

**Submerged Aquatic Vegetation and Physico-Chemical Monitoring in the Florida Bay
Mangrove Zone for CERP Assessments and Targets Refinement**

Final Project Report

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Executive Summary

Ecosystem restoration in the mangrove zone of Everglades National Park aims to reduce salinities to historical conditions and to consequently restore submerged aquatic vegetation (SAV) to previously described higher abundances (Tabb et al., 1962). The full range of pre-restoration water quality conditions and SAV abundance patterns have yet to be determined, and the relationships between SAV, water quality and nutrient pools are not fully understood. Restoration goals will be assessed in the future by comparison of salinity and SAV patterns with established benchmarks. Establishing these benchmarks will require quantifying the spatial and temporal patterns of SAV abundance and salinity and an increased understanding of the processes governing the relationships between water quality and SAV abundances. The baseline data collected by this project will be the benchmark against which the success of restoration efforts will be judged. These data are also used to produce statistical modeling tools that can be used to predict change from proposed management actions.

SAV abundance (percent cover), sediment depth, and water quality parameters (water temperature, salinity, light availability, water level, water column total nitrogen and total phosphorus concentration, and phytoplankton chlorophyll-a concentration) were measured in the mangrove sub-estuaries and upstream “lakes” of Florida Bay and the southern Everglades from May 2006 through April 2009. The spatial and temporal variability of SAV and water quality parameters have been described and will assist resource managers in efforts to restore SAV abundance to historically higher levels.

Spatially, annual mean salinity, light availability, and sediment depth to bedrock structured the SAV communities in the mangrove sub-estuaries of Florida Bay. Three distinct SAV communities (i.e., *Chara hornemannii alga* group, *Halodule wrightii* seagrass group, and a Low SAV coverage group) were identified along the Everglades - Florida Bay ecotone. These communities were differentiated along salinity and nutrient availability gradients. *Chara* communities were located in the lower salinity (mean annual salinity < 25 psu) upstream “lakes”, while *Halodule* communities were located in the more marine coastal embayments. SAV cover, particularly in the *Chara* communities, varied according to water quality differences observed between two adjacent sub-estuaries (i.e., West Lake to Garfield Bight sub-estuary and the Seven

Palm Lake to Terrapin Bay sub-estuary). These sub-estuaries were characterized by alternate states of water quality and SAV abundance. The West Lake sub-estuary was turbid, dominated by persistent algal blooms and high nutrient concentrations, and suffered from low SAV abundance. In contrast, the Seven Palm Lake sub-estuary was characterized by clear water, higher SAV cover that persisted throughout the year, and low nutrient and phytoplankton concentrations. The SAV community groups were related to water quality using a discriminant function model that predicted the type of plant community at a given site from salinity, light availability and sediment depth to bedrock. Mean salinity alone was able to correctly classify 78% of the sites and reliably separated the *Chara* group from the *Halodule* group. The addition of light availability and sediment depth to bedrock increased model accuracy to 90% and further distinguished the *Chara* group from the *Halodule* group. Light availability was uniquely valuable in separating the *Chara* group from the Low SAV coverage group. Regression analyses identified significant relationships between phosphorus concentration, phytoplankton abundance and light availability, and suggest that a decline in water transparency, associated with increasing salinity, may have also contributed to the historical decline of *Chara* communities in the region.

The clear relationships between P availability, phytoplankton abundance and light availability indicate that historic SAV communities will not be restored in the freshwater end of these estuarine systems unless water column TP concentrations are reduced, especially in the West Lake system. Though increased freshwater flow will decrease salinity and may also decrease P loading, the re-establishment of flourishing *Chara* communities in the estuaries of the southern Everglades may be inhibited by the long-term retention of P in P-limited carbonate ecosystems (Herbert and Fourqurean 2008). Because 75% of the sites characterized by *Chara* dominance exhibited median light at bottom exceeding 5% of surface light, and all sites characterized with Low SAV coverage were below this level of light availability, 5% light at bottom is a reasonable estimate for the maintenance of *Chara* communities. Using a light availability target of 5% of surface light at bottom and the regression equations relating light availability to chl *a*, and chl *a* to TP, we estimate that annual mean water column TP concentrations should be maintained at or below $2.2 \pm 1.1 \mu\text{M}$ (mean $\pm$ 95% confidence interval) to limit phytoplankton abundance and allow for the shift back to the *Chara*-dominated regime in the upstream "lakes". However, if the *Chara*-dominated and the phytoplankton-dominated regimes are distinct stable states characterized by hysteresis (Scheffer et al. 1993), a much lower

TP concentration may be required to restore a presently turbid, phytoplankton-dominated mangrove lake to a clear-water, *Chara*-dominated one.

Repeatable seasonal patterns were not evident in most SAV communities with the exception of light-limited brackish alga *Chara hornemannii* Wallman communities that experienced seasonal changes in light availability in a turbid environment. In contrast, *Chara* cover in clear water SAV-dominated environments was temporally negatively correlated with salinity and water depth. These observations suggest that water clarity may determine the importance of the salinity driver in these *Chara* communities. Cover of the more marine seagrass *Halodule wrightii* exhibited some temporal variation that was positively correlated with water temperature. This study demonstrates the differential importance of water quality and environmental drivers in estuaries distinguished by alternate regimes of phytoplankton and SAV dominance, and explains how differences in local estuarine geography may filter the response of SAV communities to environmental stressors.

Restoring higher levels of freshwater flow to the mangrove estuaries of Florida Bay may promote the spatial and temporal expansion of SAV communities if the quality of the freshwater, as indicated by low nutrient and phytoplankton content, is sufficient. Increased freshwater flow will decrease salinities and possibly decrease water column nutrient concentrations by displacing relatively phosphorus rich marine water. Decreased nutrients should increase light availability to benthic macrophytes by alleviating persistent algal blooms that are currently affecting much of the mangrove lake estuaries.

