thalassia</u> in areas of highly colored water and in areas of high concentrations of suspensates strongly suggests that this is the case.

Tannin, either dissolved or particulate, strongly absorbs blue light. In highlycolored, reddish-brown waters, where it is presumed that high concentrations of dissolved tannin were present, very little blue light penetrates more than a few centimeters into the water. Apparently, the amount of tannin is critical to whether any seagrasses are thriving or even present. It seems that very little tannin need be present to exclude <u>Thalassia</u> from an area, as shown by its rapid disappearance in Lair Channel over a relatively short distance.

Suspended mineral grains contribute to beam attenuation by scattering. Very high concentrations cause such an increase in scattering that little, if any, solar radiation would be available to seagrasses in such areas. Such situations occur at the north and south ends of Main Channel where a considerable amount of the incident light is backscattered out of the water. Two alternative explanations might account for the lack of plants at the two ends of Main Channel. First, sedimentation rates could be high enough to smother any new <u>Thalassia</u> growth in the area. Second, currents set up through the channel by wind drift could possibly prevent colonization of the area by any rooted aquatics. The presence of mangrove leaves exposed on the bottom of the channel suggests that the rate of sedimentation is not very high in this area. The mangrove leaves also indicate that the currents are not of sufficient strength to prevent rooting of <u>Thalassia</u>. Thus, we assume that sufficient amount of radiation is removed from the incident solar radiation, during passage through the water column by backscattering, that there is an insufficient amount necessary for plant growth.

Tides cause significant short-term variations in water quality at Hidden Creek and its environs. At ebb tide, organic-rich waters flow from the mangrove swamps. Efficient mixing with waters from Main Channel occurred in the area of Boston Bay. This embayment, connecting Main Channel with Hidden Creek, showed evidence of mixing of swamp and lagoonal water masses. Concentrations of mineral suspended matter in Boston Bay were lower than those in Main Channel while concentrations of organic suspended matter were intermediate between those at Main Channel and Hidden Creek. In Lair Channel, less mixing of tributary and Main Channel waters was evident. There was a distinct line between water masses of different colors. Down channel, the water shared characteristics with waters of Main Channel and was milky bluish-green. Up channel, the water was reddish-brown, revealing its source to be the swamps. The large difference in light transmission up channel and down channel becomes especially apparent at the Lair.

ACKNOWLEDGMENTS

Funding for the field work came from the Museum of Natural History Caribbean Coral Reef Ecosystem program. This is contribution #366 of the Smithsonian Caribbean Coral Reef Ecosystem Program. We wish to thank Dr. Klaus Rützler for reviewing an earlier draft of this manuscript.

REFERENCES

Hammer, W. M., Madin, L. P., Alldredge, A. L., Gilmer, R. W., and Hammer, P. P., 1975. Underwater observations of gelatinous zooplankton: sampling problems, feeding biology and behavior. <u>Limnology and Oceanography</u>. 20:907-917.

Jerlov, N.G., 1976. Marine Optics. Elsevier, New York, 231 p.

- Kirk, J. T. O., 1983. <u>Light and Photosynthesis in Aquatic Ecosystems</u>. Cambridge University Press, New York, 401 p.
- Mazda, Y., Sato, Y., Sawamoto, S., Hokcochi, H., and Wolanski, E., 1990. Links between physical, chemical and biological processes in Bashita-minato, a mangrove swamp in Japan. Estuarine, Coastal and Shelf Science. 31:817-833.
- Rützler, K. and Ferraris J.D., 1982. Terrestrial environment and climate, Carrie Bow Cay, Belize. In: Rützler, K. and Macintyre, I.G. (Eds.) <u>The Atlantic Barrier</u> <u>Reef Ecosystem at Carrie Bow Cay, Belize, I, Structure and Communities</u>. Smithsonian Contr. to Mar. Sci. 12. Smithsonian Institution Press, Washington, p. 77-91.
- Shinn, E., Hudson, J. H., Halley, R. B., Lidz, B., Robbin, D. M., and Macintyre, I. G., 1982. Geology and sediment accumulation rates at Carrie Bow Cay, Belize. In: Rützler, K. and Macintyre, I.G. (Eds.) The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I, Structure and Communities. Smithsonian Contr. to Mar. Sci. 12. Smithsonian Institution Press, Washington, p. 63-75.
- Smith, R. S. and Baker, K. S., 1981. Optical properties of the clearest natural waters. Applied Optics. 20:177-184.
- SAS Institute Inc., 1989. <u>SAS/STAT User's Guide</u>, V. 6.0, 4th Edition, Vol. 2, Cary, North Carolina, 846 p.