Causes of Light Attenuation with Respect to Seagrasses in Upper and Lower Charlotte Harbor

Final Report

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Table of Contents

List of Tables

List of Figures

Executive Summary

Little direct destruction of grasses has occurred in the Charlotte Harbor system, but although anthropogenic impacts appear minor at this time in comparison to Tampa Bay, nutrient loadings are expected to increase. The Charlotte Harbor system is also very different in hydrological and water quality characteristics from Tampa Bay, predominantly due to higher freshwater inflows. In order to evaluate the susceptibility of seagrasses in Charlotte Harbor to impacts from increased nutrients, the Southwest Florida Water Management District - Surface Water Improvement and Management Program funded a study of grasses in the Harbor with the following goals; 1) to determine the amount of light present at the deep edge of seagrass meadows, 2) to determine the amount of light reduction associated with epiphyte coverage of seagrass blades, and 3) to determine the relative importance of various light attenuators on water column clarity.

Studying both *Thalassia testudinum* and *Halodule wrightii* seagrasses, photosynthetically active radiation (PAR) and attenuation were continuously monitored for one year at the deep edges of four grass beds along a gradient of salinity (15 - 28 PSU) from the upper to lower Harbor. The morphological behavior of the grass bed (shoot density, blade area) was determined bimonthly and was used to evaluate the sufficiency of PAR received. PAR data are presented both as Moles m^{-2} yr^{-1} and as a percentage of the immediately subsurface radiation remaining in the water column at the maximum seagrass depth (%PAR_w). In addition to the continuous stations, four other stations were visited weekly for determination of water column attenuation. Monthly, measurements of water color, turbidity, phytoplankton (as chlorophyll), and epiphytic attenuation were determined for all stations. With both theoretical, literature-derived and empirically determined values, a spectrally sensitive optical model of water column attenuation was prepared to determine the relative contributions of the attenuating substances. Geographic patterns allowed an assessment of areas which may be susceptible to degradation of water clarity under increased nutrient loading scenarios. With epiphytic attenuation, PAR data could also be presented as the %PAR available to the plant (%PAR_p). Subsequent to initiation of the project, the Charlotte Harbor National Estuary Program provided additional funding for another four stations in the Pine Island Sound, Matlacha Pass, San Carlos Bay areas. The components of water column and epiphytic attenuation were determined monthly at these four stations.

Rainfall and flows during the project year were extraordinary, with winter and springtime flows as much as 20 times the long term averages and with resulting decreases in both salinity and water clarity measured at almost all stations. The biotic changes observed during the project should be interpreted with the consideration that the project year represented higher levels of attenuation following two years of comparatively better water clarity. Shoot density and blade area were used to determine significant biotic increases in seagrasses at one of the most saline stations and significant declines at the four stations furthest up the Harbor (least saline). Annual averages of epiphytic attenuation ranged from 21% to 44% of additional reduction in PAR reaching the plant, with monthly values ranging between 6% and 89%. Highest epiphytic attenuations were in the late summer and fall.

For the stations measured continuously, annualized means of light received at the maximum depth extent of seagrasses produced %PAR_w values of 29%, 20%, 16%, and 13% for stations along a gradient of increasing salinity. Annual %PAR_p for the same stations were 16%, 13%, 11%, and 11%. Biotic increases were observed at the station which received the lowest %PAR_p. In view of the net biotic changes, annual %PAR_p requirements either exhibit an inverse salinity-related gradient or salinity stress produced biotic declines in *T. testudinum* and *H. wrightii*, regardless of PAR received. The lowest salinity site experienced 16% of subsurface irradiance as %PAR_p, and still experienced biotic declines in above ground biomass. At 11% PAR_p, sites either exhibited a mix of responses (*T. testudinum*) or increased in biomass (*H. wrightii*). With one exception, stations with a mean annual salinity of below 18 PSU experienced biotic declines.

After correction for epiphytic attenuation (PAR_p), annual totals available to the plant at the canopy height (0.2 m) ranged between about 2,000 and 3,100 Moles m^{-2} yr^{-1}. Declines in biomass were observed at the lower salinity stations which received between 3,100 and 2,600 Moles m^{-2} yr^{-1}. The higher salinity sites which received near 2,000 and 2,300 Moles m^{-2} yr^{-1} of PAR_p, (*T. testudinum* and *H. wrightii*, respectively) experienced either a mixed suite of biotic changes (increased shoot density, and decreased blade area per shoot) or a significant increase in density and blade area. The annual light requirements for *T. testudinum* in lower Charlotte Harbor appear to be at least as great or greater than the PAR recorded and the light requirements for *H. wrightii* are somewhat less than that for *T. testudinum*. Seasonal distribution of PAR_p also appears critical. Under comparable salinity, sites with at least three months of the growing season in which PAR_p averaged 10 Moles m^{-2} day^{-1} maintained biomass. Low salinity stress at some stations apparently resulted in biomass decline despite having received higher PAR_p.

The results of the optical model were very good, with mean percentage agreement between modeled and observed Kd of 110%. Using water quality data from all stations as inputs, the model determined that chlorophyll, color, and turbidity accounted for 4%, 66%, and 31% of water column attenuation, respectively. The maximum annual average chlorophyll contribution was 6%, with an individual maximum of 18% during a phytoplankton bloom (143 ug l^{-1} chlorophyll). Color dominated water column attenuation, ranging from 40% to 78% to total water column attenuation. Color was still the dominant attenuator even after an arbitrary doubling of modeled chlorophyll concentrations. Stations in the lower Harbor and southern sites showed increased attenuation due to turbidity, compared to upper Harbor sites. Long term data produced similar allocations of attenuation, indicating that even under more 'typical' rainfall patterns, water column attenuation in Charlotte Harbor is dominated by color.

The results of light requirements for seagrasses, while summarized above as annual totals of PAR or $\%PAR_w$, cannot be applied indiscriminately for management efforts. Levels of light in the water column can be used as targets only if epiphytic attenuations are similar. Levels of PAR available to the plant (PAR_p, $\%PAR_p$) are more robust and biologically meaningful targets, but require that epiphytic attenuation be monitored in addition to water column parameters. The probable response of epiphytes to increased nutrients in the Charlotte Harbor system is unknown at this time. In addition, seasonal signals are strong both in physical water quality, water clarity, epiphytic growth, and seagrass growth. Light requirements that vary by season are likely and changes in water quality which disproportionately impact clarity during the growing season will have an enhanced impact on seagrass growth and survival.

Introduction

Seagrasses have been identified as keystone species that offer crucial estuarine habitat and water quality benefits. Unfortunately, substantial declines in seagrasses have been documented worldwide. Other than direct destruction, declines are most often linked to anthropogenic nutrient enrichment (Cambridge and McComb, 1984, Orth and Moore, 1983, 1984), and consequent increases in phytoplankton and epiphytic algae (Silberstein *et al.*, 1986; Neverauskas, 1987; Tomasko and LaPointe, 1991) and available light at depth. Similarly, substantial losses of seagrasses have also been identified at depth on the west coast of Florida; in Tampa (Lewis *et al.*, 1985) and Sarasota Bays (Culter and Leverone, 1993), as well as in Charlotte Harbor (Harris *et al.*, 1983; Duke and Kruczynski, 1991). Light limitation has been postulated and demonstrated as the major limiting factor and demonstrated for grassbeds in Tampa Bay (Hall *et al.*, 1990).

For Charlotte Harbor (Figure 1), however, the situation is somewhat more complex. Little direct destruction of grasses has occurred in this system and anthropogenic effects in the comparatively undeveloped watershed of Charlotte Harbor have been minor in comparison to Tampa Bay. Nutrient enrichment from point sources appears restricted to localized areas (Ardaman *et al.*, 1995; Coastal, 1995), although the far field effects of these inputs are presently unknown. Nutrients are predicted to increase (Hammett, 1988; Coastal, 1995), however, and could ultimately be expected to impact seagrasses in ways analogous to worldwide examples of nutrient enrichment. The Southwest Florida Water Management District (SWFWMD) is in the process of evaluating allowable nutrient loading scenarios for the purpose of protecting the spatial extent of grasses and other natural resources within the Harbor.

There are other differences between the Tampa Bay and Charlotte Harbor systems. The Charlotte Harbor watershed is substantially larger in relation to the receiving water area than is Tampa Bay. The watershed to bay area ratio is approximately 12:1, compared to a ratio of near 6:1 for Tampa Bay. As a result, freshwater inflows to Charlotte Harbor are large, and during the wet season, salinity values across the Harbor can be severely depressed. Many regions of the Harbor may at times be at the extreme low end of an acceptable salinity range for seagrasses. High color values (and light attenuation) are associated with the freshwater discharges, which generally display a rapid onset and a persistent presence throughout the summer wet season. In particular, grasses near the mouth of the Myakka and Peace Rivers experience the combined stresses of both low light and low salinity. The duration as well as the magnitude of both stresses undoubtedly affect seagrass persistence. While the anthropogenic development of a watershed can change the timing and flow characteristics of freshwater entering an estuary, climatological variations in annual rainfall or extreme rainfall events complicate the feasibility of watershed management for flows.

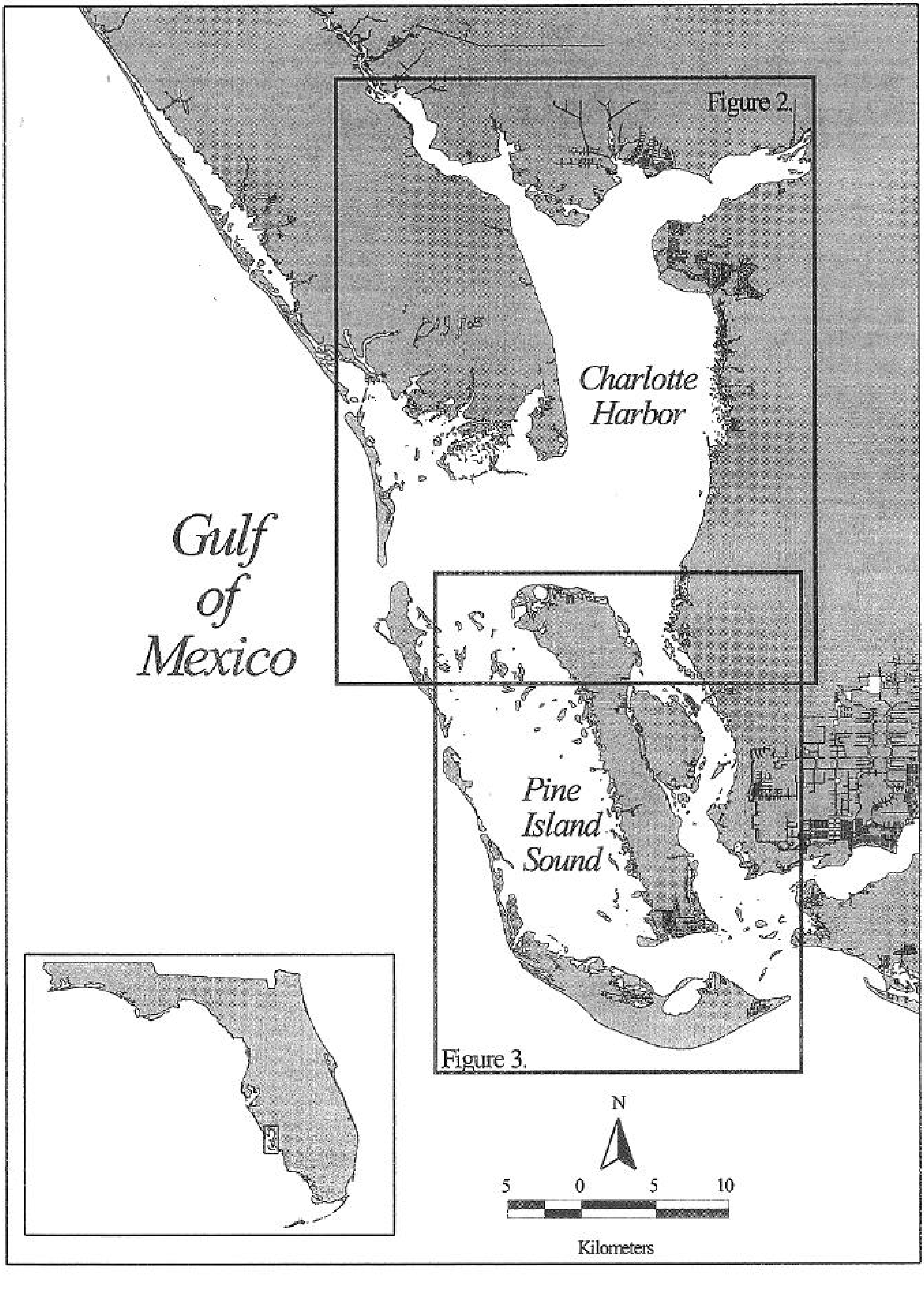

Figure 1. Charlotte Harbor study area.

The goal of the Charlotte Harbor seagrass light requirement project was threefold;

1) to determine the amount of light present at the deep edge of seagrass meadows,
2) to determine the amount of light reduction associated with epiphyte coverage of seagrass blades,
3) and to determine the relative importance of various light attenuators on water column clarity.

Light requirements of seagrasses in Charlotte Harbor were determined through a year-long empirical study, using continuous measurement of PAR at the deep edges of selected grassbeds within the Harbor. Site selection was critical for interpretation of results, *i.e.*, that the grassbeds were truly light limited. Robustness of results was dependent on the relative absence of any extreme climatological events during the year. In order to interpret resulting data in the event of an unusual year, behavior of the grassbed (measured as shoot density) was determined periodically over the course of study. The empirical approach was carried out across a variety of stations that spanned the water quality conditions experienced within the estuary. The determination of the relative contributions of water color, turbidity, phytoplankton, and epiphytic growth to light attenuation was to allow an assessment of areas which may be susceptible to degradation of water clarity under increased nutrient loading conditions.

The study represents a cooperative funding effort between the Southwest Florida Water Management District - Surface Water Improvement and Management Section (SWFWMD-SWIM) for work within the mainstem of the Harbor, and the Charlotte Harbor National Estuary Program (CHNEP) for work in the lower Harbor and Pine Island Sound. The project was carried out under a Research Quality Assurance Plan submitted (Nissanka and Dixon, 1997a) through the District to the Florida Department of Environmental Protection and under a complementary Quality Assurance Project Plan (Nissanka and Dixon, 1997b) submitted through the CHNEP to the U.S. Environmental Protection Agency.

Materials and Methods

Study Sites

Study sites were located along known gradients of salinity, nutrients, chlorophyll, color, and water clarity (SWFWMD-SWIM, unpublished data), from the Boca Grande to upper Charlotte Harbor, and in Pine Island Sound to San Carlos Bay. Near Boca Grande and Captiva Pass, the influence of coastal waters is high. Near the mouth of the Myakka, Peace and Caloosahatchee Rivers, dissolved humics in freshwater frequently result in highly colored waters, particularly in the wet season. After review of SWIM's GIS change analysis of seagrass coverage and visual inspection of 1:24,000 scale -aerial photography, sites were established in areas with generally persistent seagrasses, although year to year variations in coverage appears high. Less was known of trends in seagrass coverage in the southern Harbor. There were no bathymetric controls (*i.e.*, no offshore sandbars) at the selected sites. In some instances, sensors had to be installed a distance from the deep edge (50 m or less) of the grass beds in order to have sufficient water depth to cover the sensors. Deep edges were fast marked for reproducible sampling.

Three levels of sites were established. Four Level I sites were each instrumented with two continuous PAR sensors for a year. Sites were also visited weekly for cleaning and monthly for collection of water quality and seagrass samples. Four Level II sites were not instrumented, but were visited weekly for a year for the determination of attenuation coefficients, and monthly for water quality and seagrass samples. Four Level III sites were visited monthly for 6 months to determine water column attenuation coefficients and to collect water quality samples and seagrasses. All sites were located at the deep edges of seagrass beds. Dominant seagrasses varied by site between *Thalassia testudinum* and *Halodule wrightii*. Site designations, locations (Figures 2 and 3), and dominant grasses are listed in Table 1.

Not all grassbeds were monospecific. *H. wrightii* occurred as a non-dominant seagrass at COT and PUN sites, and *Syringodium filiforme* was present as a minor component at the PAS site near the mouth of Captiva Pass.

Instrumentation and Tides

For instrumented sites, two scalar quantum irradiance sensors (4ð; LI-COR 193SA) and a data logger were installed immediately outside the deep edge of the grassbed at each site and programmed to record 15 minute averages of photo flux. The lower sensor was located at canopy height (0.2 m above the bottom); the upper sensor was located 0.5 m above the lower. The lower sensor was shielded from bottom reflectance with a 38 cm diameter non-reflecting collar, so that attenuation coefficients determined would be representative of the water column. Data loggers were recovered monthly for data download.

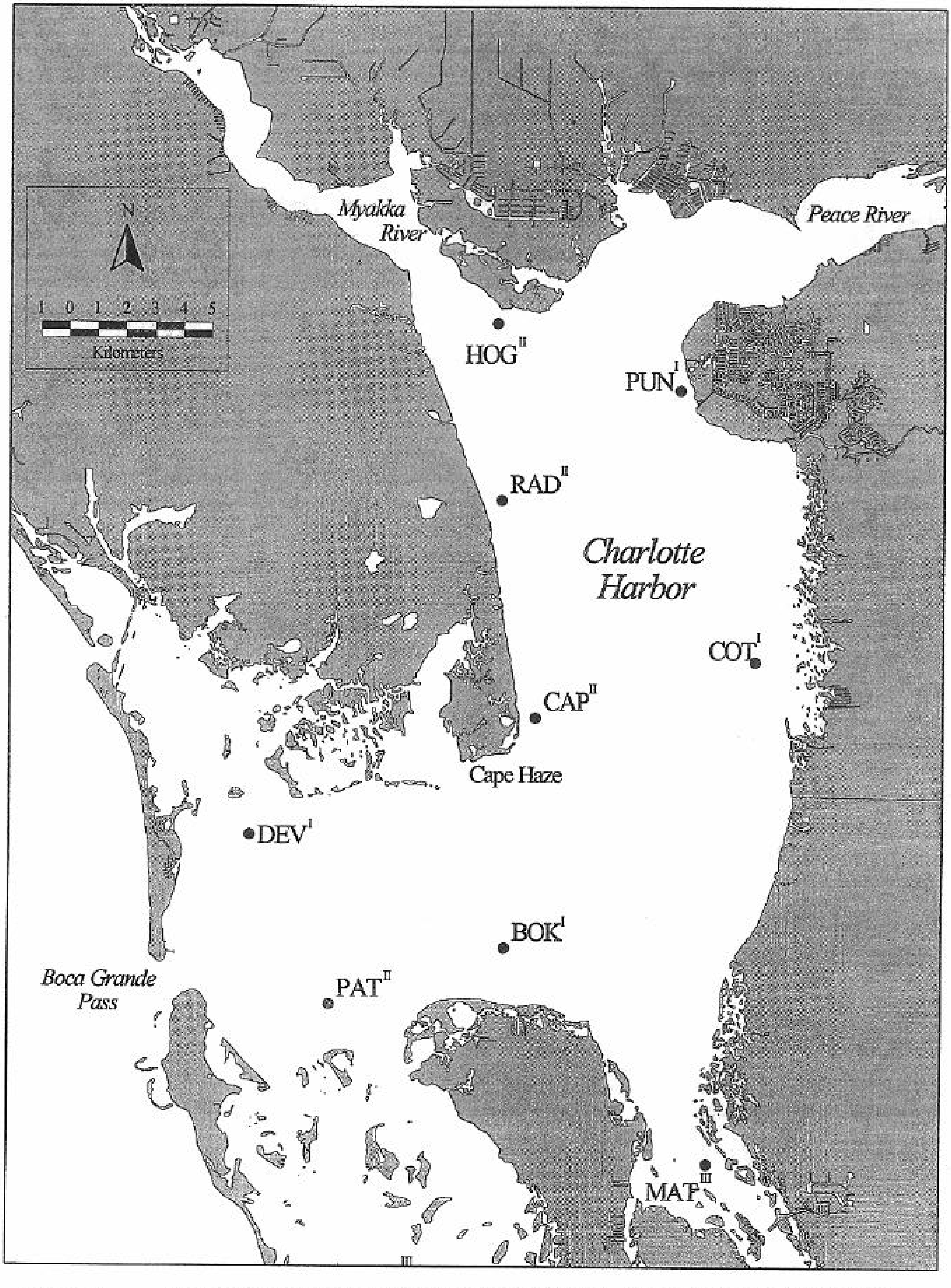

Figure 2. Northern Charlotte Harbor seagrass stations. Level I, II, and III indicate sampling regime over the course of the project year.

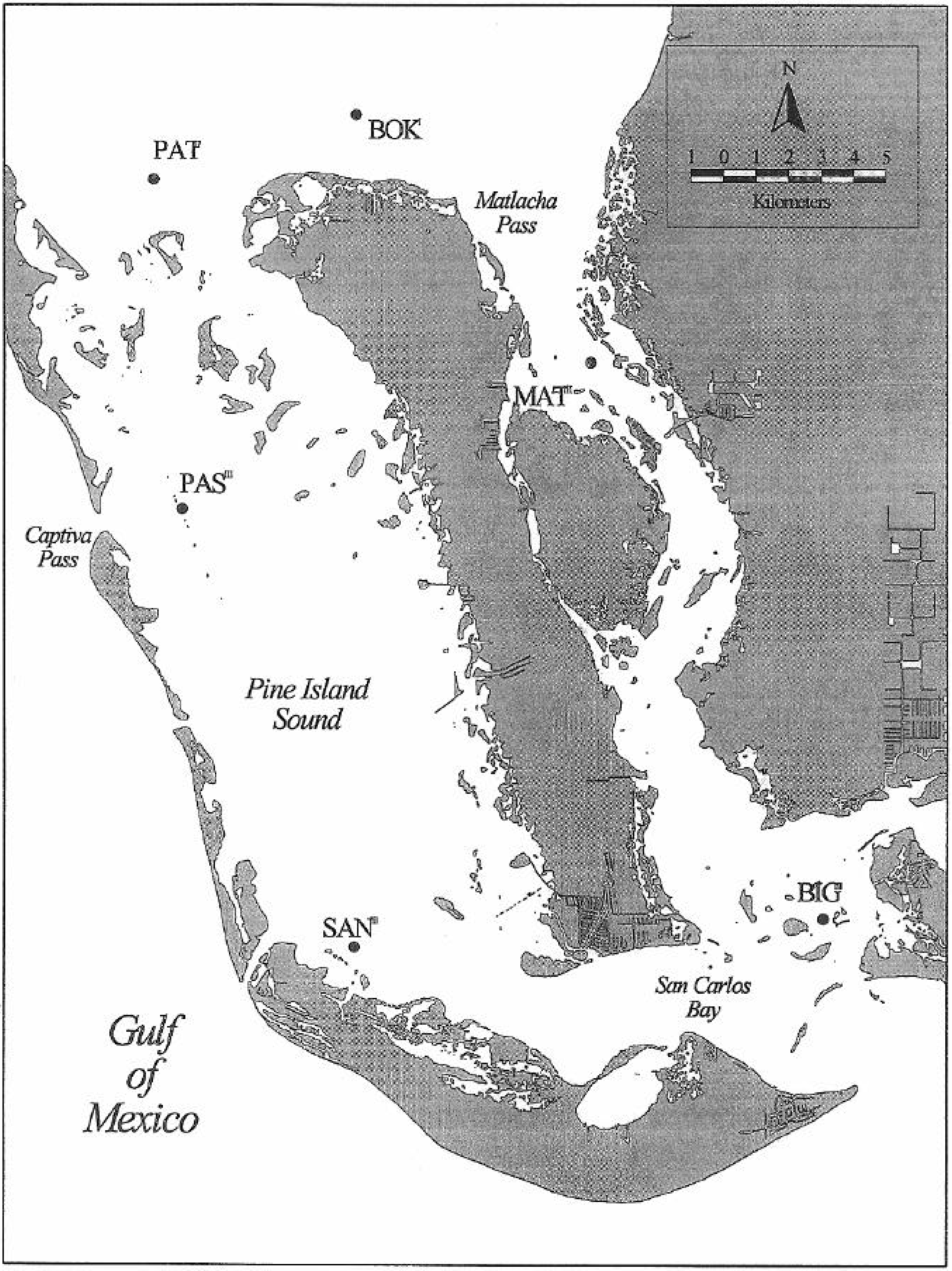

Figure 3. Southern Charlotte Harbor seagrass stations. Sites MAT, PAS, SAN, and BIG sampled for a six month period.

Table 1. Sites and sampling levels for the light requirements of seagrasses in Charlotte Harbor, April 1997 to April 1998.

Level I

PUN	-	Punta Gorda	26° 53.946'	82° 05.830'	*T. testudinum*
COT	-	Cotton Key	26° 48.780'	82° 04.386'	*T. testudinum*
BOK	-	Bokeelia	26° 43.316'	82° 09.129'	*T. testudinum*
DEV	-	Devilfish Key	26° 45.453'	82° 13.962'	*H. wrightii*

Level II

HOG	-	Hog Island	26° 55.203'	82° 09.317'	*H. wrightii*
RAD	-	Radio Tower	26° 51.841'	82° 09.224'	*H. wrightii*
CAP	-	Cape Haze	26° 47.703'	82° 08.561'	*T. testudinum*
PAT	-	Patricio Island	26° 42.234'	82° 12.452'	*T. testudinum*

Level III

MAT	-	Matlacha Pass	26° 39.239'	82° 05.247'	*H. wrightii*
PAS	-	Captiva Pass	26° 36.804'	82° 11.980'	*T. testudinum*
SAN	-	Sanibel	26° 29.543'	82° 09.158'	*H. wrightii*
BIG	-	Big Island	26° 30.023'	82° 01.407'	*H. wrightii*

Sensors were covered with clear plastic food wrap, to permit removal of fouling. Instrument arrays were operated from April 1997 through April 1998. Depths and vertical PAR profiles were recorded on each site visit with PAR sensors (LI-COR 193S [4ð] and 190SA [air, 2ð]). The profiles included additional upward and downward facing sensors (LI-COR 192SA [2ð]) to determine in-column and bottom reflectance. Salinity (Jaeger, 1973) and secchi depths were determined on each visit.

Tidal variations in water depths were estimated from tides recorded at Boca Grande and at Punta Gorda, applying the tidal variation in water depth to the mean depths observed on station (Tide Tables; U.S. Department of Commerce, 1994).

Biotic Measurements

Bimonthly, quadrat counts (n~40 per site) of the defined and fast-marked deep edge were performed. Due to the manner of station location (at the extreme deep edges of the grassbed) shoot densities were expected to be substantially lower than obtained from other regional studies. Quadrats used for *T. testudinum*-dominated stations were 0.0625 m^2 (25 cm X 25 cm), while counts at *H. wrightii*-dominated stations employed 0.0156 m^2 quadrats (12.5 cm X 12.5 cm). Blade widths and blade areas per shoots were also determined monthly in conjunction with epiphytic attenuation measurements.

Epiphytic Attenuation

The attenuation of PAR due to epiphytic materials (here referring to attached epiphytes, epifauna, and associated sediment or detritus) was determined monthly on 5 shoots per site, each collected from within 1.0 m of the deep edge. Necrotic portions were removed and the remaining blades of an entire shoot were scraped with a razor to remove all epiphytic material. The area scraped was determined as twice blade length times blade width.