Chapters 2 and 3 of this final report have been published or have been submitted for publication. The references for these publications are:

Frankovich, T. A., Morrison, D., and J. W. Fourqurean. 2010. Benthic macrophyte distribution and abundance in estuarine mangrove lakes and estuaries: relationships to environmental variables. *Estuaries and Coasts*. Published online 2010 DOI 10.1007/s12237-010-9279-0.

Frankovich, T. A., J. G. Barr, D. Morrison, and J. W. Fourqurean. In review. Differential importance of water quality parameters and temporal patterns of submerged aquatic vegetation (SAV) cover in adjacent sub-estuaries distinguished by alternate regimes of phytoplankton and SAV dominance. Submitted to *Hydrobiologia*.

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Chapter One - Introduction

The mangrove estuaries and brackish "lakes" located along the ecotone between freshwater Florida Everglades and saltwater Florida Bay, hereafter referred to as the "mangrove lakes" region of the southern Everglades, have changed during the last century. Extensive SAV beds, supporting large populations of wading birds and wintering waterfowl, once characterized these areas (Tabb et al. 1962; Craighead 1971; Ogden 1994; Simmons and Ogden 1998). Wintering waterfowl were once plentiful enough in these mangrove lakes to support a commercial hunting camp (Scottie's Hunting Camp) at West Lake (Simmons and Ogden, 1998). Present SAV, waterfowl and wading bird abundances, are all greatly reduced from historical (1931 - 1946) levels (Ogden 1994). These reductions are coincident with a 20-30 psu increase in salinity in this region (McIvor et al. 1994) caused by diminished freshwater inflows due to water management practices (Light and Dineen 1994). It is hypothesized that prolonged periods of elevated salinity in the mangrove lakes region, caused by diminished freshwater inflow volume and duration due to water management practices, have reduced the seasonal duration and spatial extent of SAV (USACE, 1999). The decline in waterfowl abundance in the mangrove zone lakes is thought to be at least partially due to this reduction in SAV (USACE, 1999). During high rainfall years, and thus increased freshwater inputs, SAV and waterfowl abundances increased in the mangrove lakes (Morrison and Bean 1997; Montague et al 1998; USACE, 1999). Because of the coincidence of increasing salinities with the decline of the dominant *Chara hornemannii* Wallman alga cover in the mangrove lakes and the lack of other historical water quality data, the temporal and spatial loss of *Chara* cover was attributed mostly to the assumed inability of the brackish *Chara* populations to tolerate elevated salinities (Morrison & Bean, 1997).

With a management goal of restoring historic SAV abundances, increased deliveries of freshwater to these mangrove lakes are proposed to maintain lower salinities as part of the Comprehensive Everglades Restoration Plan (CERP). Increased delivery of freshwater will likely change water quality (i.e., salinities, nutrient concentrations and the underwater light environments). The ability to predict how SAV communities may change as freshwater flows are restored is built upon understanding the present relationships between water quality and SAV. Successful restoration will be assessed by comparison of future SAV patterns with established

benchmarks. Establishing these benchmarks will require quantifying the spatial and temporal patterns of SAV abundance and an increased understanding of the processes governing the relationships between water quality and SAV abundances; therefore, the focus of this investigation was to describe SAV spatial and temporal distribution and abundance and its relationships with temperature, salinity climate, sediment depths to bedrock, nutrient availability and underwater light availability. This study was conducted from May 2006 through April 2009. This study also compares and contrasts the local geographies between the two adjacent sub-estuaries in the mangrove lakes region and evaluates how these inherent system attributes may have structured the ecosystem responses to reduced freshwater deliveries in both systems. The results of this study contribute towards predicting how the SAV communities will respond to proposed restoration of freshwater flow.

Study area

The geographic foci of this study are the estuarine mangrove lakes and coastal embayments located along the north shore of Florida Bay (Fig. 1.1). The 41 study sites are located along two freshwater flowpaths that drain portions of the southern Everglades. The West Lake drainage system, also referred to as the West zone, runs from West Lake through Long Lake (formerly East Lake) to "The Lungs" and finally out into central Florida Bay at Garfield Bight. Long, tenuous, mangrove creeks (Mangrove Creek and Alligator Creek), with small, shallow (< 50 cm) ponds within them, effectively separate the lakes and embayments and limit water exchange. In contrast, well-connected lakes to the adjacent east and running from Seven Palm Lake to Middle Lake to Monroe Lake and out into Florida Bay via Terrapin Bay characterize the Seven Palm drainage system, also referred to as the East zone. The watershed that drains into these flowpaths lies between the two main conduits for Everglades drainage - Shark Slough to the northwest and Taylor Slough to the northeast. Surface water flows either into or out of these mangrove-lined lakes depending on wind direction, Everglades water levels and Florida Bay sea level. Deeper areas within the most upstream lakes (West Lake and Seven Palm Lake) had exposed bedrock outcroppings with pockets of mud and sand-sized sediments while shallow sites and those in the other water bodies had mud sediments.

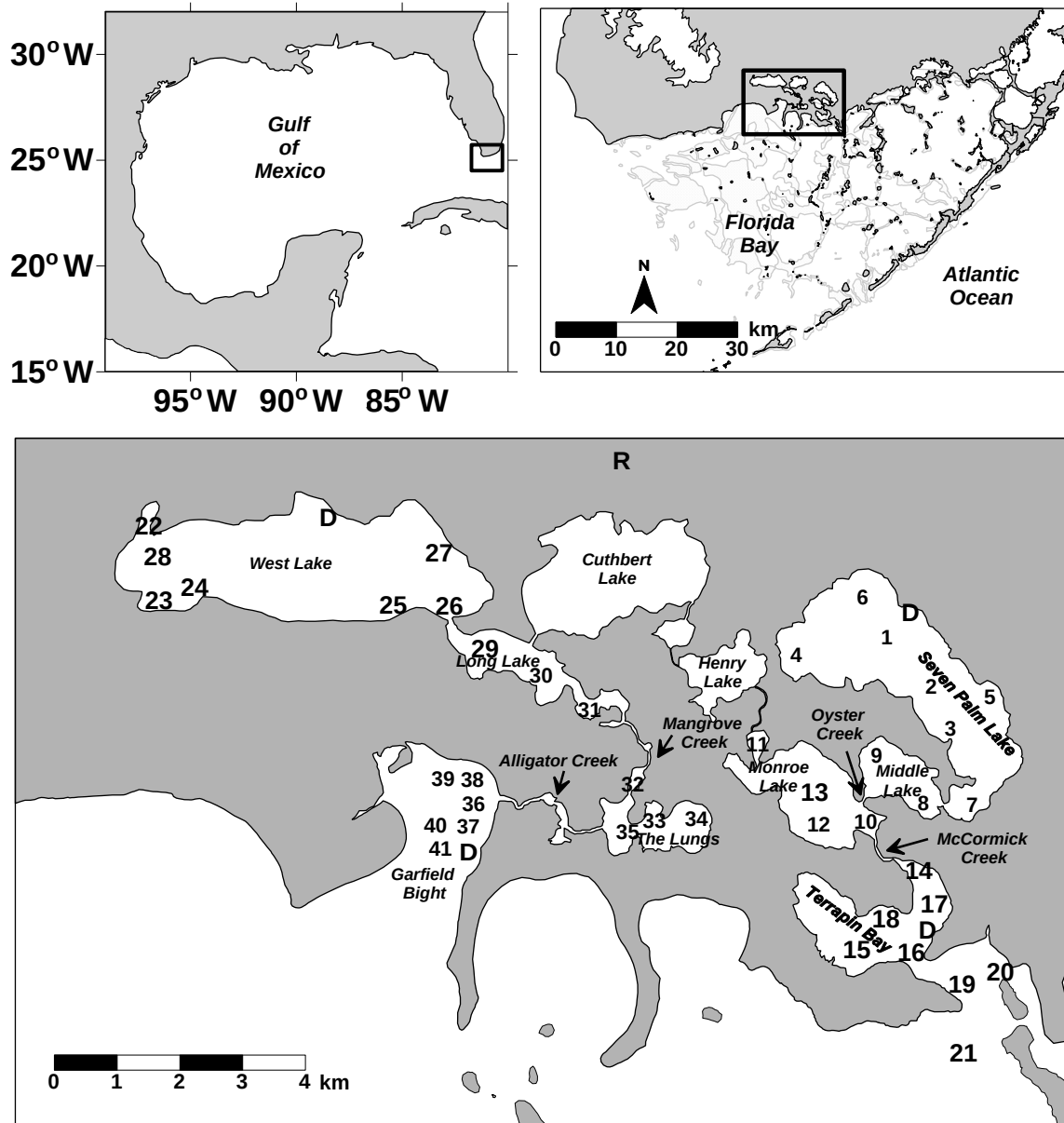


Figure 1. Location map of study sites. “S” designates Joe Bay solar insolation site. “D” designates datasonde locations. “R” designates North Cuthbert Lake (NCL) rainfall estimation location.

Chapter Two - Benthic macrophyte distribution and abundance in estuarine mangrove lakes and estuaries: relationships to environmental variables

Introduction

Through the formation of submerged aquatic vegetation (SAV) beds, benthic macrophytes provide the necessary structural habitats and nursery areas for aquatic fauna (see Heck et al. 2003 for review), stabilize sediments (Scoffin 1970; Gacia and Duarte 2001), maintain low water column nutrient concentrations (Kufel and Kufel 2002; Knight et al. 2003) and increase water clarity (Blindow et al. 2002). Additionally, the high productivity of SAV beds supports complex aquatic food webs (Fry and Parker 1979; Moncrieff et al. 1992), and in shallow areas, also provides critical seasonal energy sources for migratory waterfowl (Noordhuis et al. 2002; Michot et al. 2008). Many aquatic and estuarine ecosystems, once characterized by SAV abundance and a clear water column, have experienced regime shifts or changes in stable state to ecosystems characterized by phytoplankton dominance and increased turbidity (Orth and Moore 1983; Scheffer et al. 1993). Regime shifts have been attributed to species invasions (MacIsaac et al. 1992), salinity changes (Petersen et al. 2008) and changes in nutrient availability (Scheffer and van Nes 2007), though in many cases, the mechanisms are still unknown. For the conservation of the valuable ecosystem services provided by benthic macrophytes, an increased understanding of the environmental constraints on SAV abundance and species distributions is still needed. Successful restoration of these ecosystems will also require an understanding of the underlying mechanisms of ecosystem regime changes.

A change in light availability is one of the key features of regime shifts in shallow estuaries and lakes because adequate light availability is critical for the establishment and maintenance of SAV communities. Minimum light requirements range from less than 1% of in-water surface irradiance for most macroalgae to greater than 10% of in-water surface irradiance for seagrasses (Zimmerman 2006). Light penetration through water columns decrease with depth. In shallow environments, light attenuation by re-suspended sediments, phytoplankton, and colored dissolved substances may be more important to SAV distribution than water depth

(Hemminga and Duarte 2000). Phytoplankton compete with benthic macrophytes for light. Elevated water column nutrients may promote phytoplankton abundance, thereby decreasing light reaching the benthos and therefore decreasing SAV coverage, and once SAV coverage declines, nutrients and sediments in the water column are no longer removed by the benthos (Duarte 1995).