Epiphytic attenuation was determined by the method of Dixon and Kirkpatrick (1995), after work by following Sand-Jensen and Sondergaard (1981), with the apparatus illustrated in Figure 4. The suspension of scraped material was placed into a transparent (acrylic) dish. The dish area was matched to a typical shoot area to the extent possible, using a 71.3 cm^2 dish for epiphytes scraped from *T. testudinum* samples and a 20.3 cm^2 dish for *H. wrightii* epiphytes. The walls of the transparent dish were lined with reflective mylar, and the dish illuminated with a quartz-halogen light source (Dyna-Lume 240-350) and a white acrylic diffusing slide. A cosine PAR sensor (LI-COR 190SB) was placed 12 cm below the sample. The sensor tube was also lined with reflective mylar. For each sample, a blank reading of the irradiance passing through deionized water (E_{Blank})was followed by readings of the irradiance penetrating the epiphyte suspension (E_{Sample}). The inverse logarithmic relationship between the epiphyte suspension density and transmitted irradiance was used to correct for inequalities between dish area and blade area scraped.

$$y = \frac{\ln(E_{Sample}) - \ln(E_{Blank})}{(\text{Dish Area}^{-1})} \bullet \frac{1}{2 * \text{Blade Area}} + \ln(E_{Blank})$$

$$\text{Epiphyte Attenuation (\%)} = \frac{E_{blank} - e^{y}}{} \bullet 100\%$$

E_{blank}

Epiphytic attenuations so determined represent area-averaged conditions, *i.e.*, as if the entire epiphyte burden of the productive blades was evenly distributed across both sides of the blade surfaces. Epiphytic communities have been demonstrated to have a broad absorption spectrum (Neckles, 1991, 1993; Marrs *et al.* 1999). As a result, PAR attenuation of an epiphytic suspension is an appropriate approximation to calculate the PAR which is available to the seagrass blades, in the absence of more rigorous spectral attenuation information for water column and epiphytes, and photosynthetic action spectra for the individual grass species. Dry weights and ash free dry weights were determined on a subset of the epiphyte samples.

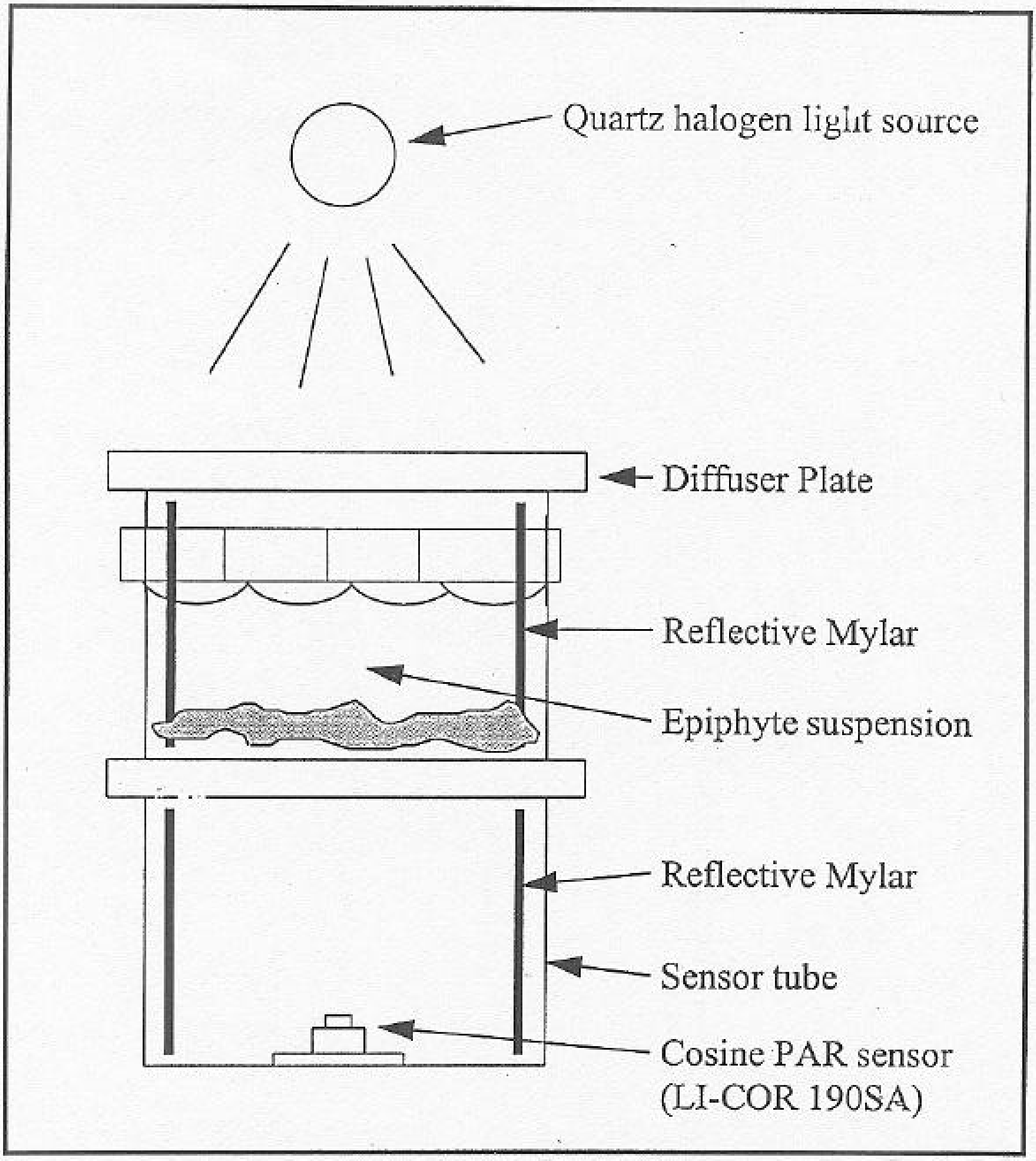

Figure 4. Apparatus for determination of epiphytic attenuation.

Continuous PAR Data Reduction

The attenuation produced by fouling communities on each continuous PAR sensor was directly measured during the monthly retrieval and download of the data loggers. Fouling removed during the remaining weekly maintenance visits was calculated by registering the times of the post- and pre-cleaning PAR readings (generally separated by 45 minutes) to the theoretical incident irradiance curve for the day. An unfouled reading at the precleaning time was calculated by the ratio of the theoretical irradiances, and compared to the actual fouled reading to obtain the degree of fouling. Fouling rates were computed as the total percentage of PAR reduction by the epiphytic community (measured or estimated) per number of days of deployment.

The attenuation due to sensor fouling was linearly interpolated for all PAR readings between endpoints of 0% at the time of cleaning to the percentage measured or estimated immediately before the time of the next cleaning. All sensor data were subsequently corrected for the interpolated fouling. Water column scalar attenuation coefficients (K_0) were calculated from corrected sensor data and were additionally examined for consistency before and after cleaning to support the validity of fouling estimates. Corrected bottom sensor readings, attenuation coefficients, depths at the bottom sensor, and depths at the deepest extent of the grassbeds were used to calculate light readings at the deep edge. Since the bottom sensors were shielded, light levels presented do not include the PAR received by seagrasses from bottom reflectance, but do include the irradiance reflectance due to materials in the water column.

Absolute levels of light received at the deep edge were computed by summation of the individual 15 minute averages of PAR at the deep edge over the various time periods of interest. Calculations of absolute light levels received by seagrasses made use of all available data points from 0500 hours until 2100 hours.

The PAR remaining at the bottom of the water column (% PAR_w), as a percentage of the immediately subsurface scalar irradiance, was computed from each attenuation coefficient (K_0) and the station water level (z) at the maximum depths of grasses.

$$\% \, PAR_w = e^{-K_0 \cdot z} \bullet 100\%$$

The percentage of PAR so calculated represents water column processes only, and does not include reductions of incident solar irradiance due to air-water surface reflection. As wind and wave conditions and solar elevation will alter the percentage of reflection, and as these properties are not subject to management actions, the percentage reduction by the water column alone was the appropriate goal of the study. Annual or seasonal light percentages were computed as the mean of percentages received, rather than from annual mean attenuation coefficients.

The effects of epiphytic attenuation were also incorporated in calculations. Absolute and percentages of PAR in the water column ($\%PAR_w$) at seagrass depth limits, already corrected for sensor fouling, were further reduced by the amount of PAR reduction effected by epiphytes to estimate the PAR actually available to the plant ($\%PAR_p$).

$$\%\ PAR_p = \quad \%\ PAR_w \bullet \left(1 - \text{Epiphyte Attenuation\%} \bullet 100^{-1} \right)$$

To maintain correspondence with other seagrass monitoring programs, seasonal and annual averages of K_0, $\%PAR_w$, and $\%PAR_p$ are based on data only between 1000 and 1400 hours. Site- and time-specific interpolated water depths obtained from tidal data were also used to compute both absolute and percentages of light remaining at the bottom of the water column under simulated tidal conditions.

Bottom Reflectance

Bottom reflectance decreases with a dark bottom type, vegetation, and when the light field reaching the bottom of the water column is diffuse. Bottom reflectance must be distinguished from upwardly scattered light (upwelling light), produced by the interaction of downwelling light and water molecules or, to a lesser extent, particulates. Upwelling light is present at all depths in the water column and is not an exclusive function of bottom reflectance. Upwelling light is attenuated similarly to downwelling light, and typically consists of between 4-10% of downwelling light (Kirk, 1994).

Bottom reflectance was of concern in this project due to the use of 4ð sensors deployed near the bottom of the water column for the determination of attenuation coefficients. In the event of substantial bottom reflectance, an attenuation coefficient determined on measurements from near the bottom of the water column would be lower than if determined for the entire water column, thus resulting in an artificially high $\%PAR_w$. The degree of the bias would increase with higher bottom reflectance and if attenuation coefficients are determined from a relatively small fraction of the water column near the bottom.

The lower continuous sensors were shielded from bottom reflectance, but manual profiles made during field visits used no shielding on any sensors. Estimates of bottom reflectance were obtained from the irradiance reflectance (ratio of upwelling:downwelling PAR) computed at all measurements depths from upward and downward facing cosine (2ð) sensors, and difference between the surface irradiance reflectance (expected to be 4-5%; Kirk, 1994) and the irradiance reflectance measured at bottom. Bottom reflectance was used compute the PAR amounts reflected, and added back to the water column values computed from attenuation coefficients, to estimate the total PAR received by seagrasses at depths 0.1 m and 0.2 m above the bottom.

Manual PAR Data Reduction

Data reduction of field measurements included calculation of the vertical diffuse attenuation coefficient (K_d) between individual depths as:

$$K_d\,(z_1,z_2) = \frac{-\ln\left(E_d(z_2)/E_d(z_1) \right)}{z_2 - z_1}$$

where E_d is the downwelling irradiance as measured by the cosine sensor at depths z_1 and z_2. The incident irradiance readings (in air) were used to normalize $E_d(z_1)$ and $E_d(z_2)$ for changing atmospheric conditions. Additionally, water column K_d values were computed as the slope of the regression of the natural log of the downwelling irradiance [$E_d(z)$] against measurement depths, ignoring the slight non-linearity produced by differential absorption of various wavelengths. Scalar attenuation coefficients (K_0) were computed similarly to K_d above, and used as a verification of continuous sensors readings and attenuation coefficients.

Downwelling irradiance, upwelling irradiance, and scalar irradiance were used to compute the average cosine of photon zenith angles for total light [$\bar{\_}(z)$ - scattering dependent], the vertical attenuation coefficient for net downward irradiance [$K_E(z)$] and the absorption coefficient [$a(z)$] (Kirk, 1992). These parameters provide an empirical means to compare the relative importance of scattering and absorbing material between sites, independent of water quality parameters, and were calculated as follows, again normalizing for changing incident conditions based on measurements in air:

$$\bar{\_}(z) = \frac{E_d(z) - E_u(z)}{E_o(z)}$$

$$K_E(z) = \frac{-\ln\left((E_d(z_2) - E_u(z_2))/(E_d(z_1) - E_u(z_1))\right)}{z_2 - z_1}$$

$$a(z) = K_E(z) \bullet \bar{\_}(z)$$

For regression analyses, ¯ and *a* were calculated as the arithmetic average of all values obtained at a station, while K_E was computed as an average of the slopes of the linear regression of the natural log of the difference between downwelling and upwelling irradiance, as a function of depth between replicate profiles.

Adjustment for Sun Angle

The size of the study area and time of travel between sites dictated that manual water column profiles were made over a substantial period of the day. Solar elevation, therefore, varied considerably between sites on a given day, as well as varying between seasons.

To allow for station intercomparisons and a more direct evaluation of attenuation coefficients as a function of water column attenuators, it was necessary to account for the longer effective path length required for light to reach a sensor at specific depth when solar elevations are lower (Miller and McPherson, 1993). Solar elevations were calculated from time (EST) and date, using the latitude of each site (Kirk, 1994). Solar zenith angle ($È_a$) and the refractive index of water were used to compute the cosine of the zenith angle in water ($È_w$) to correct K_d measurements to $K_{d\ adj}$ (Figure 5) by:

$$K_{d\ adj}(z_1,z_2) = \frac{-\ln\left(E_d(z_2) / E_d(z_1)\right)}{z_{adj}}$$

$$= K_d\ (z_1,z_2) \bullet \frac{z_2 - z_1}{z_{adj}}$$

$$= K_d \bullet \mathrm{Cos}\ (È_w)$$

The correction uses a longer path length (the effective light path length) to compute attenuation coefficients, rather than the measured vertical distances. By accounting for varying path length

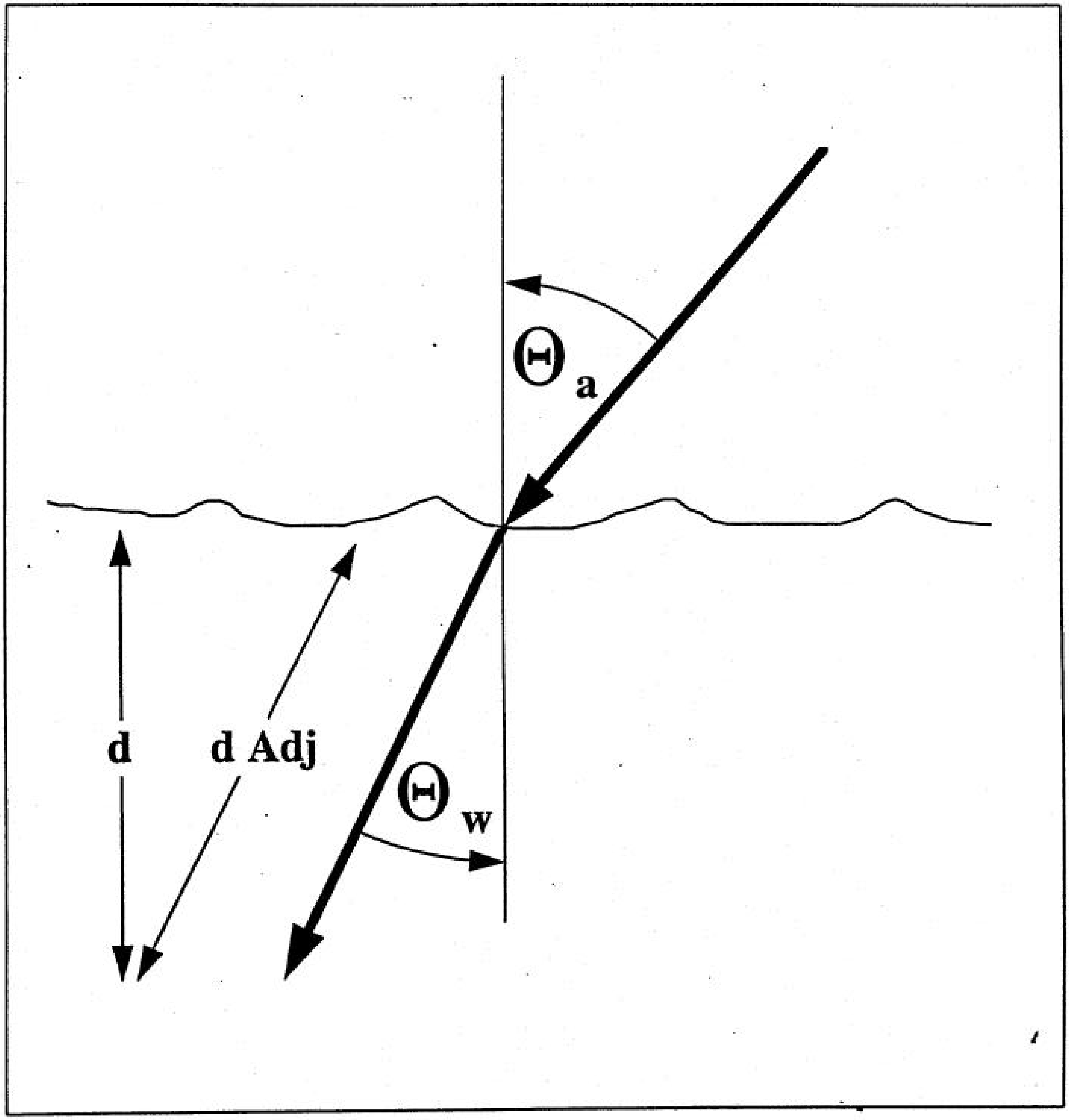

Figure 5. Geometry of longer path length for PAR under conditions of low solar elevation.

over the day, it can be seen that diurnal variation in K_0 is substantially minimized (Figure 6), a result more consistent with relatively stable water quality conditions at a given site. During wintertime at low maximum solar elevations, the effect of the adjustment is also visible between 1000 and 1400 hours. Seasonally, the longer effective paths in winter (minimal solar elevation) can decrease calculated attenuation coefficients by up to 20%.

The adjustment for solar elevations below vertical was used to compare stations sampled at differing times of day and to determine the relationship of water quality parameters to attenuation. The adjustment, however, does not account for increased scattering effects associated with decreasing sun angle and the increasingly diffuse nature of the light field. This and other factors controlling the degree of diffuseness (cloud cover, wave state, turbidity) remain as a source of variation in relating water column attenuators to the measured attenuation coefficient.

Verification of Continuous Readings

For independent verification of *in situ*, continuous sensor readings, the attenuation coefficients determined during the weekly manual PAR profiles were compared to those calculated from corrected top and bottom sensor readings. The comparisons of attenuation coefficients should be relatively robust to the differences in integration times between continuous (15 minute) and manual (5 sec) readings. Such differences may include the result of bottom reflectance, as manual readings were not shielded. Additionally, absolute light levels recorded with continuous sensors were confirmed using manually determined attenuation coefficients, the manual PAR readings at the deepest depth, and the sensor depths to calculate the PAR levels that would have been obtained from a manual profile at the continuous sensor depths. Differences in recorded and estimated PAR, however, in addition to being sensitive to bottom reflectance, may also disagree if scattered clouds produce varying readings over the 15 minute integration period.

Water Quality Sampling

Water quality samples were collected monthly as deep surface grab samples, preserved appropriately, and processed for color, turbidity, chlorophyll a. Laboratory parameters and references used in the project appear in Table 2. Conventional water quality parameters were all analyzed with EPA-approved methodologies. Methods with no EPA-approved equivalent included those for the determination of spectral absorption of the suspended and dissolved components, and the light attenuation attributable to epiphytic material, described herein.

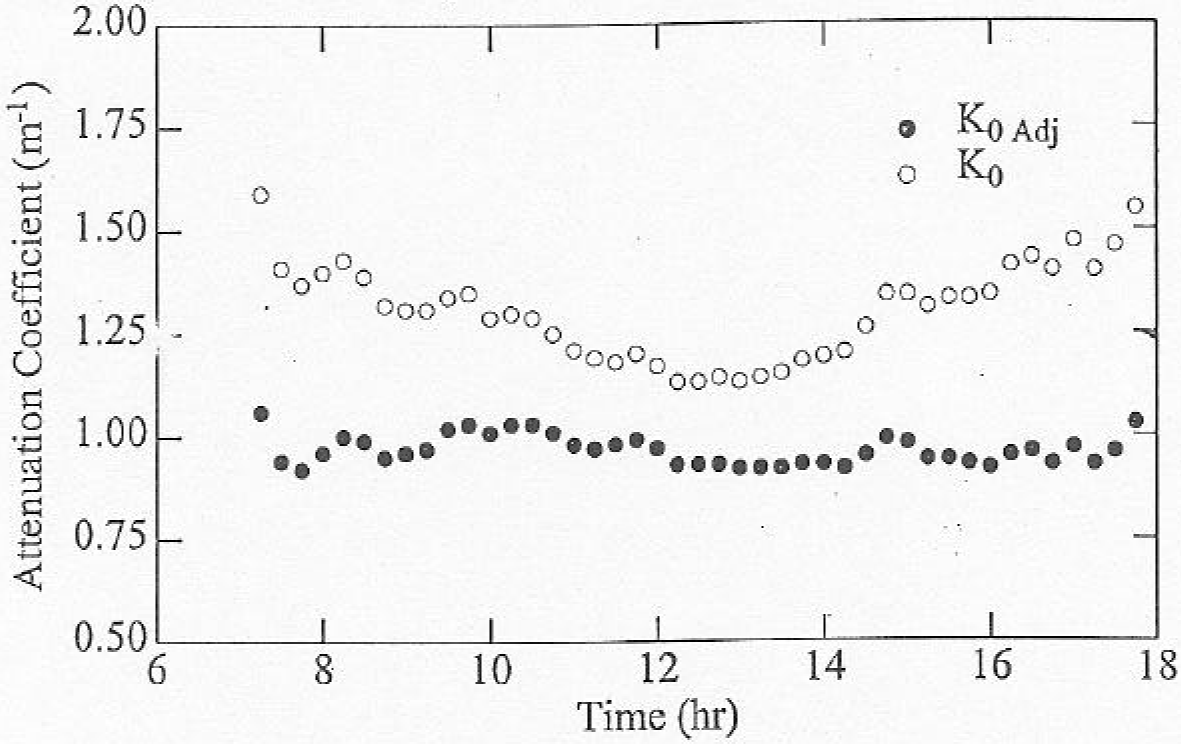

Figure 6. Example of raw and adjusted attenuation coefficients (K_0 and $K_{0\ Adj}$) at Site DEV, December 1, 1997.

Table 2. Laboratory methodologies for water quality parameters.

Parameter	Method	Description
Color	2120B[1]	Visual, nessler tube
Chlorophyll 'a'	10200H[1]	Acidification and trichromatic
Turbidity	2130B[1]	Nephelometric
Specific Conductance	120.1[2]	Electrical resistivity
Salinity	by calculation[3]	
Spectral Absorption	See Text	
Epiphytic Attenuation	See Text	

[1] APHA. 1989. Standard Methods for the Examination of Water and Wastewater, APHA, AWWA, WPCF, 17th Edition. Washington, D.C.

[2] U.S. EPA. 1983. Methods for the Chemical Analysis of Water and Wastes, EPA-600/4-79-020.

[3] Jaeger. 1973.

Suspended and Dissolved Spectral Absorption

On a monthly schedule, the raw water sample from each station was filtered through a glass fiber filter (Whatman, GF/F) and the optical density (OD) spectrum (between 400 and 700 nm) of all particulate matter (detrital, mineral and chlorophyll) on the filter pad was measured relative to a blank, wetted filter in a scanning, dual-beam spectrophotometer (Varian, DMS-80). A blank baseline was measured with no filters in the light paths before and after each set of samples and the mean of these baselines was subtracted from all scans for that sample set. The calibration of the spectrophotometer was checked against calibration standards (Milton Roy) before and after running each set of samples.

After the OD spectrum was measured for total particulate matter, each filter was placed in methanol (Kishino *et al.*, 1985) for at least 50 minutes to extract the phytoplankton pigments. Following the methanol extraction, the OD of the particulate (now only detrital and mineral) was measured again. These filter pad OD (OD_f) spectra were converted to suspension optical density (OD_s) spectra by correcting for pathlength amplification (ß; Butler, 1962) caused by multiple reflectance associated with the concentration of particles on the filters (Cleveland and Weidemann, 1993). The OD_s spectra were converted to absorption spectra using the following equation:

$$a_i(\text{ë}) = 2.3 \bullet (OD_{s,i}(\text{ë})/pl)$$

where a_i(ë) is the spectral absorption coefficient (m^{-1}) for each component (raw particulate and detrital) and *pl* is the pathlength equivalent to the volume of water filtered divided by the clearance area of the filter. Phytoplankton pigment absorption spectra (a_p) were obtained by subtracting the detrital absorption (a_d) spectra (after methanol extraction) from the raw particulate (a_{rp}) spectra (before methanol extraction).

The dissolved color absorption spectra were obtained using the water filtrates from the above filtrations. The optical density spectrum of this filtered water was measured against double distilled water in 10 cm cuvettes using the same spectrophotometer described above. The dissolved color optical density spectra were converted to absorption spectra (a_{dc}) using the above equation with OD_s replaced by the dissolved color optical density (Od_{dc}) and *pl*=0.1 m.

Optical Modeling

The optical model originated with equations presented in Kirk (1994) and Gallegos (1993) in which vertical attenuation (K_d) is a function of solar zenith angle (ì_0), scattering (b) and total absorption (a_t) with g_1=0.473 and g_2=0.218 (determined for the midpoint of the euphotic zone; Kirk, 1994).

$$K_d = \frac{1}{\text{ì}_0} [\, a_t^2 + G(\text{ì}_0) * a_t * b]^{1/2}$$

and $\quad G(\text{ì}_0) = g_1 * \text{ì}_0 - g_2$

As both scattering and absorption are wavelength dependent, the optical model developed was spectrally sensitive (1 nm increments). Analytical data (color, turbidity and chlorophyll) were used to empirically develop general relationships of absorption and scattering spectra of individual attenuators (color, detrital particles, chlorophyll). Wavelength-specific K_d values computed were integrated over 400-700 nm and compared against attenuation coefficients measured in the field to test model efficacy.

Scattering is reported to be best described as a function of turbidity (Morel and Gentili, 1991) rather than of suspended solids (Gallegos, 1994), with:

b(ë)= (550 / ë) * [Turbidity].

Total absorption (a_t) was partitioned into that attributable to water (a_w), chlorophyll or phytoplankton (a_{ph}), dissolved color (a_{dc}), and detritus (a_d).

$$a_t = a_w + a_{ph} + a_{dc} + a_d$$

Water absorption profiles [a_w(ë)]were drawn from literature values (Smith and Baker, 1981) as reported in Gallegos (1993), with 1 nm values linearly interpolated from the 5 nm values provided. Initial attempts to use literature values for chlorophyll specific absorption resulted in distributed residuals with the best agreement for chlorophyll concentrations less than 5 ug/l. Calculated spectra for samples with higher analytical concentrations were significantly higher than observed and may represent a packaging effect of more efficient absorption under lower concentrations or smaller cell size. As a result, individual spectra were normalized to the maximum absorption (~ 437-440 nm), and averaged for all samples for an overall normalized spectra. Chlorophyll-specific absorption [a_{pl}(ë)] was calculated for the model from the linear relationship between maximum absorption MA_{pl} and analytical chlorophyll concentrations as;

a_{pl}(ë) = MA_{pl} * Normalized Spectra (ë), where

MA_{pl}= 0.0209 * (Chlorophyll a, corrected) + 0.0761, n= 129, r2= 0.7647

Absorption due to dissolved color appears as a negative exponential function (Bricaud *et al.*, 1981) of absorption at 440 nm (g_{440}) and spectral slope (s_{dc}), with;

a_{dc}(ë) = g_{440} * $e^{[-s_{dc} * (\text{ë} - 440)]}$

Empirically, absorption at 440 nm was determined as a function of color (in PCU) to be;

g440 = 0.0667 * [Color], n=129, r2=0.9329

While the mean spectral slope determined during the project agreed well with literature values (0.015 compared to a range of between 0.013 to 0.018) there was a remaining dependence of slope with analytical color concentrations. Accordingly, spectral slope was also computed as a function of color (PCU) in the form;

$$s_{dc} = 0.00003 * [\text{Color}] - 0.0178,\ n = 129,\ r2 = 0.5111$$

Absorption due to detritus and other particulate material is also represented as an exponential function of turbidity (NTU) and the absorption cross section of turbidity (ó_d) in the form;

$$a_d(\text{ë}) = \text{ó}_d(\text{ë}) * [\text{Turbidity}]$$

In turn, the turbidity absorption cross section is a function of the longwave absorption cross section, ó_{bl} (*i.e.*, particulate absorption at 720 nm, normalized to turbidity), scaled to absorption at 400 nm (ó_{400}, or particulate absorption at 400 nm, also normalized to turbidity), and slope (empirically determined, s_d = 0.01125) as;

$$\text{ó}_d(\text{ë}) = \text{ó}_{bl} + \text{ó}_{400} * e^{[-s_d * (\text{ë} - 440)]}$$

In addition, ó_{400} displayed a further dependence on color, that may be attributed to the type of particulates present. The dependence of ó_{400} on color was incorporated as follows;

$$\text{ó}_{400} = 0.0014 * [\text{Color}] + 0.0731,\ n=129,\ r2= 0.4676$$

Incident irradiance spectra to initiate wavelength-specific attenuation were provided by Li-COR (1982). Intensity was seasonally adjusted using a sin function empirically fit to maximum E_0 readings (in air) collected throughout the project, and assuming no seasonal or diurnal spectral shifts. Cloudless conditions were therefore implicit in the model, and spectral shifts and loss in intensity due to surface reflectance at the air-water interface were assumed to be minimal.