Within estuaries, the relationships between benthic macrophyte species distributions and light availability and nutrients are complex and confounded by interacting relationships with mean salinity and salinity variability. Upstream freshwater SAV communities grade into downstream marine communities as salinity increases. The distributions of individual species along an estuarine gradient often reflect salinity tolerances (McMillan and Moseley 1967). In estuarine areas where freshwater flows are highly seasonal or erratic, benthic macrophyte distribution may be more reflective of salinity variability (Montague and Ley 1993). SAV species composition in estuarine areas of variable salinities may be determined by species' abilities to tolerate a wide range of salinities. Variable conditions may favor species with high fecundity, dormant seeds or spores that can withstand sub-optimal salinity conditions, and large dispersal distances. SAV species composition is also dependent upon substrate type with most seagrasses requiring sand or mud sediments as opposed to many macroalgal species that require hard substrates for attachment.

Spatially and temporally variable salinities, nutrient concentrations, and underwater light environments are characteristic of estuaries, especially in tropical and subtropical estuaries that have pronounced climate seasonality (Herrera-Silveira 1994; Boyer 2006). Climate change and sea-level rise are expected to influence salinity, water depth and nutrient availability in these transition zones between the marine and freshwater environments (Wanless et al. 1994). In addition, humans alter the delivery of freshwater, sediments and nutrients to estuaries.

As a case study, the extensive engineering of freshwater flows in the upstream Everglades ecosystem starting around the beginning of the 20th century, but accelerating in the 1950s and 1960s, have also affected the amount and timing of the delivery of freshwater and nutrients to these transition zones (Light and Dineen, 1994). The mangrove estuaries and brackish "lakes" located along the ecotone between freshwater Florida Everglades and saltwater Florida Bay have changed during the last century. Extensive SAV beds, supporting large

populations of wading birds and wintering waterfowl, once characterized these areas (Tabb et al. 1962; Craighead 1971; Ogden 1994; Simmons and Ogden 1998). Present SAV, waterfowl and wading bird abundances, are all greatly reduced from historical (1931 - 1946) levels (Ogden 1994). These reductions are coincident with increasing salinities in this region caused by diminished freshwater inflows due to water management practices (Light and Dineen 1994). With a management goal of restoring historic SAV abundances, increased deliveries of freshwater to these mangrove estuaries are proposed to maintain lower salinities as part of the Comprehensive Everglades Restoration Plan (CERP). Increased delivery of freshwater will likely change water quality (i.e., salinities, nutrient concentrations and the underwater light environments). The ability to predict how SAV communities may change as freshwater flows are restored is built upon understanding the present relationships between water quality and SAV. The focus of this investigation was to describe SAV distribution and abundance and its relationships with salinity climate, sediment depths to bedrock, nutrient availability and underwater light availability. We were particularly interested in determining potential triggers for regime shift from clear-water, SAV-dominated, to turbid, phytoplankton-dominated states. We also investigated the relationship between underwater light availability, water column nutrient concentration, and phytoplankton abundance. Our results contribute towards predicting how the SAV communities will respond to proposed restoration of freshwater flow.

Study Location

The geographic foci of this investigation are the estuarine mangrove lakes and coastal embayments located along the north shore of Florida Bay (Fig. 1.1). The 41 study sites are located along two freshwater flowpaths that drain portions of the southern Everglades. The West Lake drainage system runs from West Lake through Long Lake (formerly East Lake) to "The Lungs" and finally out into central Florida Bay at Garfield Bight. Long, tenuous, mangrove creeks (Mangrove Creek and Alligator Creek), with small, shallow (< 50 cm) ponds within them, effectively separate the lakes and embayments and limit water exchange. In contrast, well-connected lakes running from Seven Palm Lake to Middle Lake to Monroe Lake and out into Florida Bay via Terrapin Bay characterize the Seven Palm drainage system, located to the adjacent east. The watershed that drains into these flowpaths lies between the two main conduits for Everglades drainage - Shark Slough to the northwest and Taylor Slough to the northeast.

Surface water flows either into or out of these mangrove-lined lakes depending on wind direction, Everglades water levels and Florida Bay sea level. Deeper areas within the most upstream lakes (West Lake and Seven Palm Lake) had exposed bedrock outcroppings with pockets of mud and sand-sized sediments while shallow sites and those in the other water bodies had mud sediments.

Materials and Methods

The abundances of benthic macrophytes and water quality parameters were measured at 41 study sites (Fig. 1.1) from May 2006 through April 2009. These sites were chosen from historic site locations that were previously sampled in short-term SAV monitoring studies (Morrison and Bean 1997; Richards and Fourqurean 2000). Benthic macrophyte abundance at each site was surveyed by snorkeler at approximate 3-month intervals over the study period, a total of 12 times. Mean percent bottom coverage ($n = 15$ surveys) for each species present was estimated using a $1/4 \text{ m}^2$ quadrat. Bottom coverage was estimated to the nearest 5%. During each sampling, the quadrat was arbitrarily placed on the benthos at 15 locations within a 30 m radius of the study site as located using GPS. Sediment depth to bedrock was also measured for each site.

Salinity, water depth (Z), and water transparency (Secchi depth, Z_{SD}) were measured at each site at approximate monthly intervals except when low water levels prevented access by boat. Surface salinity was measured using a combination temperature-conductivity-salinity probe (YSI model 30). Sediment depth to bedrock was also measured at each site. Water and sediment depths to bedrock were measured to the nearest centimeter using a graduated PVC pipe. Water transparency was measured to the nearest 5 cm using a 20 cm diameter Secchi disc. Underwater light availability to benthic macrophytes, expressed as percent light at bottom, was estimated from Secchi depth and water depth measurements using the approximate relations:

$$K_d = 1.44 / Z_{SD} \text{ (Holmes 1970)}$$

$$\text{percent light at bottom} = 100e^{(-K_d Z)} \text{ (Kirk 1994)}$$

where K_d is the vertical attenuation coefficient for downwards irradiance of photosynthetically active radiation. Estimates of the percent light at bottom should be considered approximate

because the relationship between K_d and Secchi depth has been shown to vary (Preisendorfer 1986) especially in more turbid waters where the relation $K_d = 1.44 / Z_{SD}$ would overestimate K_d (Kirk 1994).

Additionally, water column total nitrogen (TN) concentrations, total phosphorus (TP) concentrations, and phytoplankton abundances as water-column chlorophyll-*a* (chl *a*) were determined from water samples collected at selected sites within each water body (sites 2, 8, 13, 17, 28, 30, 35, and 40; see Fig. 1.1). Sampling was performed at the same times these sites were sampled for salinity, water depth, and water transparency. TN was measured by high temperature combustion using an ANTEK 7000N nitrogen analyzer. TP was determined using a dry ashing, acid hydrolysis technique (Solórzano and Sharp 1980). Chl *a* concentrations were determined by filtering water samples (25 mm glass-fiber GF/F) and extracting the pigment from the filter using 90% acetone. Extracts were analyzed for chl *a* using a Shimadzu RF-Mini 150 fluorometer equipped with low (10 nm) half-bandwidth filters (excitation = 439, emission = 671) to maximize sensitivity to chl *a* and minimize interference from phytin *a* (Welschmeyer 1994). The fluorometer was calibrated with a chl *a* standard (Sigma-Aldrich) whose concentration was established using a Shimadzu UV Mini 1240 spectrophotometer and the spectrophotometric equations of Jeffrey and Humphrey (1975).

Statistical Analysis

A matrix of Bray-Curtis similarities was constructed from mean SAV species coverages at each site ($n = 41$) calculated from all sampling events conducted over the study period ($n = 12$, May 2006 - April 2009). To decrease the importance of the rarest species, which are "prone to random and uninterpretable fluctuations" (Clarke and Warwick, 2001), and whose occurrence in a particular study plot may be due largely to chance (McCune et al. 2002), the rarest species were removed from the matrix. Only species that had a mean abundance of at least 1%, at any of the 41 sites, were included in the cluster analysis. Hierarchical cluster analysis (McCune et al. 2002) using group average linkage and the calculated similarities was performed to identify natural groups of sites (CLUSTER, Primer-E[®] vers. 6.1.5 software). The similarity profile test (Clarke and Gorley, 2006) was used to identify significant *a posteriori* differences in multivariate structure between the identified clusters (SIMPROF, Primer-E[®] vers. 6.1.5 software).

Sequential (hierarchical) discriminant analysis (Tabachnick and Fidell 2007) was used to construct discriminant functions that would predict the occurrences of the SAV community groups identified by the cluster analysis as a function of mean salinity, mean sediment depth to bedrock, and median light availability variables calculated from all sampling events (DISCRIMINANT, SPSS vers. 11.01). Because mean salinity is a targeted performance measure for Florida Bay ecosystem restoration, it was entered first into the discriminant analysis. Mean sediment depth to bedrock and median light availability were entered simultaneously into the discriminant analysis as an additional step. The validity of the additional step in the discriminant analysis was tested using the binomial test for model improvement (Zar 1999). Site classification accuracy was assessed by cross-validation for each of the 41 sites. The discriminant functions were interpreted by examining the correlations between discriminating predictor variables and the discriminant functions. Contrasts of SAV group means were used to assess the contribution of the individual predictor variables to the separation of identified SAV groups after adjustment for the other predictors (covariates) (GLM, SPSS vers. 11.01). Type I error rate was adjusted for the number of contrasts using the Bonferroni adjustment (Tabachnick and Fidell 2007).

Linear and non-linear regression analyses (Zar 1999) were performed using water column TN, TP, and chl a concentrations to identify possible relationships between Secchi depth, light availability, phytoplankton abundance and nutrient concentrations (REGRESSION, Sigma-Plot vers. 9.01). Because it is not possible to infer Secchi depths that exceed water depths, only Secchi depths less than water depths were used in regression analyses.

Results

Four angiosperms (*Halodule wrightii* Ascherson, *Ruppia maritima* Linnaeus, *Thalassia testudinum* Banks ex König, and *Rhizophora mangle* Linnaeus) and twelve macroalgae (*Chara hornemannii* Wallman, *Batophora oerstedii* Agardh, *Acetabularia* sp., *Penicillus capitatus* Lamarck, *Udotea* sp., *Halimeda incrassata* (Ellis) Lamouroux, *Caulerpa prolifera* (Forsskål) Lamouroux, *Sargassum pteropleuron* Grunow, *Laurencia intricata* Lamouroux, *Polysiphonia* sp., and *Chondria* sp.) were observed in sample quadrats during the SAV surveys (May 2006 - April 2009). Of the 15 species, only 5 (*H. wrightii*, *R. maritima*, *C. hornemannii*, *B. oerstedii*, and *Acetabularia* sp.) exhibited mean percent bottom coverage (n = 12 sampling times)

exceeding 1% at a minimum of one site and were included in the cluster and similarity profile analyses.