The PAR spectrum at a selected depth was calculated by using the incident sunlight spectra to "illuminate" a water column of specified conventional properties (color, chlorophyll and turbidity), calculating wavelength specific absorption as described above, and integrating the both the incident and resulting spectra at depth over 400-700 nm. There were no absorption or scattering parameters computed by difference and so overall error terms were evaluated directly, by agreements with *in situ* values of attenuation coefficients, adjusted for sun angle.

Individual stations were assessed through the optical model for relative contributions of attenuating substances, referenced to the attenuation of water alone at the given depth. Using the individual sampling data, analytical concentrations of color, chlorophyll, and turbidity were successively set to zero and supplied as input to the model. Other existing data which included attenuation coefficients, turbidity, color, and chlorophyll were used to evaluate model robustness under combinations of water quality conditions that may not be represented under initiating conditions used to develop the model.

During model calibration, relationships of average cosine measurements (collected using *in situ* instrumentation and defined as downwelling irradiance divided by downward scalar irradiance, $\grave{\imath}_o = E_d / E_o$) with turbidity were examined in an attempt to improve predictive capability. In general, the diffuseness of the underwater light field is expected to increase with turbidity, increasing the apparent cosine of the zenith angle, which may improve the slight bias observed in prior applications of model results (Gallegos, 1993). Based on measurement conditions, varying incident sunlight spectra (cloudy or clear sky) was also examined to improve model accuracy.

Statistical Testing

Statistical analyses of the data were performed using SYSTAT 7.0 (SPSS, 1997) statistical analysis software with significance levels set at $p<0.05$. Analyses included t-test, and one-way ANOVA; with non-normally distributed data, Mann-Whitney, Friedman's two way ANOVA, Kruskal-Wallis, and Wilcoxon signed rank tests were used.

Results and Discussion

Climatic conditions

Rainfall during the project year was extraordinary. Examining averages from the Northern Peace, Southern Peace, and Manasota Basins (SWFWMD, 1997, 1998), cumulative rainfalls during April and May 1997 were 3 to 4 inches above historical means. For June through October, cumulative rainfalls during the project year were comparable to or slightly below historical levels. Beginning in November, however, cumulative monthly rainfall exceeded historical means, and by March 1998, rainfall received during the project year was 21 inches greater than the average amounts received during a comparable period. In addition, much of the rainfall was received in a relatively small number of storms, thus increasing runoff potential.

As expected, recorded flows mirrored rainfall. Combined flows of the Peace River at Arcadia and the Myakka River near Sarasota during the project year were plotted against the historical averages at the same stations (Figure 7). Deviations from typical conditions were slight during the initial months (April through October 1997) of the project. In November, however, combined flows rose to many times greater than historical monthly averages and by March 1998, combined flows were over 9000 cfs, in contrast to an expected 450 cfs (SWFWMD, 1998). The increased flows were evident not only in salinity regimes within the Harbor (below) but also in the water clarity measured at almost all stations.

Long-term Water Clarity

Since 1993, the SWFWMD-SWIM department has fielded a monthly water quality program in Charlotte Harbor. Parameters include attenuation coefficients and water column attenuators, as well as nutrients and other physical measurements. Stations are all in Charlotte County, ranging from the riverine portions of the Myakka and Peace Rivers to outside of Boca Grande Pass. At various times, data have been collected from up to 15 stations of which Station CH-09B is near Site RAD and Station CH-009 is near COT. Annual means of selected water quality parameters appears in Table 3. Depth of 1% surface irradiance cannot be directly converted to Kd or Kd Adj as used in this project as the depths reported are those to which 1% of the incident (in air) irradiance reaches, incorporating the loss of PAR at the air-water interface.

These data indicate that water clarity and parameters which contribute to attenuation are highly variable, not only seasonally, but between years. Attenuation coefficients, secchi depths, color, turbidity, total suspended solids, and chlorophyll a (corrected for pheophytin) all exhibit significant differences by year (Kruskal-Wallis). Salinity also varied significantly by year, while temperatures during 1993 through 1997 (the only years with complete records) displayed no significant variations. Overall salinity was depressed during 1995 and 1998, while the

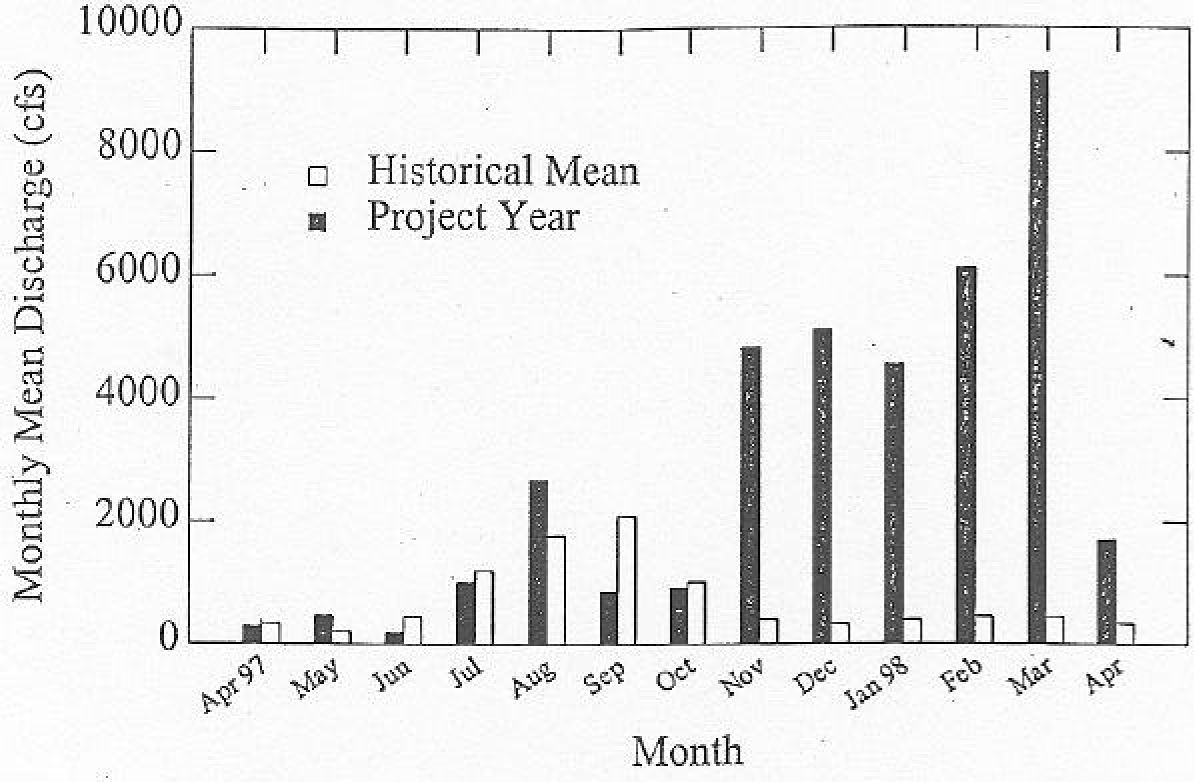

Figure 7. Combined flows of the Peace and Myakka Rivers. Historical averages and flows during the project year.

Table 3. Annual average water quality parameters from the SWFWMD-SWIM Charlotte Harbor monthly monitoring program; all stations pooled. Values from 1998 represent six months of data.

Year	Salinity (ppt)	Temperature (Deg C)	Secchi Depth (m)	Turbidity (NTU)	Color (PCU)	Total Suspended Solids (mg/l)	Chlorophyll a, Corr (ug/l)
1993	18.4	24.7	1.63	3.2	54	9.1	8.3
1994	19.3	25.3	1.63	2.5	61	7.4	6.9
1995	14.9	25.1	1.43	2.8	76	6.8	6.5
1996	19.0	24.4	1.77	3.0	35	9.2	6.6
1997	19.7	25.6	1.48	2.5	74	12.6	6.8
1998*	14.4	26.2	1.34	2.5	80	20.2	5.8

remaining years (1993, 1994, 1996, and 1997) were comparable to one another. As freshwater inflow is thought to be one of the major contributors (through highly colored humic substances) to attenuation in the Harbor, it was not surprising to see a comparable elevation of overall attenuation coefficients during 1995 and 1998 as well. (Salinity and color values were strongly correlated, and significant linear models of attenuation could be constructed with either parameter.) Annual means of attenuation coefficients at SWIM Site CH-009, adjusted for sun angle, appear in Figure 8 for 1993 through the partial year of 1998. The biotic changes observed during the seagrass project and the net gain or loss of grasses at the deep edge should be interpreted with the consideration that the project year represented higher levels of attenuation following two years of comparatively better water clarity.

Temperature and Salinity

Temperature data, gathered weekly, indicated no unusual events and displayed a typical cyclical annual pattern. Temperatures ranged from 14°C in January and February 1998 to 34°C in July and August 1997. Temperatures in April 1998 were comparable to April 1997 data, and so changes in seagrass densities between the beginning and end of the project are more likely to be attributable to light or salinity forcing functions. Differences between stations were not significant. Temperatures are illustrated for the HOG site (Figure 9A).

Salinity on the other hand responded to the record freshwater inflows to the Harbor and displayed no cyclical pattern during the project year. A gradual decline in salinity from the beginning of the project became more precipitous in late July and early August, recovered somewhat, but continued to decline from late August until the end of the study. Trends in salinity are illustrated for the HOG site, the least saline station (Figure 9B). The very wet winter produced minimum salinities during February or March 1998 for the 8 Harbor sites, with a minimum value of 2.0 PSU at HOG. Annual averages of salinity (Table 4) ranged between 14.7 (HOG) and 27.5 PSU (PAT) with the amount of variation in salinity (as either the range or standard deviation) strongly and inversely correlated with mean annual salinity values (Figure 10). In the shorter period of record available for the southern sites, the lowest salinities were generally observed in September. Table 4 also provides mean salinity values during concurrent periods of record (June through November) for all twelve sites and indicates that the HOG site again received the most freshwater, while the PAS site was under the most marine influence during this period.

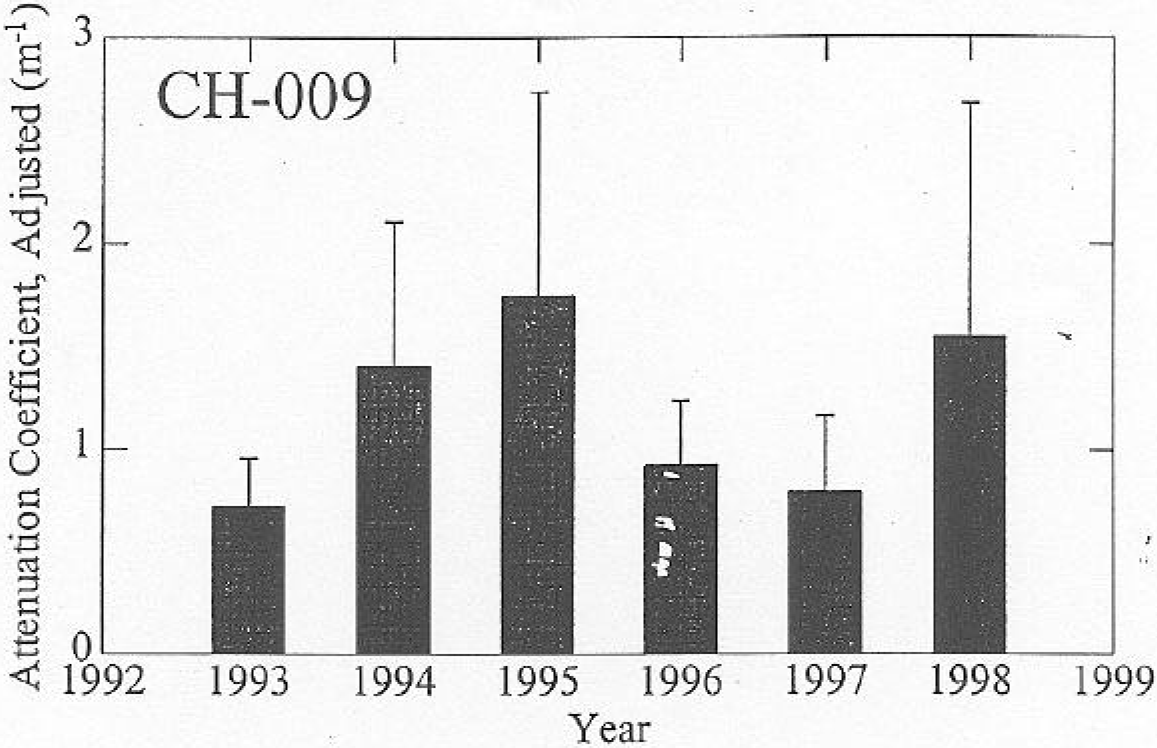

Figure 8. Annual means of water clarity from the SWFWMD-SWIM monthly monitoring program. Station CH-009 is near the COT site for this project.

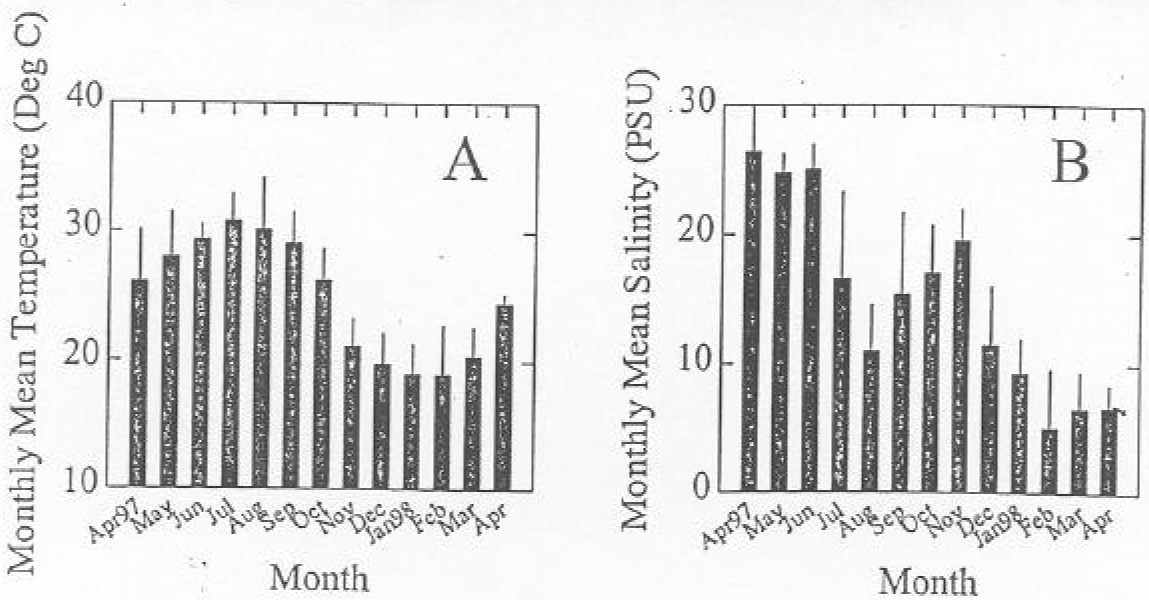

Figure 9. Monthly means and standard deviations of temperature (A) and salinity (B) at the HOG site during the project year.

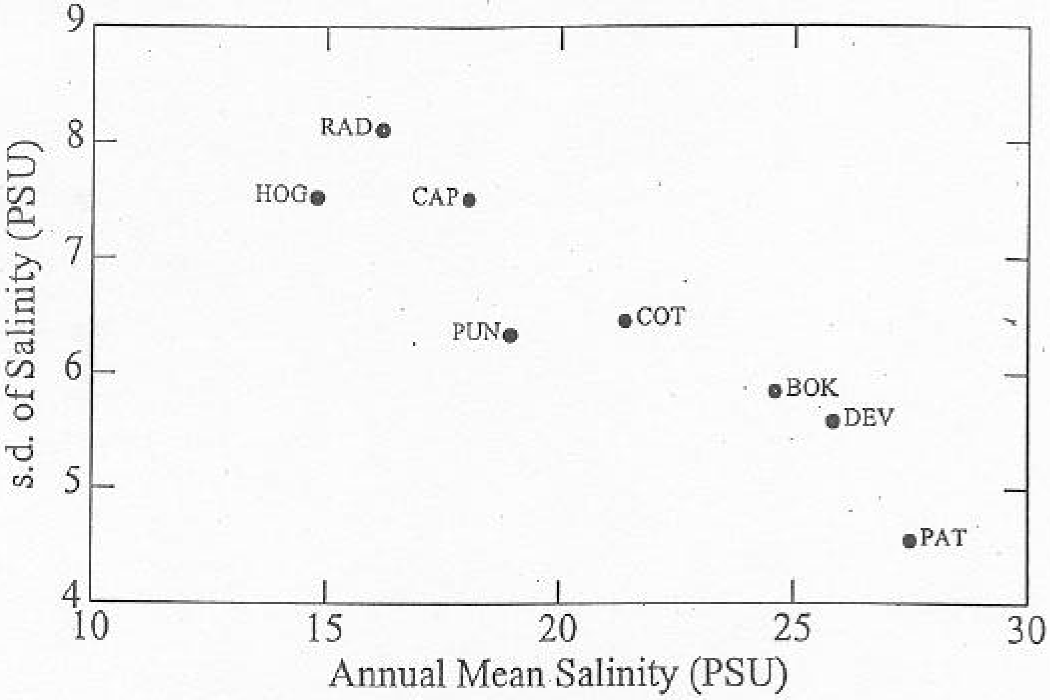

Figure 10. Standard deviation (s.d.) of salinity as a function of mean annual salinity at the eight stations sampled for the entire project year.

Table 4. Mean surface salinity (PSU) by station, for June through November, and for the project year.

June 1997 - November 1997				April 1997 - April 1998			
Site	**Mean**	**s.d.**	**n**	**Site**	**Mean**	**s.d.**	**n**
HOG	17.3	5.5	25	HOG	14.8	7.5	52
RAD	17.8	6.4	23	RAD	16.2	8.1	50
CAP	19.7	6.2	25	CAP	18.0	7.5	52
PUN	20.8	4.4	26	PUN	18.9	6.3	52
MAT	21.3	3.9	6				
COT	23.3	4.5	26	COT	21.4	6.5	53
BOK	26.3	4.2	26	BOK	24.6	5.8	53
BIG	26.6	1.2	+6				
DEV	27.0	4.9	25	DEV	25.9	5.6	52
PAT	28.2	4.2	26	PAT	27.5	4.5	52
SAN	29.2	2.9	6				
PAS	30.3	6.0	6				

Maximum Depths of Grassbeds

The maximum depth limits of sites visited during this project appear in Table 5. Values are the project means of water depths recorded at the deep edges and are assumed equal to depth below mean tide level (MTL) as samplings were random with respect to tides and as the number of station visits was large (n~50) for the eight Harbor sites. The number of visits to the southern sites in Pine Island Sound, San Carlos Bay, and Matlacha Pass were much smaller (n=6) and the depths at these stations must be considered approximate.

Table 5. Maximum depth limits of grassbeds at study sites in Charlotte Harbor and Pine Island Sound. Depths are in meters below mean tide level. * - Stations with only six observations should be considered approximations.

Site	Depth (m)	n=
HOG	0.93	53
PUN	0.95	51
RAD	1.47	51
CAP	1.69	53
COT	1.70	51
DEV	2.43	52
BOK	2.63	53
PAT	2.72	52
MAT	1.48*	6
PAS	2.32*	6
SAN	2.34*	6
BIG	2.43*	6

Maximum depths ranged from 0.9 to 2.7 m below MTL. Maximum depths, in general, increased with distance from the mouths of the Myakka and Peace Rivers and with increasing salinity (Figure 11). (Salinity in the Charlotte Harbor system, as discussed below, has a highly significant inverse relationship with light attenuation.) Of the eight sites with 12 months of data, the PUN site was shallower than would be expected based on salinity alone. Shoot density at the maximum depth was also higher than the remaining *T. testudinum*-dominated sites, indicating that this station may not have been light limited. Additionally, the higher epiphytic loading at this site may have contributed to the shallower depths at this station (see below). The deepest sites were on the southern side of the Harbor near Bokeelia (BOK) and Patricio Key (PAT). The southern, less frequented stations appeared to increase in maximum depth from north to south (from 1.5 to 2.4 m) with the deepest site (BIG) near the mouth of the Caloosahatchee River.

Seagrass Response

Species-specific shoot densities were substantially lower than for other work on *T. testudinum* and *H. wrightii* (Hall *et al.*, 1991; Czerny and Dunton, 1995; Tomasko and Dunton, 1995). Dixon and Leverone (1995) have demonstrated the sensitivity of shoot density to proximity to the deepest edge in a light limited bed, as counts at 1 m from the edge were substantially greater than at the defined deepest edge. The design of this project, working at the deepest edge of the various stations, would be expected to have minimal values of shoot

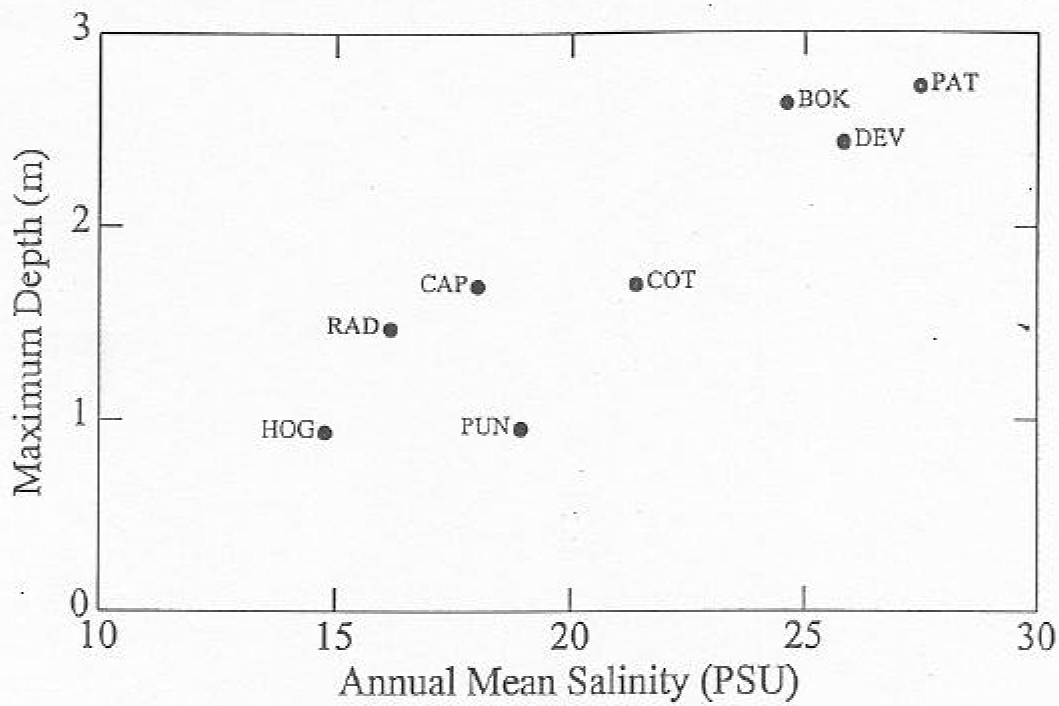

Figure 11. Maximum depths of seagrass beds as a function of mean annual salinity at the eight stations sampled for the entire project year.

density. The variation in density between stations with similar grasses may represent a true difference in shoot density at the deep edge, or may be a result of marking the deepest edge with a series of straight segments. The linearity of the edge of the grassbed determined the number of quadrats of bare sand counted and would contribute to variations in apparent density. It should be emphasized, however, that the same deep edge at each station was consistently sampled, and so observed changes in density at a given station represent meaningful change. For comparison of all 12 sites, Table 6 provides mean shoot densities by species for June, August, and October, combined, while Table 7 lists minimum, maximum, and annualized shoot densities for the sites sampled over a 12 month period.

Table 6. Mean shoot density (# m^{-1}) for June, August, and October for all stations. H = *Halodule wrightii*; T = *Thalassia testudinum*.

Site	**Species**	**Mean**	**s.d.**
BIG	H	49	24
SAN	H	75	41
MAT	H	86	20
HOG	H	112	49
RAD	H	164	77
CAP	H	294	164
DEV	H	383	162
PAT	T	21	6
BOK	T	29	10
PAS	T	39	6
COT	T	50	14
PUN	T	109	35

Table 7. Mean annual average shoot density (# m^{-1}) for the stations sampled over a 12 month period. H = *Halodule wrightii*; T = *Thalassia testudinum*.

Site	**Species**	**Mean**	**s.d.**
RAD	H	112	67
HOG	H	116	44
CAP	H	198	133
DEV	H	314	128
PAT	T	21	6
BOK	T	29	14
COT	T	52	13
PUN	T	122	30

Shoot density along the marked deep edge over the course of the project was used as one of the primary biotic indicator of seagrass bed persistence. Non-parametric tests (Kruskal-Wallis one way analysis of variance) of initial (early May 1997) and final (late April 1998) shoot densities by site indicated that of the instrumented sites, PUN and COT experienced no significant change, while DEV and BOK both recorded significant increases (Table 8). Of the remaining non-instrumented sites sampled over a 12 month period, only the PAT site displayed a significant increase, while HOG, RAD, and CAP were statistically unchanged.

Table 8. Change in shoot density (# m^{-1}) between May 1997, and April 1998. (H=*Halodule wrightii*, T=*Thalassia testudinum*.)

		May 1997		**April 1998**		**Signif.**	
Site	**Species**	**Mean**	**s.d.**	**Mean**	**s.d.**	**Change**	**p=**
HOG	H	182	364	88	124	-	>0.05
RAD	H	75	130	67	80	-	>0.05
CAP	H	131	171	71	92	-	>0.05
DEV	H	142	150	269	152	Incr	0.000

PUN	T	114	88	112	116	-	>0.05
COT	T	40	42	46	66	-	>0.05
BOK	T	7	16	36	27	Incr	0.000
PAT	T	11	17	26	27	Incr	0.002

During the project year, there were statistically significant changes in shoot density by month for the *T. testudinum* and the *H. wrightii* sites. Seasonal signals in shoot density were suppressed at the *T. testudinum* stations (Figure 12), PUN, COT, BOK, and PAT, compared to *H. wrightii* sites and compared to non-light limited sites studied elsewhere (Hall *et al.*, 1991; Dixon and Leverone, 1995). The comparative lack of seasonal signal was consistent with other work on *T. testudinum* at maximum depth limits (Dixon and Leverone, 1995). Lowest *T. testudinum* shoot densities were, in general, observed in October, approximately 2 months following substantive increases in attenuation coefficient, rather than during the coldest months as noted in other work (Dixon and Leverone, 1995).