The cluster analysis and similarity profile test identified three significant ($P < 0.05$) benthic communities defined by species composition and percent bottom cover (Fig. 2.1). The largest group contained 22 sites and was characterized by the dominance of *Chara* (33% mean bottom cover) within the SAV community (Fig. 2.1). Also present within the *Chara* community at mean percent bottom cover greater than 1%, was *Batophora* (2%) that occurred both as an epiphyte and attached to exposed bedrock. The second largest group contained 15 sites and was characterized by the dominance of *Halodule* within the SAV community (Fig. 2.1). *Batophora* was also present in the *Halodule* community (6% mean bottom cover) where it was attached epiphytically or to hard substrates (e.g., shell fragments). The third group contained 4 sites and was characterized by very low SAV coverage (<1%) (Fig. 2.1).

A spatial pattern was evident in the distribution of benthic community groups (Fig. 2.2). The *Chara* communities were found exclusively within the upstream "lakes" (i.e., West Lake, Long Lake, The Lungs, Seven Palm Lake, Middle Lake, and Monroe Lake) while the *Halodule* communities were found predominantly in the Florida Bay coastal embayments (Fig. 2.2). The Low SAV coverage communities were found exclusively in the West Lake drainage in western West Lake and eastern Long Lake (Fig. 2.2). *Ruppia* and *Acetabularia* occurred sporadically and at low mean percent bottom coverages throughout the study area with *Ruppia* occurring on mud substrates and *Acetabularia* attaching to exposed bedrock (Seven Palm Lake) or shell fragments.

Water quality characteristics were variable at the study sites (Table 2.1). Mean annual salinities ranged from 14.1 psu at site 4 in Seven Palm Lake to 35.1 psu at site 21 in Terrapin Bay. Mean annual salinities increased from the *Chara* communities in the upstream locations (Seven Palm Lake and West Lake) to the *Halodule* communities in the downstream coastal embayments (Terrapin Bay and Garfield Bight) (Table 2.1; Fig. 2.3a). Median light availability (percent light at bottom) ranged from 1% at sites 27 and 28 in West Lake to >24% (24% is the maximum possible estimate using Secchi disc measurements) at most sites in the Seven Palm Lake drainage system (Table 2.1). Median light availabilities were lowest at sites within the Low SAV coverage group (Fig. 2.3b) and were generally lower in West Lake, Long Lake, and The

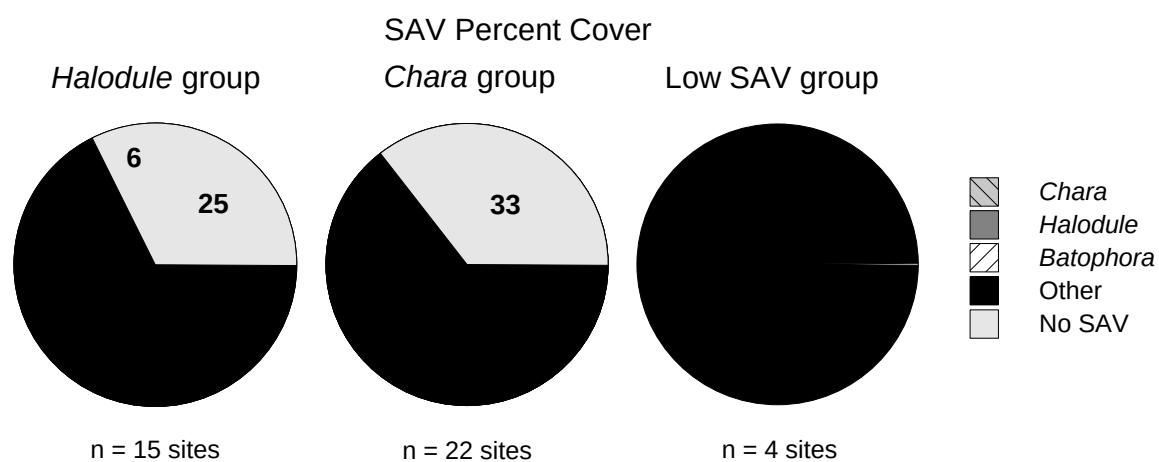


Figure 2.1 Taxa composition of SAV community groups identified by cluster analysis. "Other" represents the species of low abundance not represented within an individual pie chart and is a unique combination of species for each SAV community group.

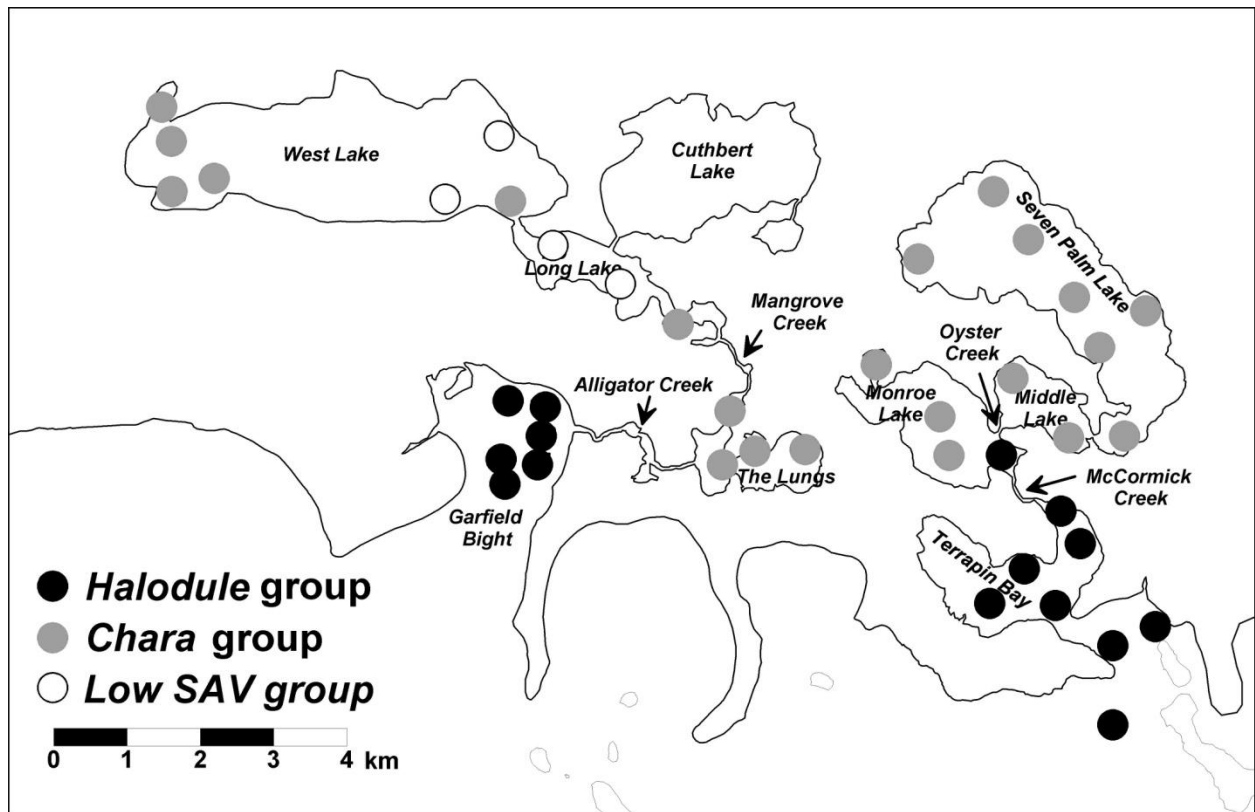


Figure 2.2 Spatial distribution of SAV community groups in the study area.

Table 2.1 Water quality characteristics and sediment depths to bedrock at all study sites. Data collected from May 2006 - April 2009.

									Light availability		
									Light at bottom	Sediment depth to	
Site	Drainage	n	Salinity		Water depth (cm)		Secchi depth (cm) ^b		(%) ^c	bedrock (cm) ^d	
	System ^a		Mean	Range	Mean	Range	Median	Range	Median	Mean	Range
1	S	29	14.9	4.4 - 30.6	139	119 - 165	Bottom	35 - Bottom	24	2	0 - 5
2	S	29	15.3	4.2 - 30.8	147	120 - 170	Bottom	35 - Bottom	24	2	0 - 8
3	S	29	15.7	4.0 - 31.9	157	135 - 180	150	35 - Bottom	21	7	0 - 20
4	S	29	14.1	2.7 - 29.6	127	110 - 145	Bottom	35 - Bottom	24	7	0 - 25
5	S	29	15.7	4.0 - 32.6	119	95 - 119	Bottom	35 - Bottom	24	45	30 - 50
6	S	29	14.7	4.1 - 30.1	138	110 - 160	145	35 - Bottom	22	3	0 - 5
7	S	29	16.9	4.4 - 34.0	108	75 - 130	Bottom	35 - Bottom	24	53	40 - 70
8	S	29	19.7	4.6 - 37.0	124	100 - 145	Bottom	35 - Bottom	24	50	40 - 60
9	S	29	20.4	4.9 - 36.8	116	93 - 140	Bottom	35 - Bottom	24	56	50 - 60
10	S	29	25.6	6.4 - 46.4	70	50 - 90	Bottom	30 - Bottom	24	102	90 - 115
11	S	22	24.6	6.0 - 41.0	78	50 - 95	65	15 - Bottom	17	88	65 - 110
12	S	29	23.9	6.0 - 43.0	113	95 - 135	105	30 - Bottom	20	47	40 - 55
13	S	30	24.8	6.1 - 46.0	121	100 - 145	108	30 - Bottom	19	27	15 - 35
14	S	28	27.2	6.3 - 46.4	60	42 - 85	Bottom	30 - Bottom	24	122	120 - 125
15	S	27	29.5	8.3 - 46.0	82	63 - 104	Bottom	40 - Bottom	24	119	75 - 140
16	S	27	30.5	8.2 - 46.8	89	70 - 115	Bottom	30 - Bottom	24	82	35 - 105
17	S	30	29.4	6.6 - 48.0	83	65 - 109	Bottom	20 - Bottom	24	101	95 - 110
18	S	27	29.8	8.1 - 46.0	85	70 - 106	Bottom	35 - Bottom	24	95	90 - 105
19	S	27	32.5	9.5 - 47.1	72	55 - 92	Bottom	35 - Bottom	24	113	100 - 120
20	S	27	33.7	12.4 -	69	50 - 95	Bottom	40 - Bottom	24	121	115 - 125
21	S	28	35.1	23.9 -	125	110 - 152	Bottom	55 - Bottom	24	41	35 - 50
22	W	32	17.6	11.6 -	53	30 - 95	38	15 - Bottom	14	115	115
23	W	32	17.2	11.5 -	92	60 - 132	30	15 - 65	2	95	90 - 105
24	W	32	17.3	11.5 -	96	68 - 135	38	20 - 60	3	78	70 - 85
25	W	32	17.5	11.4 -	130	107 - 130	40	20 - 60	4	34	20 - 50