Sites composed predominantly of *H. wrightii* (RAD, CAP, and DEV) generally displayed more seasonal variation in shoot density (Figure 13) than *T. testudinum* sites. Maximum *H. wrightii* densities were recorded in either June or August. Again, density appeared to decline following the onset of decreased water clarity rather than in response to temperature declines. In contrast, *H. wrightii* densities at the HOG site were lower overall, and there were no significant differences in density by month. The HOG site was the site with the lowest overall salinity, highest salinity variation (either absolute or as a percentage of the mean), and the highest annual attenuation coefficient.

Blade area per shoot also changed significantly over the project (Table 9). Of the eight upper Harbor stations, all but CAP and DEV exhibited significant net declines between April 1997 and March 1998. After an initial increase in blade area between May and June, areas at both *T. testudinum* and *H. wrightii* sites declined steadily. Over the course of the study, blade areas at *T. testudinum* stations were reduced by approximately 38%, while leaf areas at *H. wrightii*-dominated stations declined by 17%. Shoot density and blade area per shoot were combined into leaf area index (LAI; $cm^2\ m^{-2}$). While not testable, LAI increased at sites BOK, PAT, and DEV between April 1997 and March 1998, and decreased at the remaining sites. Of the continuously instrumented sites, only DEV exhibited significant increases in both shoot density and blade area per shoot. Both the PUN and COT sites had decreased blade area and unchanged shoot density for a presumed net decline in above ground biomass. The net change is unclear at the BOK site, which experienced decreased blade area together with increased shoot density. Biotic changes are summarized by species for all sites in Figures 14 and 15. Overall biotic change assessment used to interpret measured light levels appears in Table 10. Stations in the upper Harbor experienced declines in comparison to the lower Harbor stations, with decline typically produced by loss of blade area per shoot.

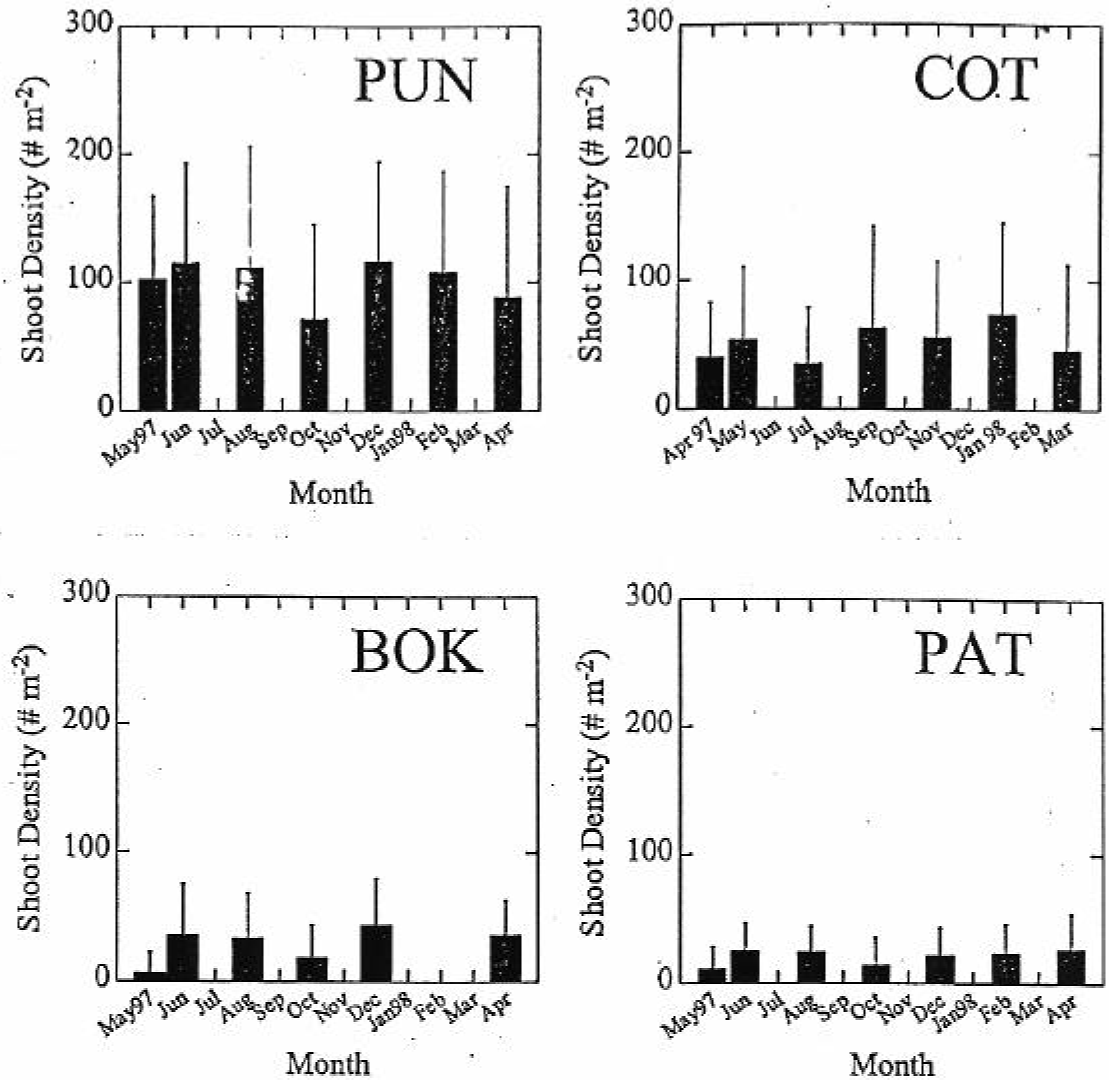

Figure 12. Shoot density (# m^{-2}; mean and standard deviation) observed at the maximum depths of *Thalassia testudinum* beds over the project year.

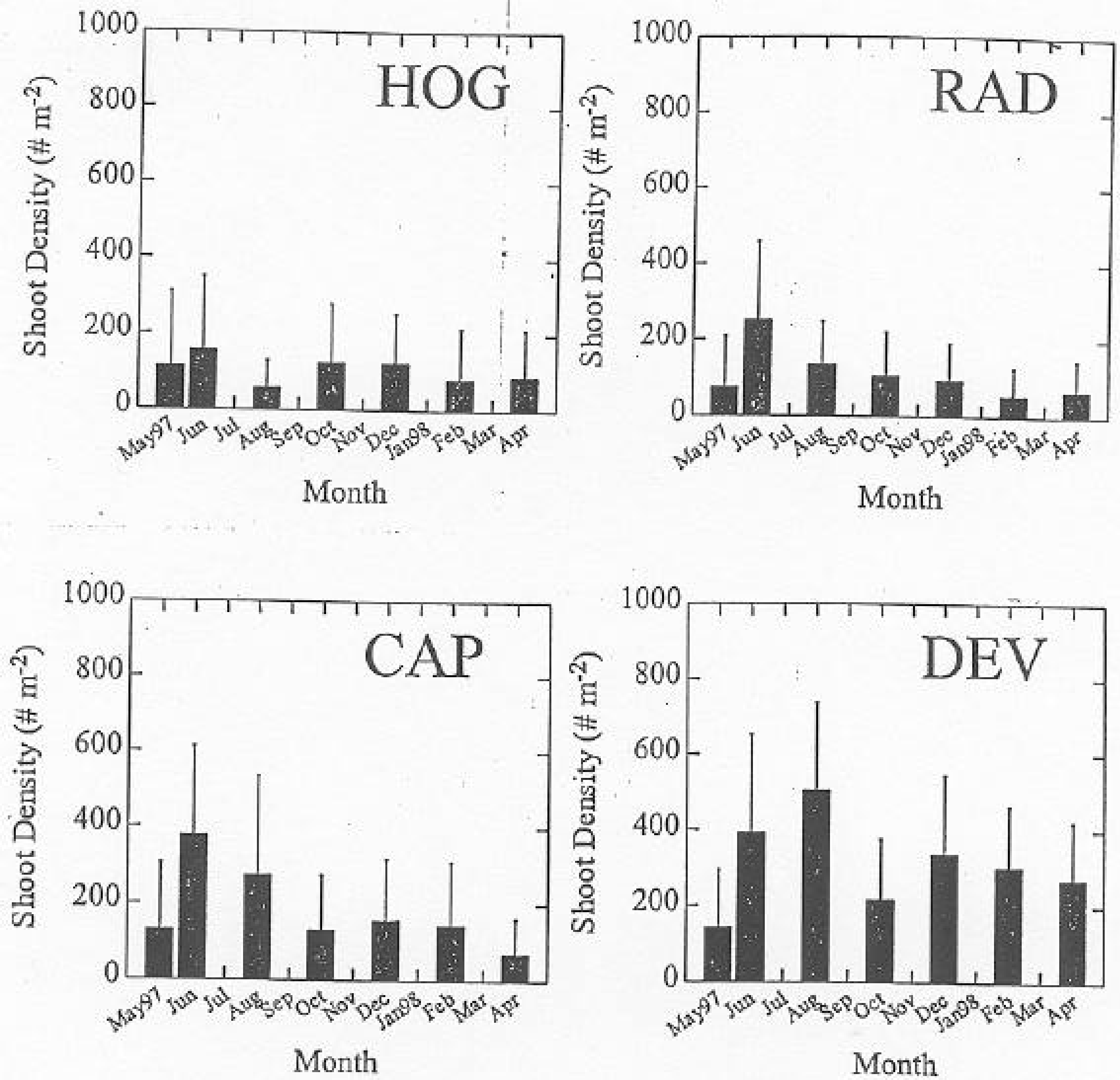

Figure 13. Shoot density (# m^{-2}; mean and standard deviation) observed at the maximum depths of *Halodule wrightii* beds over the project year.

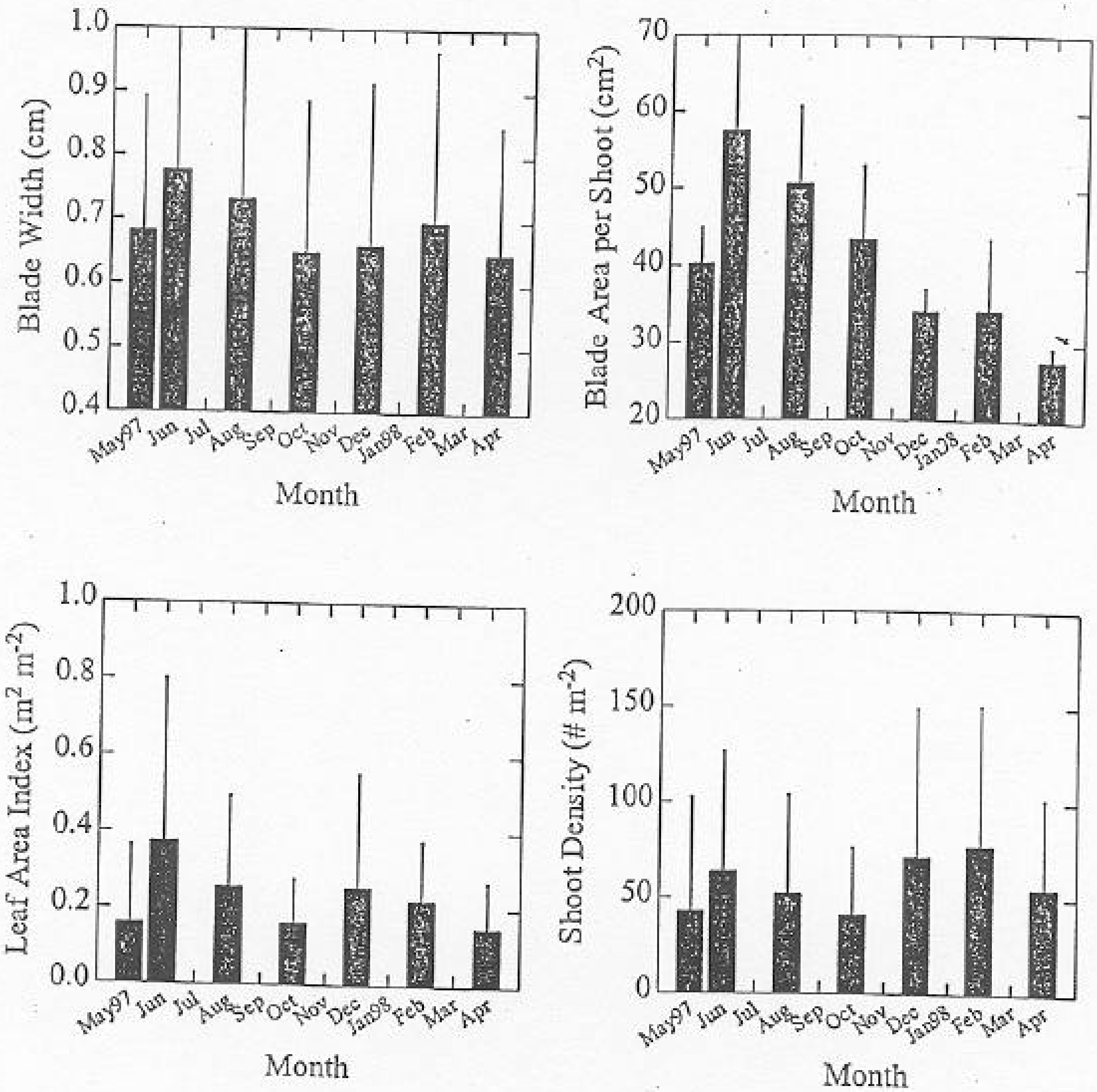

Figure 14. Biotic response (blade widths, blade areas per shoot, leaf area index, and shoot density) observed at the maximum depths of *Thalassia testudinum* beds over the project year. Means and standard deviations of individual station means.

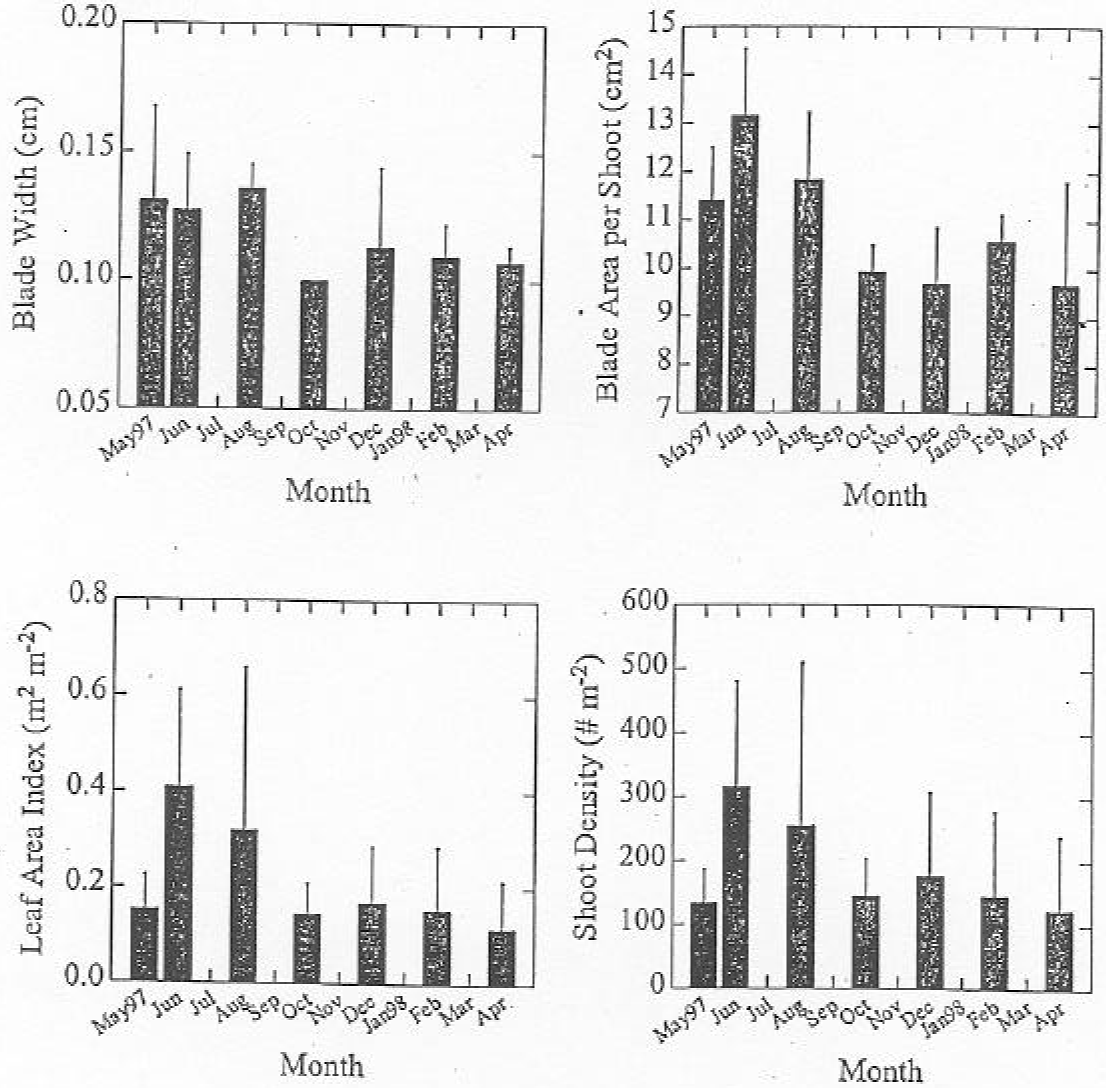

Figure 15. Biotic response (blade widths, blade areas per shoot, leaf area index, and shoot density) observed at the maximum depths of *Halodule wrightii* beds over the project year. Means and standard deviations of individual station means.

Table 9. Change in blade area per shoot (cm^2 $shoot^{-1}$) between May 1997 and April 1998. (H=*Halodule wrightii*, T=*Thalassia testudinum*.)

		May 1997		**April 1998**		**Signif.**	
Site	**Species**	**Mean**	**s.d.**	**Mean**	**s.d.**	**Change**	p=
HOG	H	12.5	0.9	10.7	1.2	Decr	0.028
RAD	H	11.0	2.2	7.6	2.1	Decr	0.028
CAP	H	10.4	1.6	11.6	2.4	-	>0.05
DEV	H	11.7	2.8	8.8	1.3	Decr	0.028
PUN	T	34.8	2.3	26.2	5.6	Decr	0.016
COT	T	41.7	10.0	29.6	4.0	Decr	0.028
BOK	T	43.8	9.1	28.3	3.3	Decr	0.009
PAT	T	40.6	5.4	27.1	8.3	Decr	0.047

Table 10. Summary of biotic changes at seagrass stations between May 1997 and April 1998.

Site	**Species**	**LAI (m^2 m^{-2})**	**Blade Area Per Shoot (cm^2 $shoot^{-1}$)**	**Shoot Density (# m^{-2})**	**Net Change**
HOG	H	D	D	-	D
PUN	T	D	D	-	D
RAD	H	D	D	-	D
COT	T	D	D	-	D
CAP	H	D	-	-	-
BOK	T	I	D	I	?
PAT	T	I	D	I	?
DEV	H	I	-	I	I

Changes, or lack thereof, at the southern sites sampled for a 6 month period are more difficult to interpret. Of the three sites recording a net increase over a 12 month period, one was a *H. wrightii* site and the other two dominated by *T. testudinum*. Each exhibited declines in shoot density between June and October that may have been associated with declines in water clarity. Of the four stations sampled for 6 months, three exhibited no change in shoot density between June and October (the last sampling common to all 12 stations), while at the SAN site, shoot density declined. As the SAN site was not the most affected by decreasing water clarity during this period, and as the decline in shoot density did not appear deleterious based on the 12 month stations, the four 6 month stations were assumed to represent stable grassbeds.

Epiphytic Attenuation

Epiphytic attenuation varied widely over the course of the project with maximum attenuation observed in August and September 1997 (Figure 16). Seasonal patterns were most pronounced at the upper Harbor sites, HOG, PUN, and RAD, while lower Harbor and southern sites were relatively consistent over the time periods sampled. There were significant differences in epiphytic attenuation both among stations, between months, and by species, with attenuations for *T. testudinum* samples slightly higher than *H. wrightii* samples. During the months with highest epiphytic attenuation (August and September 1997), higher attenuations were associated with lower salinity values (Figure 17).

Among the sites sampled for a 12 month period (Figure 18), PUN experienced the highest annual mean attenuation due to epiphytes, at 44%. Of the *H. wrightii* sites, RAD recorded the highest annual epiphytic attenuation, at 40%. The minimum fouling for either species was observed at the DEV site, with an annual mean of 21%. Individual monthly values of epiphytic attenuation ranged from 6% to 71% for *H. wrightii* sites, and 6% to 89% for *T. testudinum* sites. There was no overall trend of annual epiphytic attenuation against mean annual salinity. In examining monthly epiphytic attenuation values as a function of other monthly water quality parameters, higher epiphytic attenuations were generally present under moderate color values (50-150 PCU), moderate salinity values (10-20 PSU), shallower depths (1-2 m), and mid-range water column attenuation (1-2 m^{-1}).

Of the southern stations, the SAN site recorded the lowest epiphytic attenuation for the six month period (13%), while the PAS site, under the most marine influence, recorded 29%. Summary data for the eight sites with 12 months of data and for all sites during the summer period appear in Table 11. Linear interpolation between monthly, site-specific epiphytic attenuation were used to generate plant-available PAR levels from continuous sensor data.

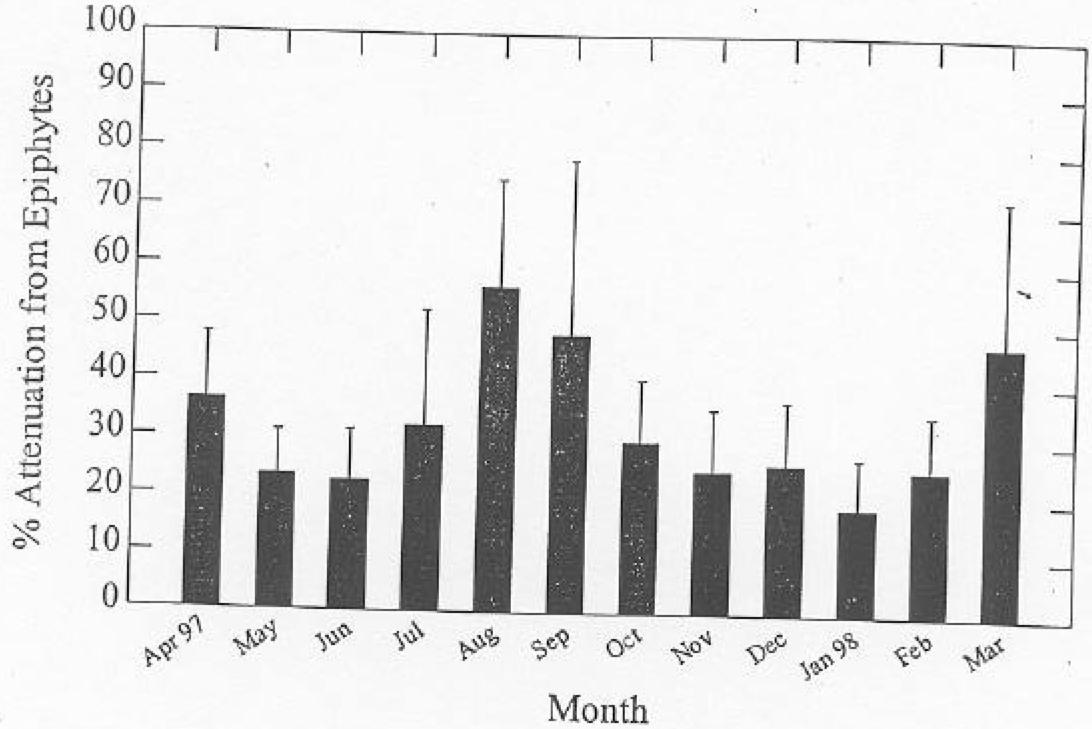

Figure 16. Epiphytic attenuation of PAR at the maximum depths of seagrass beds over the project year. Means and standard deviations of individual station means.

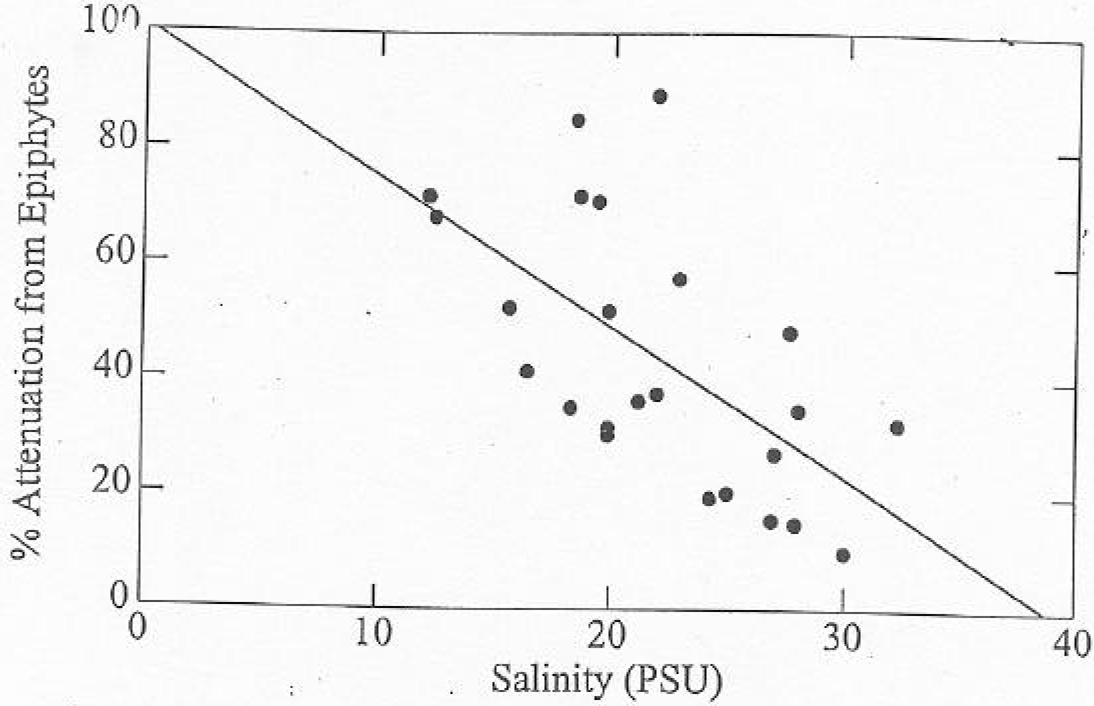

Figure 17. Epiphytic attenuation of PAR as a function of monthly mean salinity during August and September, 1998, for both northern and southern stations.

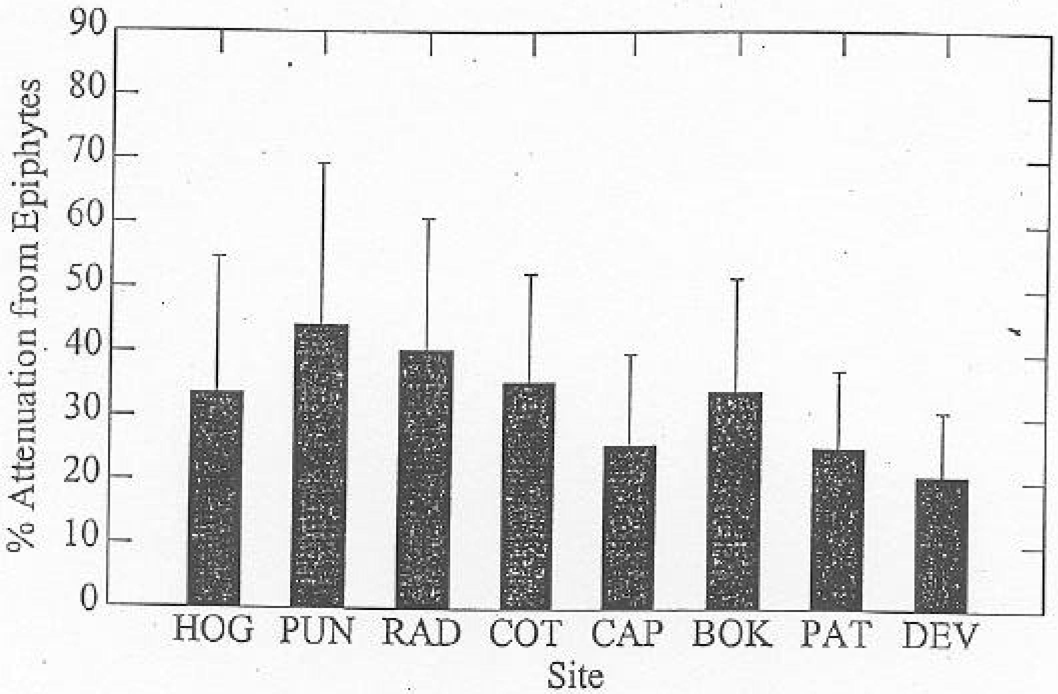

Figure 18. Annual station means and standard deviations of the epiphytic attenuation of PAR for the project year.

Table 11. Epiphytic attenuation (as % reduction of PAR) for all sites, June through November, and for the eight sites sampled over a 12 month period.

June 1997 -November 1997				April 1997 - April 1998			
Site	**Species**	**Mean**	**s.d.**	**Site**	**Species**	**Mean**	**s.d.**
RAD	H	46.0	19.1	RAD	H	40.4	20.7
HOG	H	44.8	24.3	HOG	H	34.3	21.0
CAP	H	27.4	14.2	CAP	H	25.9	15.4
MAT	H	27.5	10.9	DEV	H	20.8	9.7
DEV	H	22.7	12.7				
BIG	H	21.6	7.3				
SAN	H	13.5	3.5				
PUN	T	58.8	22.6	PUN	T	44.3	23.9
COT	T	35.1	16.0	COT	T	35.3	16.9
BOK	T	28.3	8.2	BOK	T	33.9	17.4
PAT	T	21.4	13.4	PAT	T	25.1	12.4
PAS	T	29.2	7.8				

Fouling rates on continuous sensors displayed seasonal patterns consistent with the monthly epiphytic attenuation values. Implied is that blade turnover was relatively consistent over time, a result supported by the low seasonal signals observed in shoot density and leaf area indices.

Four of the monthly sets of epiphytic attenuation samples were processed for dry weights with loads (as mg cm^{-1}) computed from seagrass blade areas. While epiphytic loads did not vary significantly by species, there were significant seasonal and station differences that were even more pronounced than the differences in attenuation (Figure 19). This result is due to the composition of the epiphytes, which in the case of HOG, RAD, and PUN, consisted of a large proportion of calcareous material (*i.e.*, limpets, barnacles, etc.).

The general relationship of epiphytic attenuation to loading was similar to that observed previously for Tampa Bay (Dixon and Leverone, 1995) although the range in the optical properties of the various epiphytic types produced a large amount of scatter in the results. The

regression between attenuation and the natural log of loadings was significant (Figure 20), although the curve produced differed from that for Tampa Bay (Dixon and Leverone, 1995), and for that derived for other species and regions (Sand-Jensen and Borum, 1983; Odum, 1985; Kemp *et al.*, 1988; Burt *et al.*, 1995; Neckles, 1993; Fong and Harwell, 1994). In general, the largest amount of scatter in the relationship was associated with those stations where the calcareous epiphytes were prevalent.
Fig 19

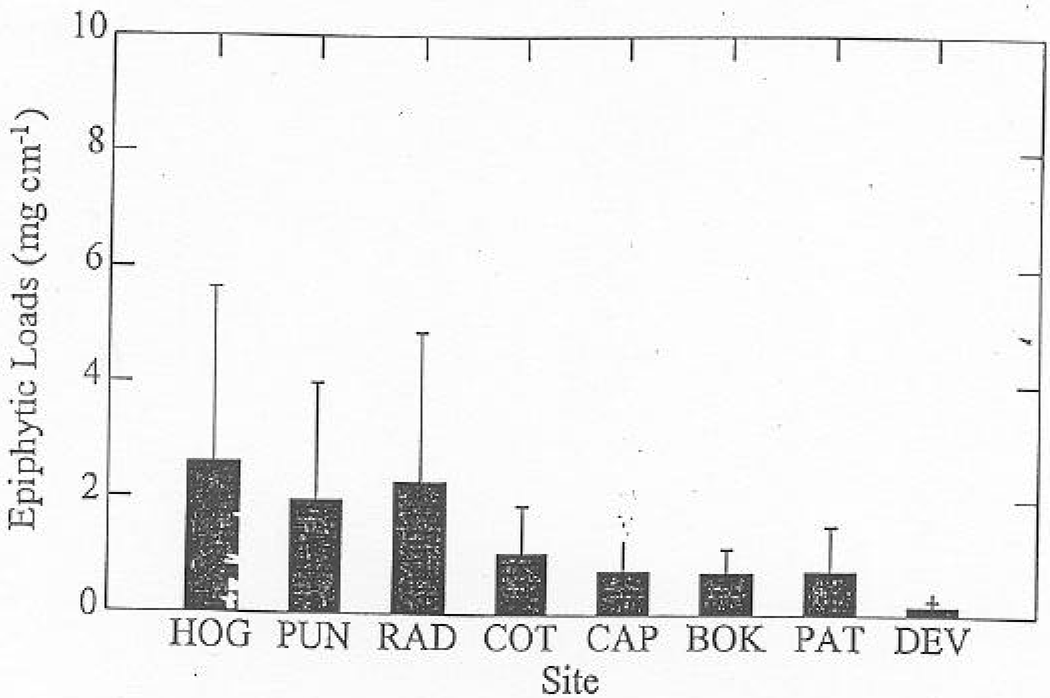

Figure 19. Annual station means and standard deviations of the epiphytic loads on seagrasses. Means and standard deviations from four samplings, May, August, and October of 1997, February 1998.

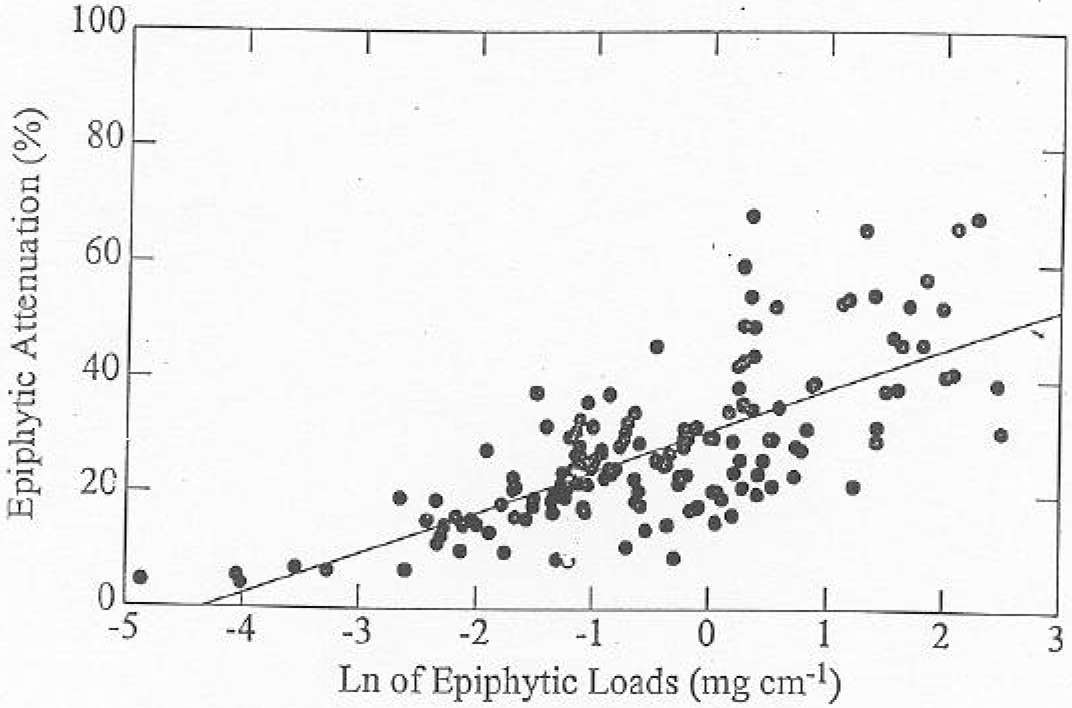

Figure 20. Epiphytic attenuation of PAR as a function of epiphytic loading.

Attenuation Coefficients - Continuous Data

Accuracy of attenuation coefficients determined with continuous instrumentation was assessed by comparison with the weekly *in situ* profiles. Differences between the two quantities could result from changing water clarity over the 15 minute integration period of the continuous recorder, non-homogeneity of the water column, bias in the correction of continuous data for fouling, and individual biases of both the upper and lower continuous sensors and the field profiling sensor. Despite the multiple potential sources for error, the slope between continuous attenuation coefficients and manual profiles was 0.95, with the 95% confidence interval ranging between 0.90 and 1.00. A slope of 1.00 indicates perfect agreement. Differences did not appear attributable to the shielding of the continuous sensors.

As salinity declined over the project year, scalar attenuation coefficients ($K_{0\ Adj}$) collected with continuous sensors increased for the region as a whole. Figure 21 illustrates the monthly means of mean daily adjusted attenuation coefficients between 1000 and 1400 hours, with standard deviations indicating the variation between the four continuous stations. Corrected for sun angle, the coefficients are smaller than typical coefficients (K_0) during the winter months. Depressions in salinity in August were matched by increased attenuation during this month. From October 1997 through March 1998, water clarity steadily declined, with only a slight improvement in April 1998. Monthly values of adjusted and unadjusted attenuation coefficients appear in Table 12 for the four continuous stations.

%PARw and %PARp - Continuous Data

The attenuation coefficients measured at 15 minute intervals and mean station depths were used to compute the percentage of immediately subsurface PAR reaching the maximum depth limits of seagrasses ($\%PAR_w$) and after attenuation by epiphytic loads ($\%PAR_p$; Table 12). Again data were limited to 1000-1400 hours, and monthly means are the calculated from daily means to reduce the impacts of missing data. Monthly values of %PARw ranged between 56% at PUN during June 1997 to less than 1% at DEV during March 1998. Values of %PARp ranged between 38% and 0.3%for the same stations and time periods. Annualized means produced %PARw values of 29.0%, 19.8%, 16.2%, and 13.2% for PUN, COT, BOK, and DEV, respectively, while annual %PARp for the same stations were 15.9%, 13.2%, 11.0%, and 10.6%. The PUN site received substantially more PAR at depth than the remaining stations (Figure 22). Even with the PUN site data included, however, agreement between stations, measured as %RSD, was better for %PARp than for %PARw, emphasizing the utility of incorporating epiphytic attenuation in determination of light requirements.

In view of the net biotic changes, annual %PARp requirements for *T. testudinum* appear to exhibit a salinity-related gradient. The PUN site, the lowest salinity site, experienced 16% of subsurface irradiance as PAR_p, and still experienced biotic declines in above ground biomass. Similarly, the COT site received even less %PARp (13%), with similar biotic declines. At

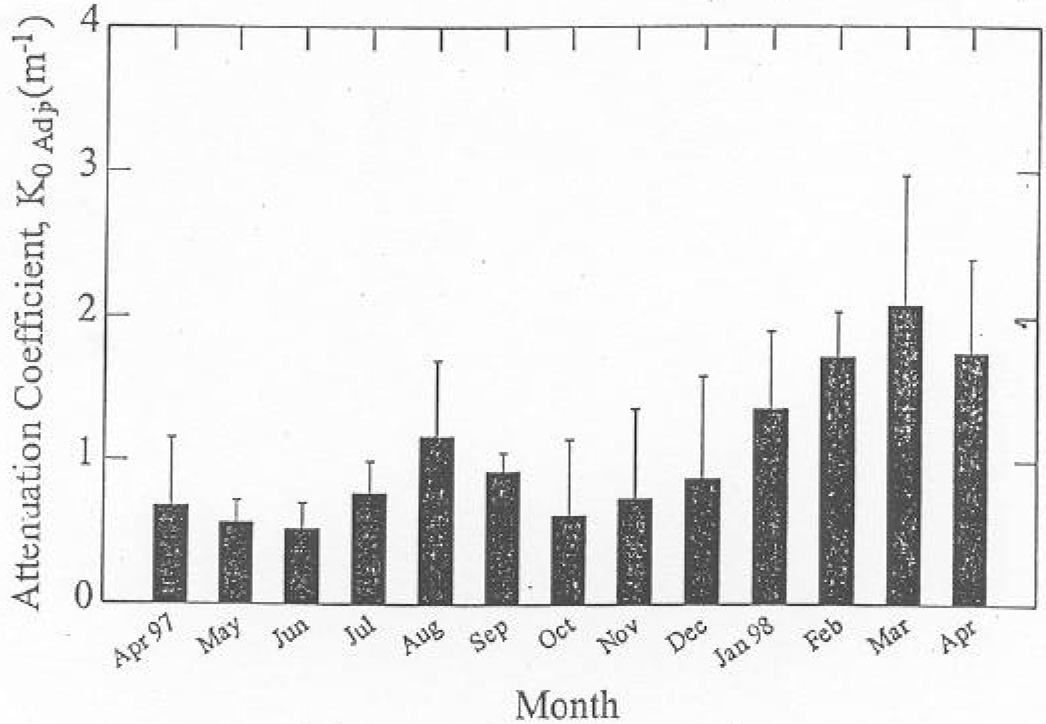

Figure 21. Monthly means and standard deviations of adjusted attenuation coefficients ($K_{0\ Adj}$) measured with continuous instrumentation.

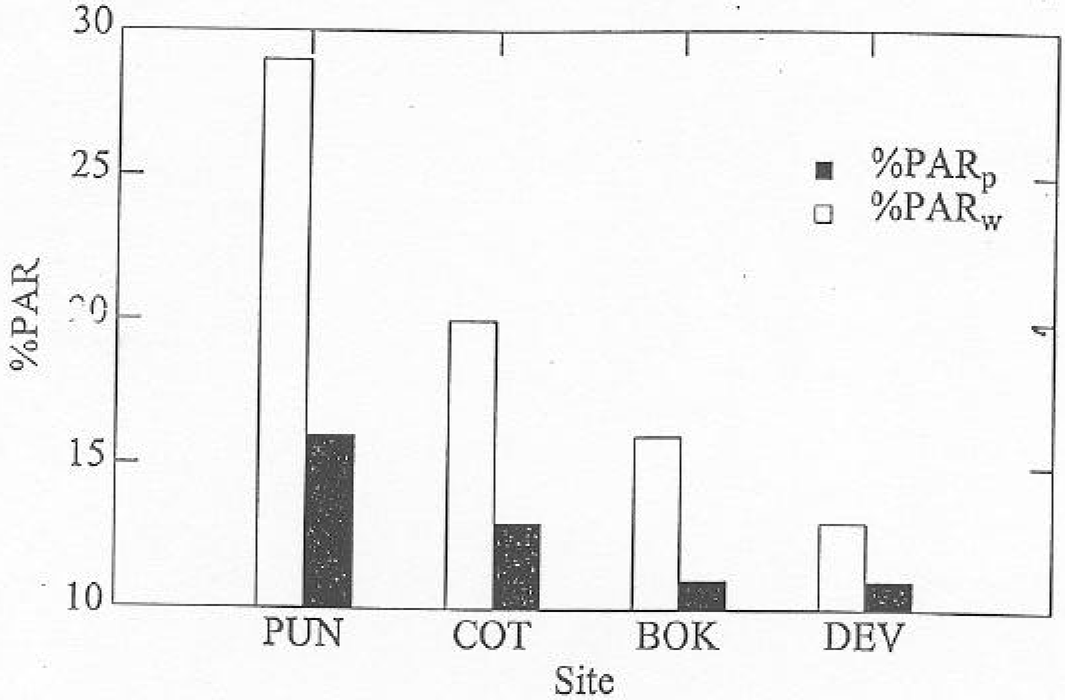

Figure 22. Annualized %PAR$_w$ and %PAR$_p$ for the stations with continuous instrumentation.

Table 12. Monthly and annualized water clarity parameters from continuous instrumentation, 1000-1400 hours.

Site	Month	Mean Sun Angle (Degrees)	Mean K_0 (m^{-1})	Mean $K_{0\ Adj}$ (m^{-1})	Mean PAR_w	Mean PAR_p
PUN	Apr-97	68.19	1.30	1.24	34.4	21.1
	May	72.48	0.63	0.61	55.7	38.4
	Jun	74.71	0.71	0.69	51.5	34.0
	Jul	73.83	0.95	0.92	42.3	21.5
	Aug	69.35	1.81	1.74	19.4	5.1
	Sep	60.82	1.19	1.11	34.5	4.8
	Oct	50.31	1.15	1.00	34.3	15.0
	Nov	41.53	1.55	1.28	25.0	14.6
	Dec	37.32	1.71	1.37	22.7	13.8
	Jan-98	39.47	2.46	2.00	13.8	11.9
	Feb	46.40	2.43	2.08	15.5	12.2
	Mar	56.22	2.60	2.35	9.9	5.9
	Apr	64.42	2.66	2.51	9.9	5.7
Annual Mean			1.60	1.42	28.9	15.9
COT	Apr-97	68.39	0.58	0.55	39.7	23.1
	May	72.49	0.70	0.68	36.3	26.6
	Jun	74.75	0.55	0.54	39.8	32.4
	Jul	73.65	0.88	0.85	26.3	20.1
	Aug	69.39	1.00	0.96	21.8	12.5
	Sep	62.65	1.03	0.96	21.1	9.5
	Oct	49.17	0.99	0.86	19.3	12.4
	Nov	41.54	1.09	0.90	17.6	12.3
	Dec	37.30	1.80	1.44	6.5	4.6
	Jan-98	39.56	1.65	1.07	7.3	5.5
	Feb	46.25	1.80	1.54	5.9	3.9
	Mar	56.24	1.55	1.40	9.0	3.4
	Apr	63.85	1.83	1.72	6.7	2.8
Annual Mean			1.19	1.03	19.5	13.0

Table 12. (Continued)

Site	Month	Mean Sun Angle (Degrees)	Mean K_0 (m^{-1})	Mean $K_{0\,Adj}$ (m^{-1})	Mean PAR_w	Mean PAR_p
BOK	Apr-97	68.26	0.34	0.33	43.0	20.4
	May	72.31	0.44	0.42	37.0	24.5
	Jun	74.26	0.37	0.36	37.3	27.9
	Jul	73.71	0.88	0.86	26.4	20.0
	Aug	69.37	1.32	1.27	3.7	2.5
	Sep	59.93	0.86	0.80	16.5	12.7
	Oct	50.50	0.69	0.61	18.2	12.4
	Nov	41.53	0.94	0.77	12.3	8.4
	Dec	37.24	1.38	1.11	4.0	2.5
	Jan-98	39.15	1.50	1.22	2.7	2.0
	Feb	46.30	1.75	1.50	1.5	1.1
	Mar	56.20	1.69	1.53	2.2	0.7
	Apr	64.14	1.33	1.25	5.3	1.7
Annual Mean			1.05	0.94	15.5	10.5
DEV	Apr-97	67.99	0.64	0.61	23.0	18.1
	May	72.46	0.60	0.58	27.0	22.1
	Jun	74.62	0.55	0.53	28.7	24.7
	Jul	73.88	0.53	0.51	31.7	29.0
	Aug	65.63	0.77	0.74	15.5	9.9
	Sep	60.56	0.97	0.90	12.3	8.0
	Oct	50.31	1.05	0.93	10.3	7.0
	Nov	41.51	1.09	0.90	8.1	6.5
	Dec	37.33	1.32	1.06	6.4	5.2
	Jan-98	39.18	1.50	1.22	3.7	2.8
	Feb	41.69	2.08	1.72	1.3	1.0
	Mar	56.64	3.31	3.00	0.4	0.3
	Apr	64.35	1.61	1.52	4.6	3.9
Annual Mean			1.24	1.10	13.3	10.6

11% PAR_p, the BOK site exhibited a mix of responses, although with a net increase in LAI. The only instrumented *H. wrightii* site, DEV, experienced increased biomass with only 11% PAR_p.

Weekly and Monthly Data

Monthly mean adjusted attenuation coefficients computed from weekly visits and from continuous data were compared (paired t-tests) to assess the robustness of conclusions using weekly data. For the four sites as a whole, there were no significant differences between the two methods, and the monthly attenuations determined with the continuous data averaged only 0.04 m^{-1} higher that the monthly attenuations determined from weekly visits. By station, the COT site was the only one with a significant difference; monthly attenuation computed from continuous data averaged 0.29 m^{-1} lower than the mean weekly profile. In using the annualized attenuation to compute %PAR at depth, the COT site could be in error by as much as much as 12% (*i.e.*, 16% PAR annualized value based on weekly visits, versus 28% PAR based on continuous data). The remaining stations would be in error by only between 0.6% and 6% PAR. It is obvious that some degree of caution is needed, but in general, the weekly samplings appear to be a relatively robust approach to sampling a large number of stations.

Monthly and annual mean adjusted attenuation coefficients based on weekly profiles appear in Table 13 for all sites. Adjusted attenuations were used since not all sampling could take place between 1000 and 1400 hours. Annual attenuation coefficients ranged from 0.80 to 1.79 m^{-1}. Temporal patterns of attenuation were comparable at all of the northern stations with a steady decline in water clarity over the course of the project. The southern sites were sampled for a shorter period of time but did not exhibit the same degree of attenuation increase over time as did the northern sites and so the mean attenuation obtained was used as a surrogate for annual values in the subsequent analyses.

Viewing all sites and data together, a simple yet highly significant model of mean monthly adjusted attenuation coefficient can be produced with mean monthly salinity alone (Figure 23), perhaps in part due to the range in salinities experienced in this atypical year. Varying slopes between the northern and southern regions also highlight the effects of the differing sources, amounts, and color of freshwater to the respective areas. Surprisingly, color was not as significant a predictor of attenuation overall as was salinity.

Maximum depth limits of all sites sampled are illustrated as a function of annual mean adjusted attenuations (Table 13) in Figure 24A. The generalized logarithmic relationship illustrated supports water column light limitation as the controlling physical factor on maximum depth, but the increased scatter in the relationship at high attenuation (and low salinity) could indicate other controlling factors as well. The mean %PARw for all sites was 17.6% of the immediately subsurface PAR, ranging from 10.1% (BIG) to 26.2% (PUN).

Fig 23

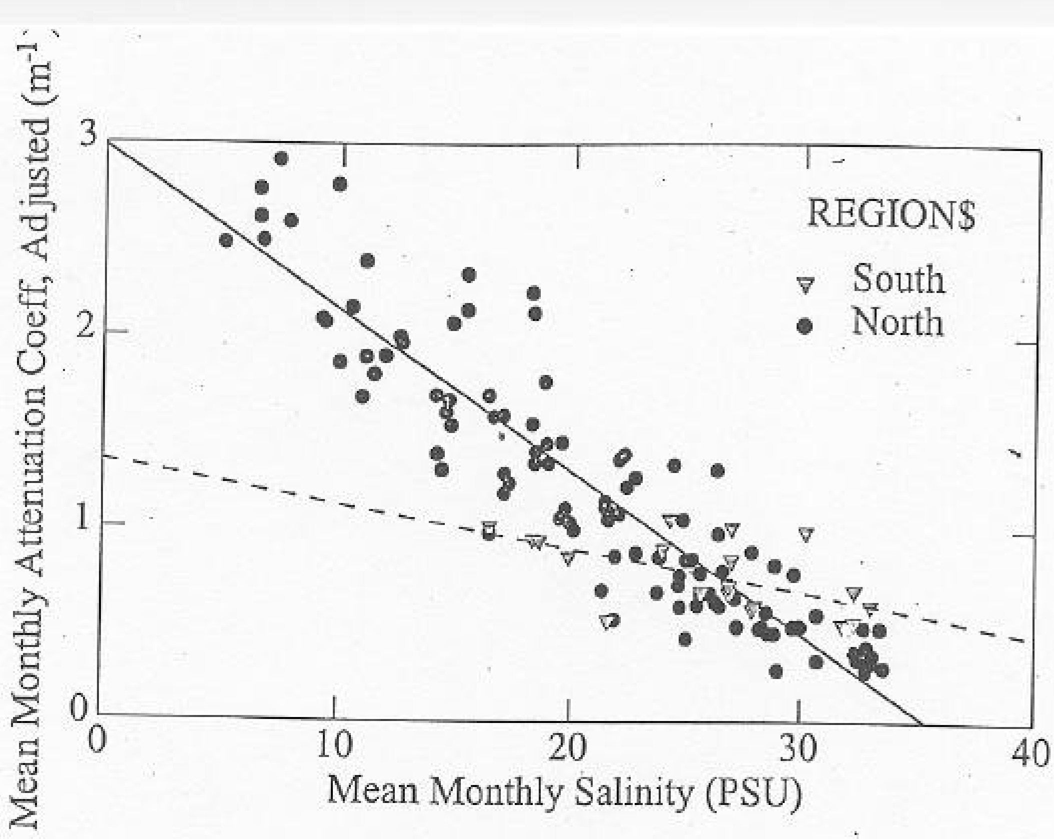

Figure 23. Mean monthly adjusted attenuation coefficients ($K_{0\ Adj}$) as a function of mean monthly salinity values for all stations using weekly or monthly data.

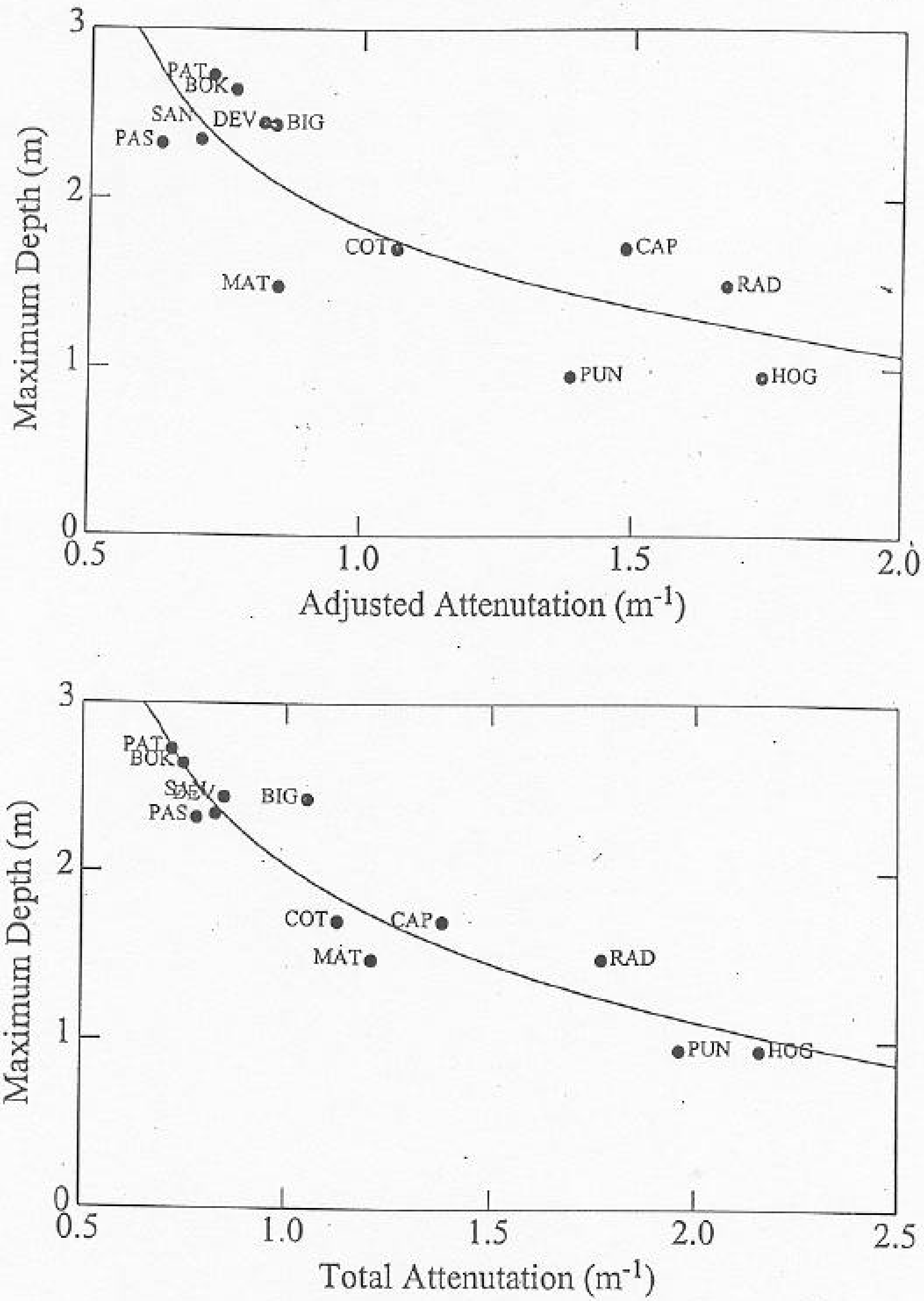

Figure 24. Maximum seagrass depths as a function of adjusted attenuation coefficients ($K_{0\ Adj}$; A) and as a function of total attenuation coefficients (K_{total})which incorporate epiphytic attenuation (B). Based on weekly or monthly data.

Table 13. Monthly and annualized adjusted attenuation coefficients ($K_{0\ Adj}$; m^{-1}) from weekly observations. Except as noted, n~50 for each station.

Site	HOG	PUN	RAD	COT	CAP	BOK	PAT	DEV	MAT*	PAS*	SAN*	BIG*
Apr-97	1.31	0.81	0.48	0.32	0.49	0.27	0.28	0.48				
May	0.76	0.64	0.66	0.49	0.49	0.33	0.34	0.49				
Jun	0.84	0.67	0.60	0.46	0.57	0.36	0.31	0.39				
Jul	1.59	1.27	1.06	0.62	0.85	0.27	0.55	0.46	0.94	0.68	0.68	0.71
Aug	1.69	1.54	2.39	0.98	1.31	0.53	0.43	0.69	1.02	0.95	0.67	1.01
Sep	2.33	1.04	1.39	1.22	1.24	0.67	0.61	0.71	0.86	0.52	0.58	1.05
Oct	1.19	1.11	1.29	0.86	1.59	0.60	0.49	0.84	0.53	0.50	0.99	0.84
Nov	1.45	1.14	2.13	0.86	2.23	0.77	0.88	0.77	0.90	0.51	0.61	0.60
Dev	1.81	1.55	1.77	1.35	1.61	1.05	0.78	0.88				
Jan-98	2.09	2.07	2.78	1.40	2.00	1.10	1.05	1.12				
Feb	2.48	1.97	2.59	1.70	1.90	1.34	1.36	1.44				
Mar	2.62	2.08	2.76	1.90	2.92	1.70	1.39	1.33				
Apr	2.50	2.15	1.86	1.68	2.14	1.00	0.98	1.08				
Annual Mean	1.79	1.44	1.73	1.12	1.55	0.80	0.75	0.84				
Max Depth	0.93	0.95	1.47	1.70	1.69	2.63	2.72	2.43	1.48	2.32	2.34	2.43

* - n=6

Monthly mean adjusted attenuation, monthly epiphytic attenuation, and mean maximum depths were used to compute mean monthly %PARp (Table 14) and an annual %PARp at each site. A "total attenuation" coefficient (K_{total}) was then computed for each station from annualized %PARp values and station depths. The total attenuation coefficient incorporates the effects of epiphytic attenuation, but only pertains to the depth for which is was calculated. It is presented in Figure 24B as a device to illustrate the necessity of including epiphytic attenuation, as the scatter between stations is substantially reduced.

The logarithmic fit illustrated in . 24B represents an annualized plant requirement of 13% of the immediately subsurface PAR, with individual stations ranging between 16.8% (MAT) and 7.3% (RAD). The mean %PARp at all 12 sites from weekly data (13%), was very comparable to the mean annual %PARp computed from continuous data at four sites (12.7%) and consistent with earlier work in Tampa Bay (Dixon and Leverone, 1995) which reported annual mean %PAR_p values between 13.0% and 14.2%.

Annualized values of %PAR_p appear in Figure 25. *T. testudinum* stations were closely grouped, receiving roughly between 13.9% and 15.7%PAR_p annually. A trend of increasing %PAR_p with decreasing salinity was observed and declines in biomass noted even for the station receiving the highest %PAR_p (PUN). The range in %PAR_p at *H. wrightii* stations was broader and somewhat lower, between 7.3 and 13.1%PAR_p. Biomass declines were noted for stations with up to 15.7%PAR_p (PUN). With the exception of CAP, stations with mean annual salinities below 18 PSU experienced biotic declines.

PAR Annual and Daily Totals - Continuous Data

Individual PAR readings (15 minute averages) and attenuation coefficients were used to compute the PAR at maximum depths and available to the seagrasses after epiphyte attenuation. The values represent PAR calculated at the deep edge of each grassbed and do not include any PAR received by the grassbed after reflectance off of the bottom. Values were summed over a day at each of the four instrumented sites and daily totals averaged by month. Monthly means were further averaged and multiplied by 365 to compute annual totals of PAR and to minimize impacts of any missing data. Monthly and annual values by site appear in Table 15, together with the effects of tidally varying water depths. Applying tidal variation during the study year produced mixed results in that some stations received lowered PAR_w and PAR_p (2-4%) while at the PUN site, annual PAR_p was increased by 5%. As there was no clear bias, the remaining data analyses were performed using fixed water depths.

In an effort to report biologically meaningful PAR_p levels, PAR_w was computed for depths 0.1 m and 0.2 m above the bottom (canopy heights), including estimates of the PAR reflected from the bottom. Bottom reflectance was obtained from field measurements of irradiance reflectance at surface and at bottom, and used to calculate the absolute quantities of PAR reflected. Bottom reflectance was typically less than 10%, and while there were station to

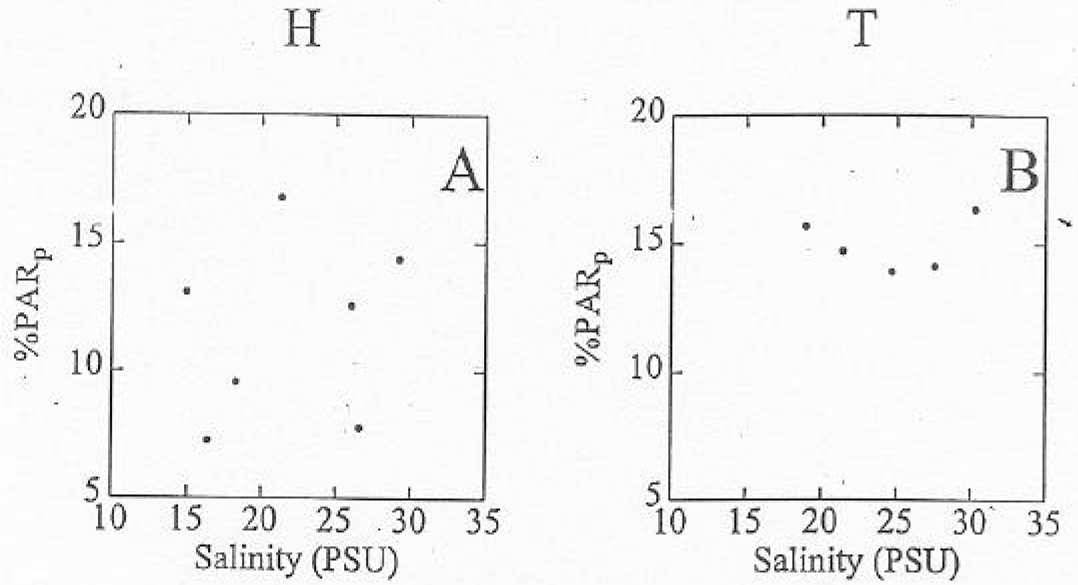

Figure 25. Annualized %PARp by site, segregated by seagrass species. T = *Thalassia testudinum*, H = *Halodule wrightii*. Based on weekly data.

Table 14. Monthly and annualized $\%PAR_p$ at seagrass depth limits. Except as noted, n~50 for water column observations and n=12 for epiphytic attenuation.

Site	HOG	PUN	RAD	COT	CAP	BOK	PAT	DEV	MAT*	PAS*	SAN*	BIG*
Apr-97	27.0	30.4	20.2	41.7	27.8	28.9	33.3	23.5				
May	41.9	39.7	24.7	33.1	36.2	31.1	29.6	26.5				
Jun	34.6	32.7	28.8	33.1	32.3	23.6	27.2	33.7	26.7	9.7	7.6	2.2
Jul	10.1	13.5	16.4	28.9	18.5	38.6	18.1	31.4	17.3	14.6	17.9	12.8
Aug	6.1	4.0	1.1	11.9	7.1	18.3	18.9	12.3	13.0	7.1	17.7	6.3
Sep	5.9	4.4	3.1	6.9	8.3	12.5	19.4	10.2	19.2	20.4	21.8	6.2
Oct	25.5	21.6	8.9	17.1	8.3	13.7	23.2	12.8	33.5	23.5	8.6	10.9
Nov	23.7	20.9	7.7	17.4	8.6	15.5	15.8	14.9	20.2	24.4	20.7	17.6
Dev	16.1	13.7	8.5	8.3	6.9	4.5	11.1	10.6				
Jan-98	14.7	19.9	2.9	7.9	3.9	6.1	4.9	5.4				
Feb	8.5	12.4	3.5	4.3	4.3	2.9	1.7	3.1				
Mar	7.7	7.8	0.8	1.8	0.6	0.8	3.3	3.7				
Annual Mean	18.5	18.4	10.5	17.7	13.5	16.4	17.2	15.7	21.6	16.6	15.7	9.4

* - n=6

Table 15. The effect of tidally varying water column depths on mean daily PAR_w and annual PAR_w received at depth. Unless specified, units are Moles m^{-2} day^{-1}.

Site / Month	Mean PARw		Mean PARw		Site / Month	Mean PARw		Mean PARw	
	Fixed depth		Tidal Depth			Fixed depth		Tidal Depth	
PUN	Mean	s.d.	Mean	s.d.	BOK	Mean	s.d.	Mean	s.d.
Apr-97	20.2,	9.5	19.9,	9.5	Apr-97	20.7,	8.1	20.5,	8.1
May	28.8,	8.3	27.3,	8.0	May	20.3,	6.2	19.7,	6.0
Jun	26.4,	8.7	23.8,	7.6	Jun	18.2,	7.5	17.4,	7.2
Jul	17.6,	7.1	15.5,	6.7	Jul	12.3,	5.8	11.3,	5.6
Aug	4.7,	2.0	4.0,	1.9	Aug	4.0,	1.9	3.4,	1.5
Sep	9.3,	5.5	9.3,	6.1	Sep	4.6,	2.4	4.3,	2.3
Oct	9.2,	4.4	10.1,	5.4	Oct	4.5,	1.7	4.6,	1.7
Nov	7.5,	4.0	9.9,	6.3	Nov	3.6,	2.5	4.0,	2.7
Dec	3.3,	3.3	4.9,	5.0	Dec	0.9,	0.7	1.1,	0.7
Jan-98	4.4,	2.4	8.7,	6.9	Jan-98	0.6,	0.3	0.8,	0.4
Feb	3.8,	1.8	6.3,	3.3	Feb	0.4,	0.2	0.5,	0.3
Mar	5.2,	3.3	7.3,	5.2	Mar	0.6,	0.4	0.6,	0.4
Apr	4.0,	3.0	4.8,	3.4	Apr	1.6,	1.3	1.6,	1.2
Mean Daily PAR ($M\ m^{-2}\ d^{-1}$)	11.0		11.6			6.8		6.6	
Annual PAR ($M\ m^{-2}\ yr^{-1}$)	4023		4244			2466		2392	
COT	Mean	s.d.	Mean	s.d.	BOK	Mean	s.d.	Mean	s.d.
Apr-97	19.7,	8.7	19.5,	8.7	Apr-97	14.6,	6.1	14.3,	6.1
May	22.7,	6.4	21.6,	6.2	May	17.1,	6.6	16.3,	6.5
Jun	22.2,	6.7	20.4,	6.2	Jun	18.9,	6.3	17.5,	6.0
Jul	14.0,	4.3	12.5,	4.0	Jul	13.8,	3.2	12.8,	3.3
Aug	5.2,	1.9	4.6,	1.7	Aug	6.6,	1.1	5.7,	0.8
Sep	7.1,	3.1	6.8,	2.9	Sep	5.0,	2.3	4.8,	2.1
Oct	6.4,	2.4	6.6,	2.6	Oct	3.9,	2.2	4.0,	2.3
Nov	5.9,	2.9	7.2,	4.1	Nov	3.4,	2.0	3.8,	2.2
Dec	2.2,	1.8	2.9,	2.3	Dec	1.9,	1.9	2.2,	2.2
Jan-98	1.5,	0.9	2.2,	1.3	Jan-98	0.9,	0.5	1.1,	0.7
Feb	1.1,	0.7	1.5,	1.0	Feb	0.4,	0.6	0.5,	0.6
Mar	1.4,	1.0	1.6,	1.1	Mar	0.5,	0.5	0.5,	0.6
Apr	1.7,	1.1	1.8,	1.0	Apr	2.5,	1.6	2.5,	1.6
Mean Daily PAR ($M\ m^{-2}\ d^{-1}$)	8.4		8.2			6.7		6.5	
Annual PAR ($M\ m^{-2}\ yr^{-1}$)	3055		2999			2460		2362	

station differences, there were no relationships observed to either cloud cover, time, sun angle, attenuation coefficient, color, chlorophyll, turbidity, incident irradiance, or measured cosine angle of irradiance. Accordingly, monthly mean values of bottom reflectance were calculated for each site and used to compute PAR_p at the canopy height.

The reflected PAR was attenuated through 0.2 m using measured attenuation coefficients (K_0) and the resulting quantity added to the downward propagating PAR_w. The resulting PAR_w at 0.2 m shallower ranged between 20% and 30% higher than the values at the maximum depth limits, with the most obvious increases noted at the shallow PUN station. Subsequently, epiphytic attenuation was used to reduce PAR to compute the PAR_p at the canopy height (Table 16). These data reductions permitted comparisons with previous work and other investigators in which sensors were unshielded and at canopy heights.

Annual totals received at the canopy depth (PAR_w) ranged from 5,287 Moles m^{-2} yr^{-1} at the PUN site to 2,871 Moles m^{-2} yr^{-1} at DEV. Sites DEV (*H. wrightii*-dominated) and BOK (*T. testudinum*-dominated) were very similar in PAR_w, while the COT site received 3,770 Moles m^{-2} yr^{-1}. After correction for epiphytic attenuation (PAR_p), annual totals available to the plant at the canopy height (0.2 m) ranged between 1,982 and 3,051 Moles m^{-2} yr^{-1}. Declines in biomass (Table 10, above) were presumed at PUN and COT sites, which received 3,051 and 2,609 Moles m^{-2} yr^{-1}, respectively. The BOK site, with 1,982 Moles m^{-2} yr^{-1} of PAR_p, experienced a mixed suite of biotic changes (increased shoot density, and decreased blade area per shoot) although with an increase in LAI over the study. The annual light requirements for *T. testudinum* in Charlotte Harbor appear to be at least as great or greater than the PAR recorded and again light requirements appear to increase with decreased salinity.

Annual PAR_p at canopy height (Figure 26) was 2,334 Moles m^{-2} yr^{-1} at the DEV site, which, accompanied by an increase in density and blade area, indicate that *H. wrightii* light requirements are somewhat less than that for *T. testudinum*. The PAR_w at the DEV site was 2,871 Moles m^{-2} yr^{-1} and *H. wrightii* at this site exhibited biotic increases over the project, primarily through shoot density increases. The PAR_w of the site was greater than the 2,200 to 2,400 Moles m^{-2} yr^{-1} identified by Dunton (1994) as insufficient to maintain a positive carbon balance, and also greater than the 1,600-2,000 Moles m^{-2} yr^{-1} measured when *H. wrightii* died within 9 months (Czerny and Dunton, 1995). The range between the PAR_w and PAR_p is a further examples of the importance of including epiphytic attenuation, as the levels of Texas epiphytes and PAR_p are unknown.

Czerny and Dunton (1995) also defined 1,900 Moles m^{-2} yr^{-1} as a necessary annual PAR_w level for *T. testudinum* in Texas. Previous work in Tampa Bay on *T. testudinum* sites (Dixon and Leverone,

1995) recorded PAR_w levels between 3,600 and 4,900 Moles m^{-2} yr^{-1}, and PAR_p levels between 2,200 and 3,100 Moles m^{-2} yr^{-1} with shading effects noted for the one station which received less than 3000 Moles m^{-2} yr^{-1}. Stations in Tampa Bay which received near 3,100 Moles m^{-2} yr^{-1} experienced biotic changes that were consistent with no net change and the seasons sampled. The annual PAR_p at the BOK *T. testudinum* site, however, was 1,982

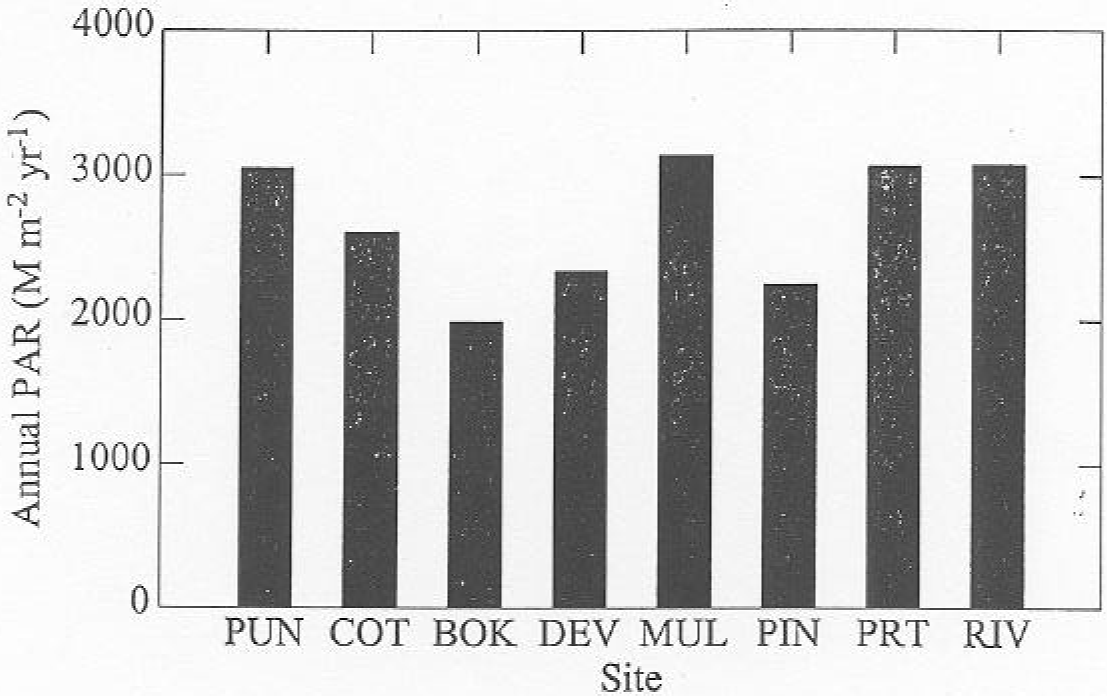

Figure 26. Annualized PARp (at canopy height) from continuous instrumentation in Charlotte Harbor and Tampa Bay, Florida.

Table 16. Estimation of PAR_w and PAR_p (including bottom reflectance) at seagrass canopy heights for comparison with previous work. Unless specified, units are Moles m^{-2} day^{-1}.

Site / Month	Mean PAR_w		Mean PAR_p		Mean PAR_w		Mean PAR_p		Mean PAR_w		Mean PAR_p	
	At maximum depth limits				At 0.1 m above bottom				At 0.2 m above bottom			
PUN	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Apr-97	20.2	9.5	12.4	5.8	23.4	10.7	14.4	6.6	26.0	11.5	16.0	7.1
May	28.8	8.3	19.9	5.7	31.9	9.3	22.0	6.3	34.0	9.9	23.5	6.8
Jun	26.4	8.7	17.3	5.3	29.4	9.7	19.3	5.9	31.5	10.5	20.7	6.4
Jul	17.6	7.1	9.0	4.3	20.1	7.7	10.3	4.7	21.9	8.0	11.2	4.9
Aug	4.7	2.0	1.1	0.6	5.7	2.4	1.3	0.6	6.9	2.9	1.6	0.7
Sep	9.3	5.5	1.2	0.7	10.8	6.3	1.4	0.8	12.1	7.0	1.6	0.9
Oct	9.2	4.4	3.8	1.9	10.6	5.1	4.3	2.2	11.8	5.7	4.8	2.4
Nov	7.5	4.0	4.4	2.3	9.1	5.0	5.3	2.9	10.6	6.0	6.2	3.5
Dec	3.3	3.3	1.9	1.9	4.0	4.0	2.3	2.3	4.7	4.6	2.8	2.7
Jan-98	4.4	2.4	3.8	2.0	6.2	3.5	5.4	3.0	8.7	5.4	7.6	4.7
Feb	3.6	1.8	2.9	1.5	4.8	2.3	3.9	2.0	6.5	3.2	5.2	2.8
Mar	5.2	3.3	3.0	1.9	6.9	4.2	4.1	2.5	8.8	5.3	5.2	3.1
Apr	4.0	3.0	2.3	1.7	5.2	3.8	3.0	2.2	6.6	4.6	3.8	2.7
Mean Daily PAR (M m^{-2} d^{-1})	11.0		6.3		12.8		7.4		14.5		8.4	
Annual PAR (M m^{-2} yr^{-1})	4017		2304		4676		2688		5287		3051	

COT	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Apr-97	19.7	8.7	11.3	4.9	22.5	9.7	12.9	5.5	23.5	10.0	13.6	5.7
May	22.7	6.4	16.6	4.6	26.0	7.4	19.0	5.3	27.6	7.9	20.1	5.7
Jun	22.2	6.7	18.0	5.5	24.6	7.3	20.0	6.0	25.9	7.6	21.0	6.2
Jul	14.0	4.3	10.7	3.4	15.9	4.8	12.2	3.8	17.2	5.2	13.1	4.1
Aug	5.2	1.9	3.0	1.3	6.0	2.2	3.5	1.6	6.6	2.5	3.8	1.7
Sep	7.1	3.1	3.2	1.4	8.0	3.4	3.6	1.5	8.8	3.6	4.0	1.6
Oct	6.4	2.4	4.2	1.6	7.5	2.8	4.9	1.9	8.2	3.0	5.3	2.1
Nov	5.9	2.9	4.2	2.0	7.1	3.6	5.0	2.5	7.9	4.1	5.5	2.9
Dec	2.2	1.8	1.5	1.2	2.6	2.1	1.8	1.4	3.0	2.3	2.1	1.6
Jan-98	1.5	0.9	1.1	0.7	1.9	1.1	1.4	0.8	2.2	1.2	1.6	0.9
Feb	1.1	0.7	0.7	0.5	1.4	0.9	0.9	0.6	1.6	1.0	1.1	0.7
Mar	1.4	1.0	0.5	0.3	1.7	1.2	0.6	0.4	2.0	1.3	0.7	0.4
Apr	1.7	1.1	0.7	0.5	2.1	1.2	0.9	0.6	2.5	1.3	1.1	0.7
Mean Daily PAR (M m^{-2} d^{-1})	8.4		5.8		9.6		6.6		10.3		7.1	
Annual PAR (M m^{-2} yr^{-1})	3055		2122		3500		2427		3770		2609	

Table 16. (Continued)

Site / Month	Mean PAR_w		Mean PAR_p		Mean PAR_w		Mean PAR_p		Mean PAR_w		Mean PAR_p	
	At maximum depth limits				At 0.1 m above bottom				At 0.2 m above bottom			
BOK	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Apr-97	20.7	8.1	10.0	4.2	23.6	9.2	11.3	4.7	24.3	9.3	11.7	4.8
May	20.3	6.2	13.6	4.3	22.7	6.9	15.2	4.8	23.5	7.1	15.7	4.9
Jun	18.2	7.5	13.6	5.6	20.2	8.3	15.1	6.2	20.9	8.5	15.6	6.4
Jul	12.3	5.8	9.3	4.4	13.9	6.4	10.5	4.8	14.6	6.5	11.0	4.9
Aug	4.0	1.9	2.8	1.4	4.9	2.2	3.3	1.7	5.4	2.5	3.7	1.9
Sep	4.6	2.4	3.4	2.0	5.2	2.6	3.9	2.1	5.5	2.7	4.2	2.2
Oct	4.5	1.7	3.0	1.1	4.9	1.8	3.4	1.2	5.2	1.9	3.6	1.2
Nov	3.6	2.5	2.5	1.7	4.2	2.8	2.9	1.9	4.4	3.0	3.1	2
Dec	0.9	0.7	0.5	0.4	1.0	0.7	0.6	0.5	1.1	0.8	0.7	0.5
Jan-98	0.6	0.3	0.4	0.3	0.7	0.4	0.5	0.3	0.8	0.4	0.6	0.3
Feb	0.4	0.2	0.3	0.2	0.5	0.3	0.3	0.2	0.5	0.3	0.4	0.2
Mar	0.6	0.4	0.2	0.1	0.8	0.5	0.2	0.2	0.8	0.6	0.3	0.2
Apr	1.6	1.3	0.5	0.5	2.0	1.5	0.6	0.5	2.2	1.6	0.7	0.6
Mean Daily PAR (M m^{-2} d^{-1})	6.8		4.6		7.6		5.2		8.0		5.4	
Annual PAR (M m^{-2} yr^{-1})	2466		1673		2787		1888		2925		1982	
DEV	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Apr-97	14.6	6.1	11.5	4.8	16.1	6.7	12.7	5.2	17.1	7.0	13.5	5.5
May	17.1	6.6	14.0	5.4	19.3	7.2	15.8	6.0	20.2	7.4	16.6	6.1
Jun	18.9	6.3	16.3	5.4	21.2	6.9	18.2	5.9	22.3	7.1	19.1	6.1
Jul	13.8	3.2	12.6	3.0	15.5	3.6	14.1	3.2	16.3	3.7	14.8	3.4
Aug	4.4	3.9	2.8	2.5	4.7	4.2	3.0	2.7	5.1	4.5	3.3	2.9
Sep	5.0	2.3	3.3	1.5	5.7	2.5	3.7	1.6	6.2	2.7	4.0	1.8
Oct	3.9	2.2	2.6	1.5	4.5	2.5	3.0	1.7	4.9	2.6	3.3	1.8
Nov	3.4	2.0	2.7	1.6	3.8	2.3	3.1	1.7	4.2	2.4	3.4	1.9
Dec	1.8	1.9	1.5	1.6	2.2	2.2	1.8	1.8	2.4	2.4	1.9	2
Jan-98	0.9	0.5	0.7	0.4	1.0	0.6	0.8	0.5	1.2	0.7	0.9	0.5
Feb	0.4	0.6	0.3	0.4	0.5	0.7	0.4	0.5	0.6	0.8	0.5	0.6
Mar	0.5	0.5	0.4	0.4	0.6	0.6	0.5	0.5	0.8	0.7	0.7	0.6
Apr	2.5	1.6	2.1	1.4	3.0	1.9	2.5	1.6	3.4	2.0	2.8	1.7
Mean Daily PAR (M m^{-2} d^{-1})	6.6		5.3		7.4		6.0		7.9		6.4	
Annual PAR (M m^{-2} yr^{-1})	2393		1948		2695		2193		2871		2334	

Moles m^{-2} yr^{-1}, less than that observed at the shaded site in Tampa Bay. The lack of a definitive decline in biomass at BOK indicates that there may be specific seasonal light requirements which were satisfied during the project year or that there were confounding effects of additional stressors (*i.e.*, salinity).

Additional support for the concept of a growing season has been developed for seagrasses in Charlotte Harbor (Tomasko and Hall, 1999). In that work, regardless of water clarity and/or salinity, substantial growth of seagrasses did not occur once temperatures were below 20 °C. Other confounding seasonal signals include epiphytic attenuation which, in other systems (Sarasota Bay, Tampa Bay), has reached maximum values during periods of low growth (wintertime). When considering light requirements for grasses, therefore, it is likely that annual totals of PAR or annual percentages of PAR have critical seasonal distributions - a wintertime minima needed to maintain oxygenated conditions and support little additional growth and a growing season minima to replace lost tissues and build to the seasonal biomass peak. It is critical to keep in mind the underlying plant physiology determining light requirements and recognize that the annual totals determined in this and other projects represent an integrated value. It is conceivable that under some conditions, annual totals could be maintained, but if particular seasonal totals were insufficient, might still permit an overall decline of grasses.

To investigate seasonal light levels, the average daily values of PAR_p at canopy height were examined by month for both Tampa Bay and Charlotte Harbor (Figures 27A and 27B). The two studies exhibited a very different temporal pattern of water clarity and PAR received at depth, some of which can be attributed to the unusually high rainfall received in 1997-1998. In Tampa Bay, maximum water clarity was between March and May. For the Tampa Bay site with shading effects (Site 2), there were no months in which the mean daily PAR exceeded 10 Moles m^{-2} day^{-1}. The remaining sites of Tampa Bay each experienced at least three months in which mean daily PAR_p exceeded 10 Moles m^{-2} day^{-1}.

April (1997) through July in Charlotte Harbor was the time of maximum water clarity, with all sites experiencing three months in which mean daily PAR_p exceeded 10 Moles m^{-2} day^{-1} and PUN and COT receiving more than 20 Moles m^{-2} day^{-1} on average during two months. All sites also experienced eight consecutive months (August through March) in which mean daily PAR_p was generally less than 5 Moles m^{-2} day^{-1}. It is evident in Figure 27B that the BOK site consistently received lower daily PAR_p totals than did the other *T. testudinum* sites, and yet, unlike the BOK site, both PUN and COT exhibited biotic declines.

Examination of a seasonal mean daily PAR_p (Figure 28) further illustrates the differences between the Tampa Bay and Charlotte Harbor stations. For Tampa Bay, differences in PAR_p were maximized between the shaded and stable sites in Tampa Bay for a four month period (April through July). The defined "growing season" also coincided with the period when shading effects were first noted for Tampa Bay. Mean daily PAR_p during the growing season exceeded 10 Moles m^{-2} day^{-1} for stable Tampa Bay sites and was less than 8 Moles m^{-2} day^{-1} for

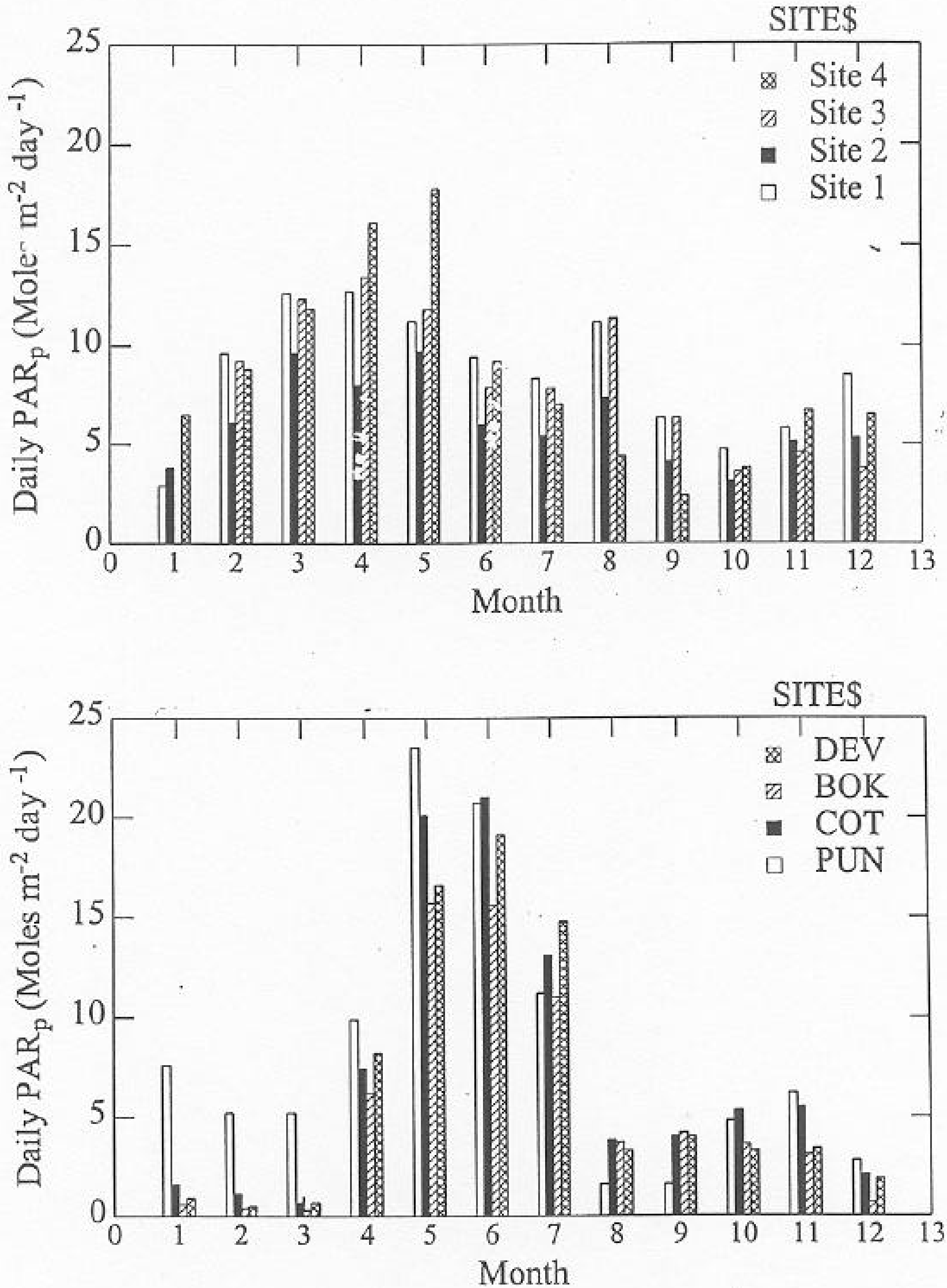

Figure 27. Mean daily PARp (at canopy height) from continuous data in Tampa Bay (A) and Charlotte Harbor (B).

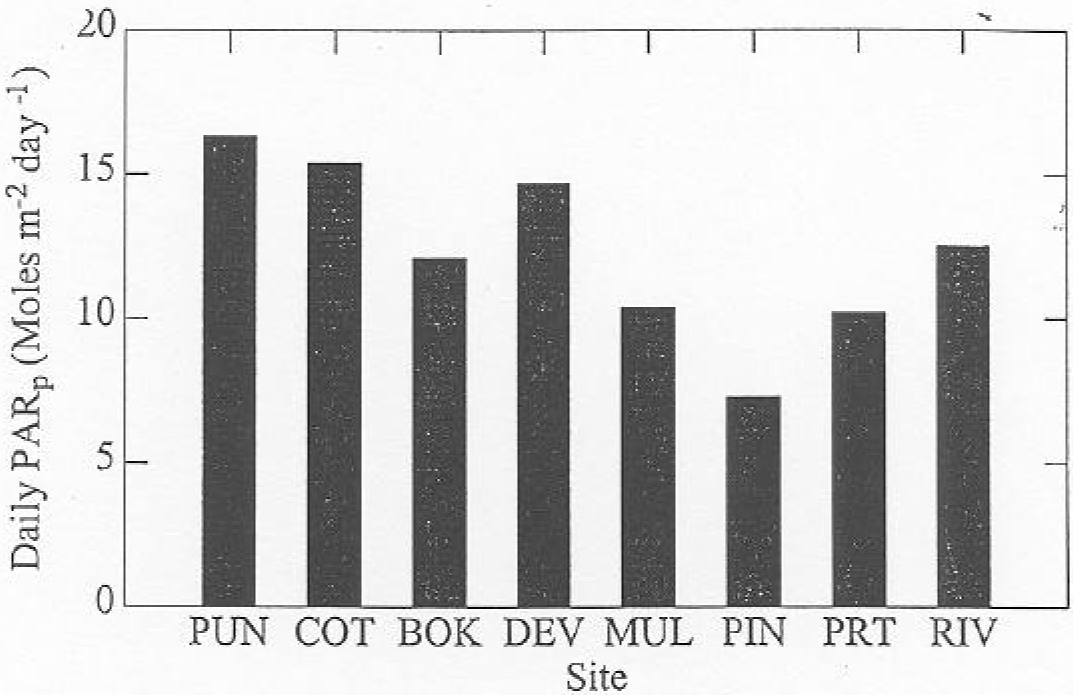

Figure 28. PARp (at canopy height) during the growing season (April through July) from continuous instrumentation in Charlotte Harbor and Tampa Bay, Florida.

the site with shading effects. The PAR_p received by all of the Charlotte Harbor *T. testudinum* sites, however, was at least as great as the mean growing season PAR_p received by stable Tampa Bay sites, despite having clear declines in biomass at both PUN and COT.

Biotic declines over the course of the study at the PUN and COT sites were controlled by a decline in blade area per shoot. Monthly values of blade area per shoot were examined as a function of mean monthly salinity and mean monthly $\%PAR_p$ to examine the results of salinity stress. Due to the correspondence of salinity and water column attenuation, both salinity and $\%PAR_p$ individually accounted for a significant amount of variation in blade area, but in multivariate regression, salinity was not significant once the variation attributable to $\%PAR_p$ was removed. The same was true for the DEV site, in that $\%PAR_p$ was a stronger predictor of blade area for *H. wrightii* than was salinity, although blade area did not decline between the beginning and end of the study.

Despite the relationship of blade area with $\%PAR_p$, the differences between PAR_p observed in Tampa Bay and Charlotte Harbor for both seasonal and annual totals deserve consideration. Sudden low salinity stress has resulted in etiolation of *T. testudinum* in other studies (Dixon and Leverone, 1995). It is possible that the depressed salinities observed in the Harbor reduced the above-ground biomass and that the resulting ambient light levels and/or below-ground reserves were insufficient to restore "lost" biomass. This hypothesis is consistent with the elevated seasonal PAR_p values observed in Charlotte Harbor and may also account for the net above-ground biomass declines at PUN which received comparable annual amounts of PAR_p as the stable Tampa Bay stations. The annual PAR_p received by the stable BOK site, roughly 2,000 Moles m^{-2} yr^{-1}, is also very different from the Tampa Bay values, but it is possible that the continued above-ground biomass at this site was supported by underground reserves.

Water Quality Data

Water quality data collected during this project appear in Appendix A and are summarized in Figures 29 and 30. Turbidity values were low overall and ranged between 0.4 and 16.9 NTU. Two values of chlorophyll a were unusual (143.3 ug/l at PUN and 49.2 ug/l at HOG) with the remainder typically below 20 ug/l and a median value of 6 ug/l. Color values were quite high at times in the upper Harbor, with a maximum value of 200 PCU at HOG. The relationship of scalar attenuation coefficient (K_0) to secchi depth (where secchi was less than overall water depth) was strong enough (Figure 31) to provide an alternative approach to estimating water column attenuation from historical data sets. Spatial distributions of selected parameters for the six month period when all 12 stations were sampled appears in Figures 32 through 34 and illustrate the persistence of freshwater, high color, and higher chlorophyll values along the western side of upper Charlotte Harbor.

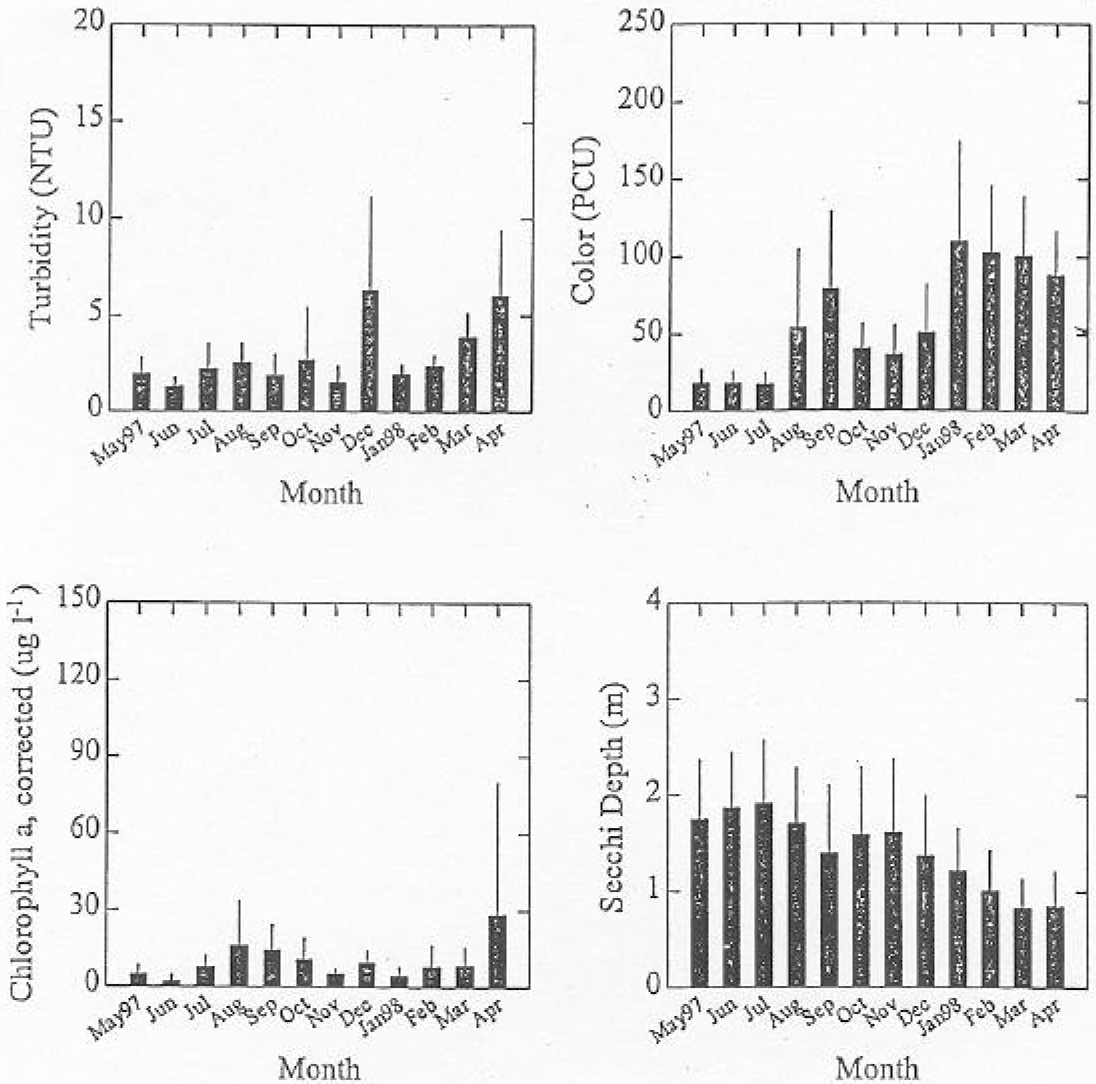

Figure 29. Mean and standard deviations of water quality parameters over the project year for northern Charlotte Harbor stations.

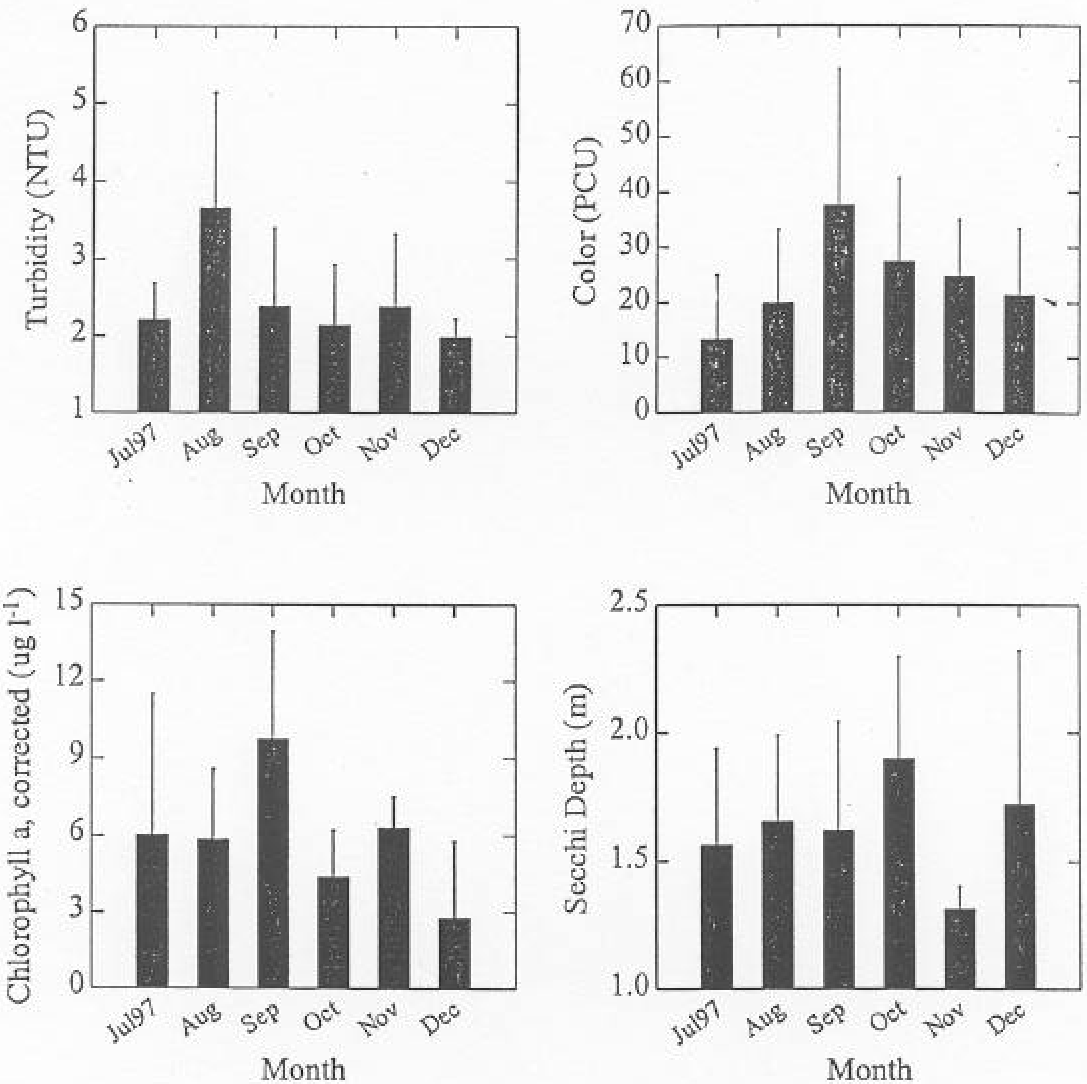

Figure 30. Mean and standard deviations of water quality data for the southern Charlotte Harbor stations.

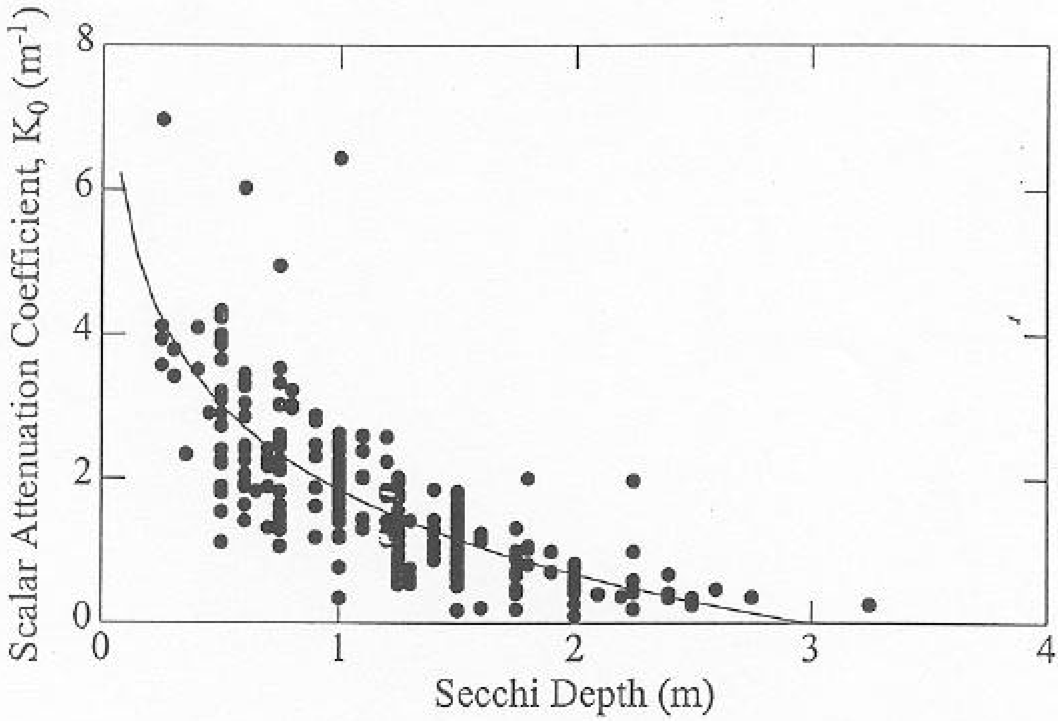

Figure 31. Scalar attenuation coefficient (K_0) ad a function of secchi depths when secchi depths were less than or equal to overall water column depth.

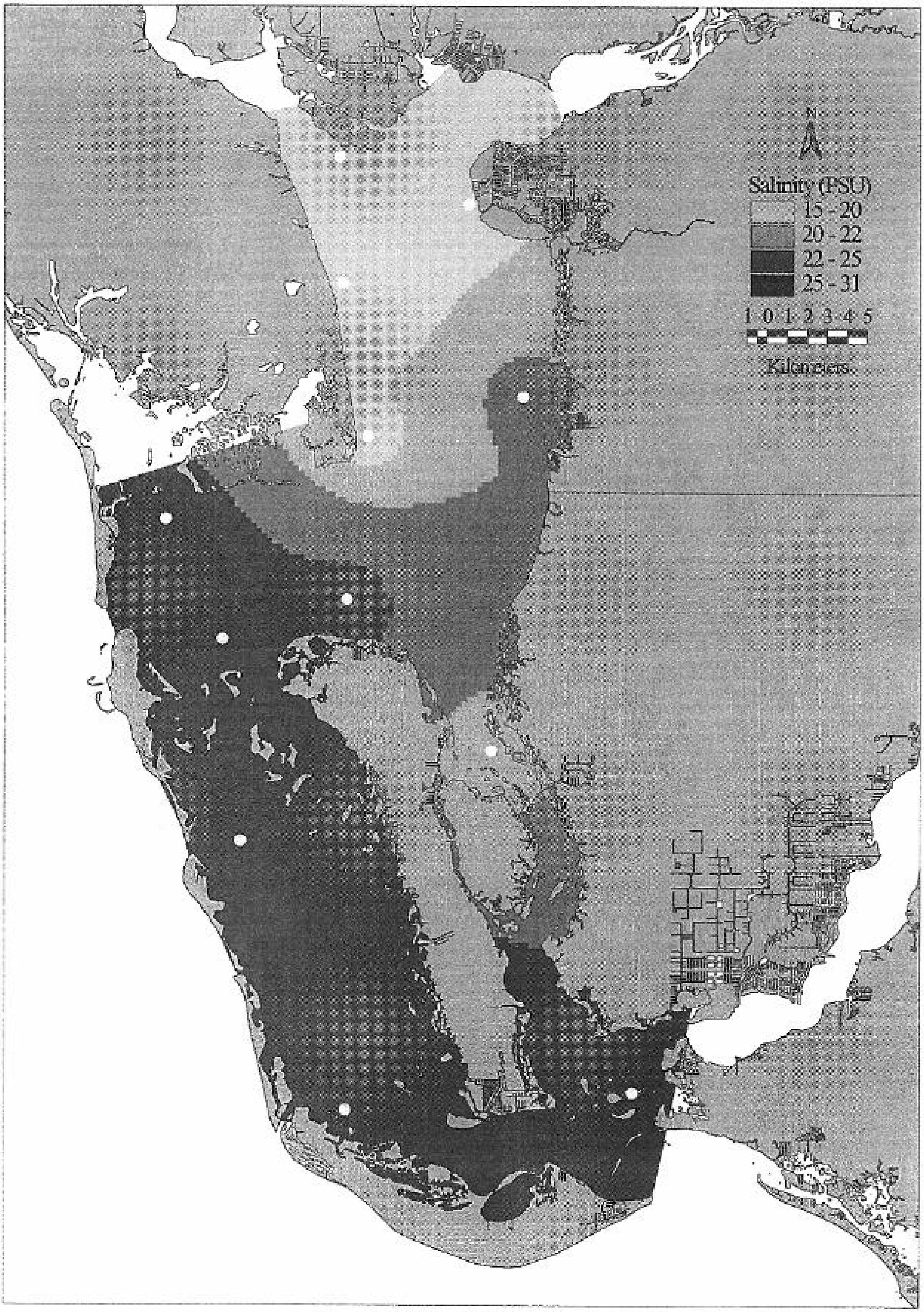

Figure 32. Mean spatial distribution of salinity between June and November. Based on weekly data for the northern stations and monthly data for the southern stations.

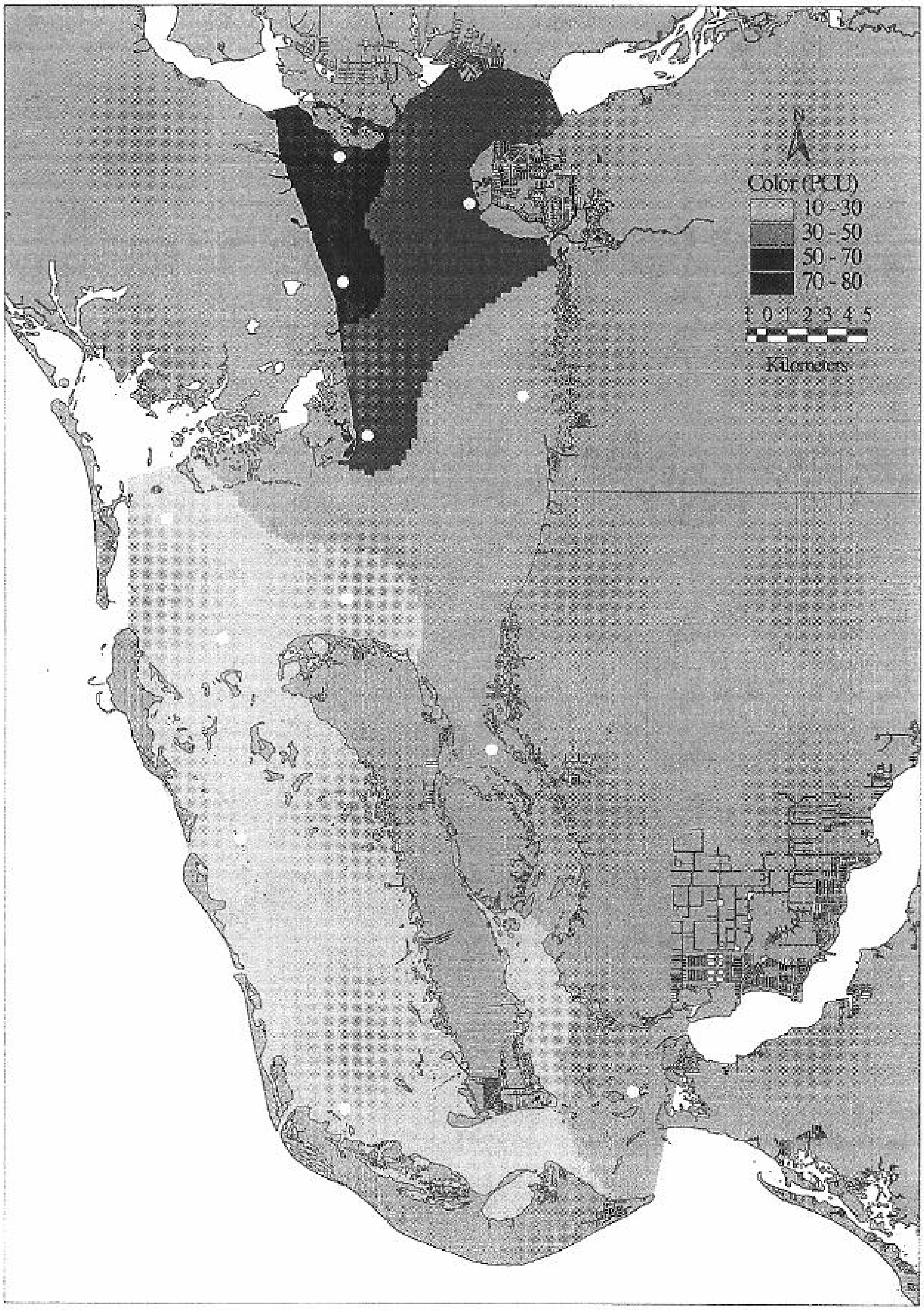

Figure 33. Mean spatial distribution of color between June and November. Based on weekly data for the northern stations and monthly data for the southern stations.

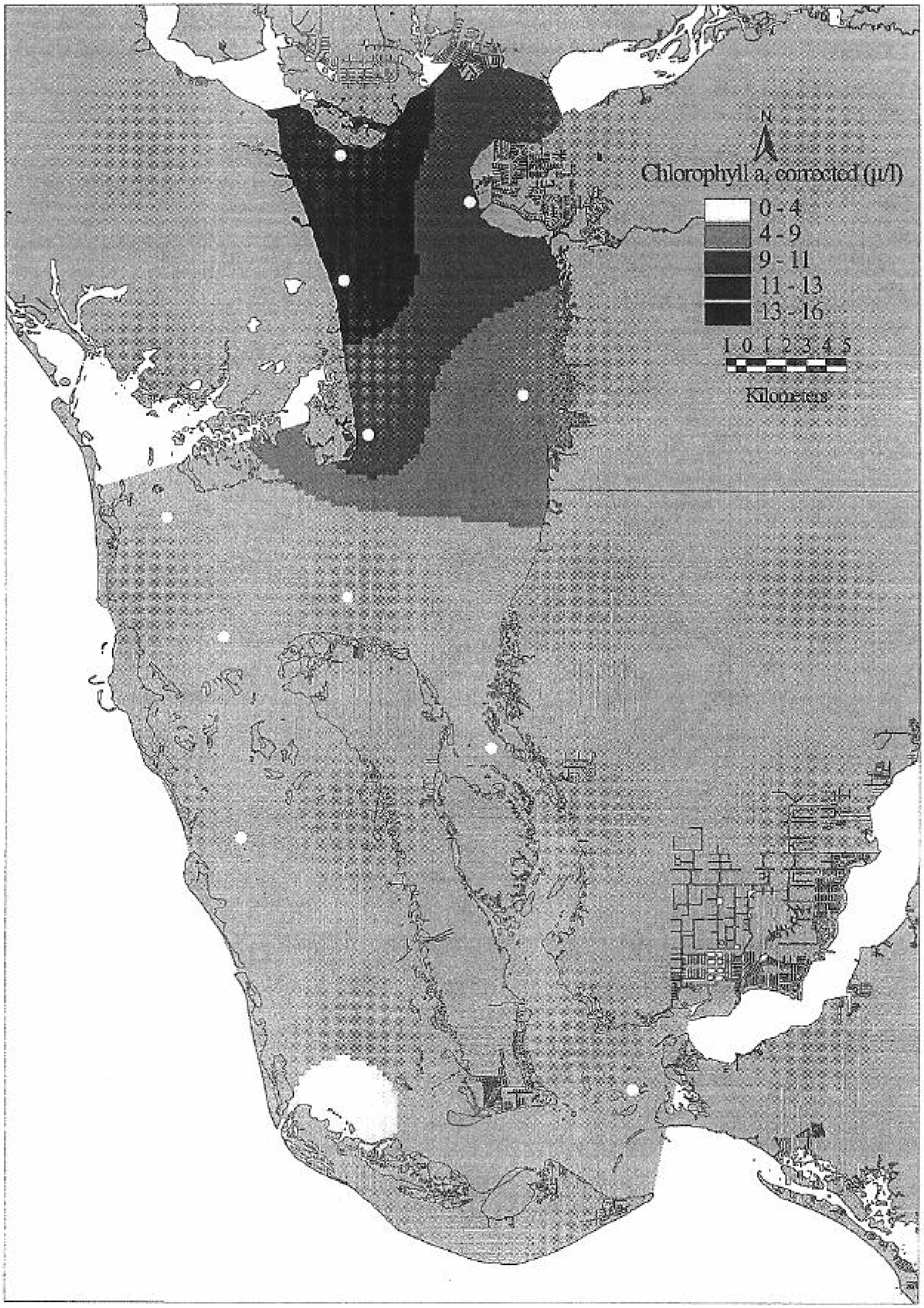

Figure 34. Mean spatial distribution of chlorophyll between June and November. Based on weekly data for the northern stations and monthly data for the southern stations.

Optical Model

The spectrally sensitive attenuation coefficients ($K_{d(PAR)}$) computed by the optical model from water depths, color, chlorophyll, and turbidity agreed well with the individual Kd values measured *in situ* (Figure 35) with an overall slope near unity. Mean percentage agreement between modeled and observed Kd was 110%, with the 95% confidence interval ranging from 104% to 115%. Paired t-tests indicate an overall positive bias of 0.08 m^{-1} in the modeled values, direction and degree of bias comparable to previous application of similar techniques (Gallegos, 1993).

The largest bias was typically restricted to data sets in which color was greater than 100 PCU (15 of 120 samples). The residuals from color-dependent relationships incorporated into the model do not explain the bias of these samples. A factor which may have contributed to this result is that samples were collected from just below the water surface, while field measurements of attenuation coefficients extended throughout the water column. It is possible that salinity stratification occurred under high flow (and high color) conditions, with the result that color samples collected were representative only of the upper water column. This is supported by several of the *in situ* profiles in which depth integrated attenuation deviated from modeled attenuation. As a result of the correlation of color with model bias, stations with some of the highest color values (HOG, RAD, and CAP) reported the some of the largest differences between modeled and measured attenuation. There were, however, no significant distributions of bias by station, indicating that site-specific relationships of the components of light attenuation (Pierce, *et al.*, 1986; Gallegos, *et al.*, 1990; Gallegos, 1994) have been adequately represented by the model.

Observed bias between modeled and observed Kd values was also correlated with sun angle. Some portion of this dependence can be attributed to varying spectral distribution with solar elevation, a factor which was not incorporated in the model. Spectral variations with sun angle can include increasing atmospheric effects with decreasing solar elevation, such as increased pathlength, increasing contributions of short wavelength skylight to total irradiance with decreasing solar elevation, and the decreased proportion of short wavelength light in direct solar beams with decreasing elevations (Kirk, 1984). Additionally, bias may be produced by the literature constants employed in the cosine dependent $G(\hat{\imath}_0)$ variable. Constants available were for the depths to which 10% radiation penetrates rather than 20% which would be more appropriate for seagrasses. Biases are uncorrelated with chlorophyll or turbidity, indicating that the model approach has successfully incorporated these values. Remaining sources of non-agreement between modeled and measured Kd values could also include the Li-COR sensor used for field measurements as the sensor departs from a quantum response at the extremes of the 400-700 nm spectrum.

The modeled attenuation was repeated with the analytical parameters of chlorophyll, color, and turbidity successively set to zero to compute the individual contributions to total attenuation. The effects of depth and water column attenuation are held constant and are not included in this

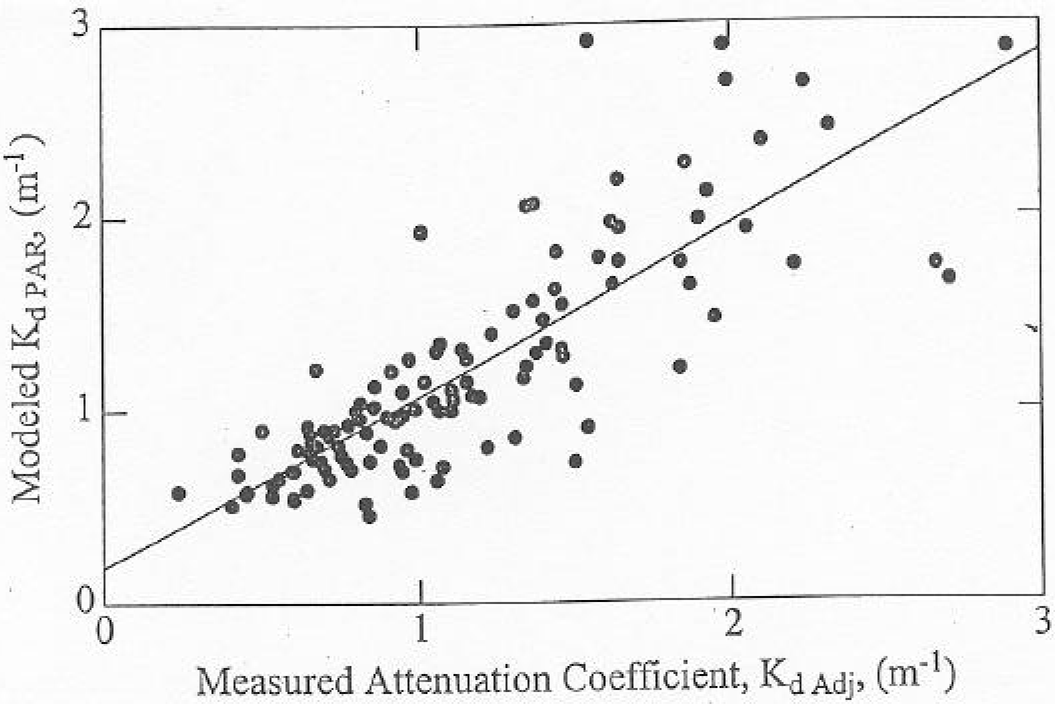

Figure 35. Agreement between modeled diffuse attenuation coefficient (K_{dPAR}) and adjusted attenuation coefficients ($K_{d\ Adj}$) measured in the field.

apportionment. Annual averages by station of modeled contributions to attenuation appear in Table 17 and Figures 36 and 37 with the diameter of the station symbol proportional to the water column attenuation coefficient. Overall, chlorophyll, color, and turbidity accounted for 4%, 66%, and 31% of attenuation, respectively. The PUN site recorded the maximum annual average chlorophyll contribution of 6%, followed by the COT site with 5%. The individual maximum chlorophyll contribution of 18% was also at PUN, during a phytoplankton bloom with a chlorophyll concentration of 143 ìg l^{-1}. Color generally dominated water column attenuation, with attenuation due to chlorophyll becoming substantial only under phytoplankton bloom conditions. Stations in the lower Harbor (PAT and DEV) showed increased attenuation due to turbidity, compared to upper Harbor sites. For the southern sites, a much larger portion of attenuation was produced by turbidity during the six months sampled, up to 55% for the PAS site. Due in part to lesser influence of freshwater and the time period sampled, attenuations were also lower overall for the southern sites. Even in the southern sites, however, the chlorophyll component of attenuation was small, between 3% and 6%. The observed spatial distribution of attenuation and it's dependence on color is consistent with the general findings of McPherson and Miller (1987; 1994) for Charlotte Harbor in which attenuation coefficients were partitioned via other methods. Contributions of chlorophyll to attenuation, however, were much greater in McPherson and Miller (1994) at over 16%, than in either their earlier work or in this project.

Table 17. Percentage contribution to water column attenuation. Data collected during this project (1997-1998) and by the SWIM water quality monitoring project (1993-1998).

Site	**Chlorophyll**	**Color**	**Turbidity**	**Site**	**Chlorophyll**	**Color**	**Turbidity**
HOG	3	78	19	CH001	8	85	14
PUN	6	72	22	CH002	3	76	20
RAD	3	77	21	CH02B	6	67	27
COT	5	71	24	CH029	1	84	15
CAP	3	74	24	CH004	5	71	24
BOK	3	72	25	CH005	5	68	27
PAT	4	63	33	CH05B	4	67	28
DEV	3	59	38	CH006	5	71	24
MAT	5	73	23	CH09B	3	73	24
PAS	6	40	55	CH007	4	71	25
SAN	4	48	48	CH009	5	70	24

BIG	3	60	37	CH011	4	56	40
				CH013	4	35	61
				CH014	7	40	54

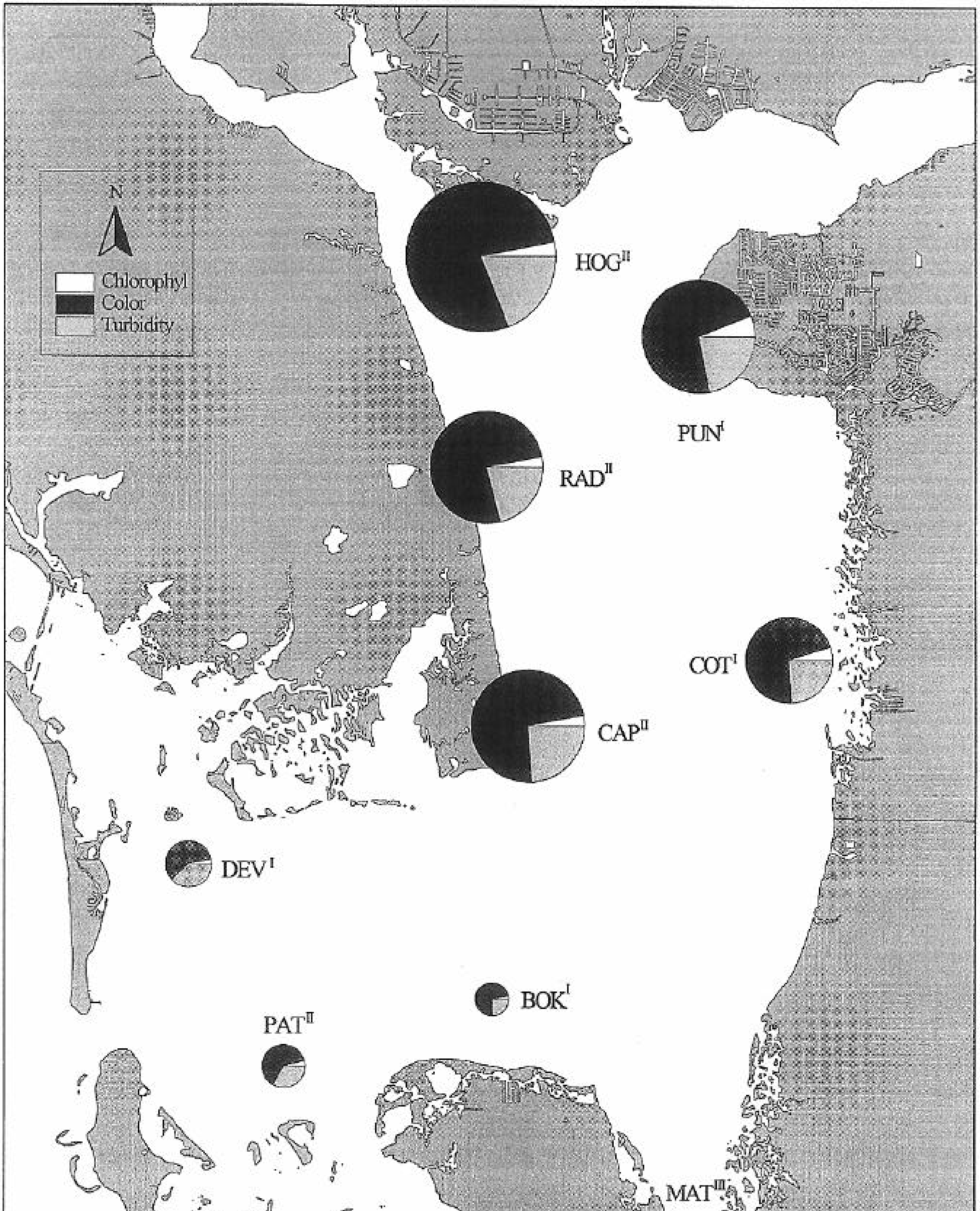

Figure 36. Annual proportions of water column attenuation contributed by chlorophyll, color, and turbidity for the northern Charlotte Harbor stations. Diameter is proportional to the annual adjusted attenuation coefficients ($K_{d\ Adj}$).

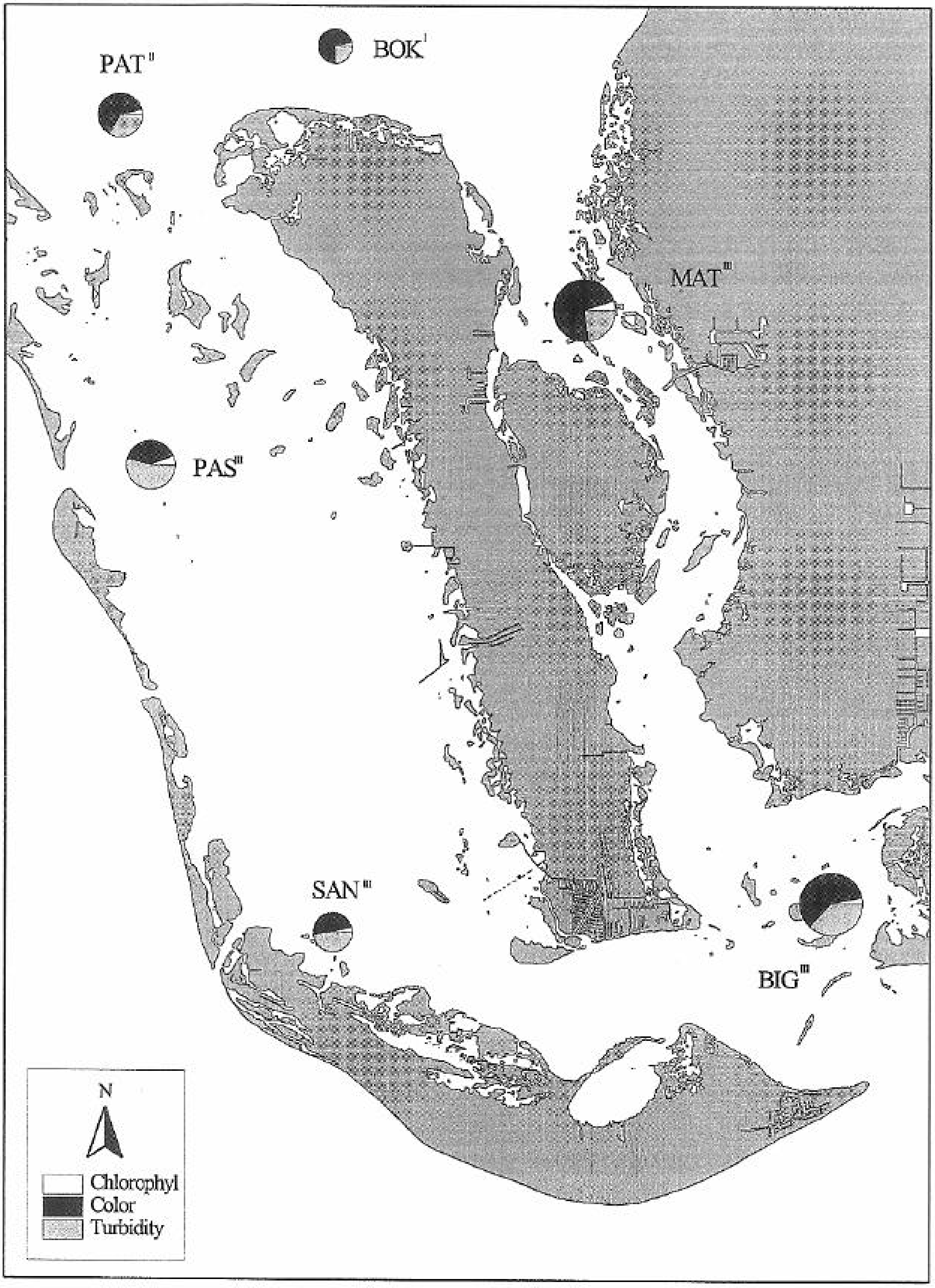

Figure 37. Annual proportions of water column attenuation contributed by chlorophyll, color, and turbidity for the southern Charlotte Harbor stations. Diameter is proportional to the annual adjusted attenuation coefficients ($K_{d\ Adj}$).

To provide a rough estimate of attenuation under increased nutrient loading levels, chlorophyll concentrations in the model were arbitrarily doubled for all monthly data. As a result, the percentage of attenuation attributable to chlorophyll doubles, with a concomitant reduction in the proportion of attenuation due to color. This is somewhat of an underestimate of total water column attenuation under increased chlorophyll regimes, as there would undoubtedly also be an increase in turbidity due to increased phytoplankton. The impact of increased chlorophyll alone, however, should be fairly represented. Under the arbitrary chlorophyll projections, the contribution to water column attenuation now is as great as 12% annually at PUN and 11% at the COT site. Modeled Kd at the PUN site decreases from 1.78 to 1.66 m^{-1}, or $\%PAR_p$ is reduced form 21.4% to 19.1%. What is unknown, however, is the net impact of the increased nutrient loads on epiphytic loading of seagrasses.

Using the SWIM water quality data from other stations in the Harbor as input to the model, long term patterns in attenuation were examined to determine if the unusual rainfall of the project year altered the partitioning of attenuation. Recognizing that not all stations were sampled in all months and years, monthly averages were prepared from available data on chlorophyll, turbidity, and color concentrations. Attenuation was partitioned by month, and the distribution averaged across the twelve monthly periods (Figure 38). Surprisingly, while water column attenuation was much greater during the project year, the partitioning of attenuation between chlorophyll and the remaining attenuators was very similar. There are portions of the upper Myakka and Peace Rivers (CH-001 and CH-004) where the largest relative influence of chlorophyll appears. For co-located stations in the upper Harbor, color accounted for somewhat more attenuation during the project year, but was still the dominant attenuator in the long-term SWIM data set. This result would indicate that, even during year with lower rainfall, color should persist as the dominant attenuator within Charlotte Harbor

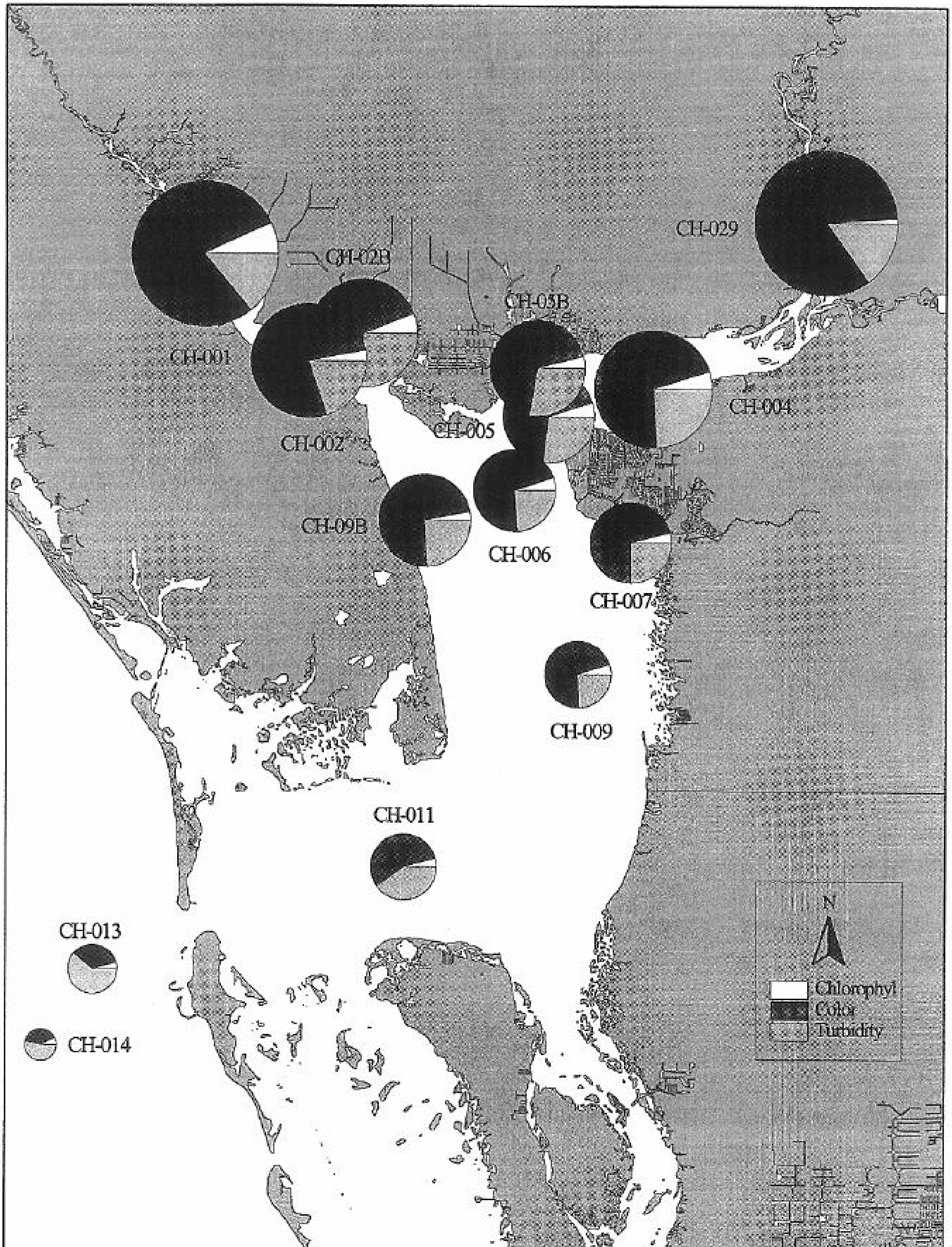

Figure 38. Long term (1993-1998) proportions of water column attenuation contributed by chlorophyll, color, and turbidity for the SWFWMD-SWIM Charlotte Harbor monitoring stations. Diameter is proportional to approximate mean adjusted attenuation coefficients ($K_{d\ Adj}$).

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Appendix A