26	W	32	17.6	10.4 -	101	75 - 132	35	20 - 70	2	61	50 - 78
27	W	33	17.6	11.3 -	148	125 - 190	40	25 - 75	1	9	5 - 10
28	W	34	17.3	11.4 -	138	110 - 180	35	15 - 60	1	43	40 - 45
29	W	33	22.7	9.9 - 53.3	106	78 - 145	40	25 - 60	2	54	52 - 55
30	W	34	23.1	9.6 - 57.2	97	70 - 127	40	20 - 70	3	62	55 - 65
31	W	33	24.2	9.8 - 59.9	88	65 - 158	40	20 - Bottom	5	96	93 - 100
32	W	32	25.7	9.4 - 51.7	55	30 - 85	35	10 - Bottom	12	121	118 - 125
33	W	32	26.6	8.9 - 53.0	70	50 - 97	35	20 - Bottom	7	93	85 - 100
34	W	32	27.5	9.6 - 53.8	68	45 - 105	40	20 - Bottom	8	88	80 - 100
35	W	33	26.2	8.7 - 52.0	78	55 - 108	35	25 - Bottom	5	81	80 - 82
36	W	17	27.2	15.7 -	45	28 - 60	50	15 - Bottom	24	163	160 - 170
37	W	17	29.5	14.1 -	50	32 - 65	Bottom	20 - Bottom	24	157	153 - 160
38	W	16	26.4	13.0 -	44	20 - 56	40	15 - Bottom	15	154	145 - 160
39	W	15	27.6	14.4 -	48	30 - 60	20	15 - Bottom	9	146	140 - 150
40	W	18	31.3	17.4 -	53	35 - 68	Bottom	15 - Bottom	24	148	145 - 152
41	W	18	32.5	19.1 -	61	45 - 80	Bottom	20 - Bottom	24	130	125 - 132

^a Drainage system letters "S" and "W" indicate the Seven Palm and West Lake drainage systems, respectively.

^b Bottom indicates Secchi depth exceeding water depth.

^c Light at bottom determined from the relation $K_d = 1.44/\text{Secchi depth (m)}$ and the equation $\% \text{ light at bottom} = e^{(-K_d * \text{water depth})} * 100$.

^d n for sediment depth to bedrock data ranges from 1 to 4.

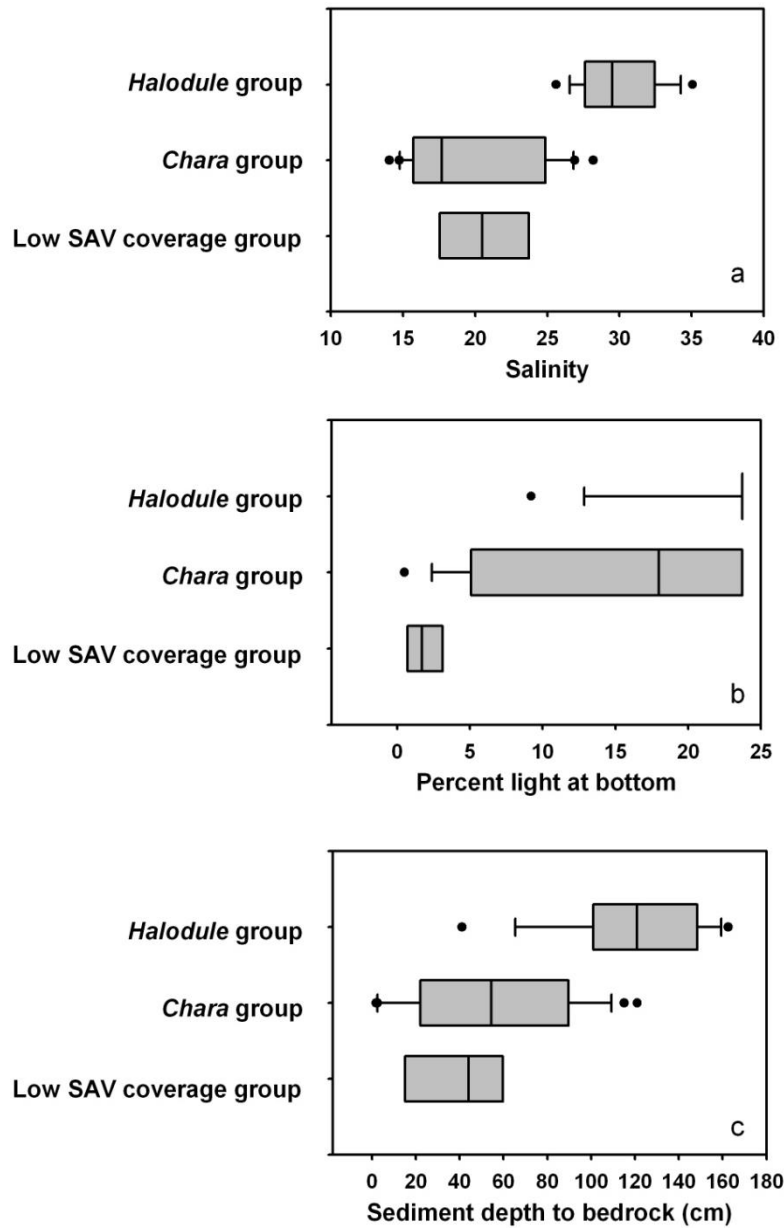


Figure 2.3 Descriptive statistics of water column salinity (a), light availability (percent light at bottom) (b), and sediment depth to bedrock (c) of the identified SAV community groups. *Halodule* group: n = 15; *Chara* group: n = 22; Low SAV coverage group: n = 4. Boxes indicate 25th and 75th percentiles, error bars indicate 10th and 90th percentiles, vertical lines within boxes indicate median values, and dots are outliers.

Lungs (sites 22-35, median light availability range = 2% - 12%) compared to the rest of the study area (sites 1-21, 36-41, median light availability range = 9 - 24%) (Table 2.1). Low water transparencies (Secchi depths) during persistent phytoplankton blooms contributed to low light availabilities in West Lake, Long Lake, and The Lungs (Table 2.1). Light availabilities and Secchi depths declined with increasing phytoplankton abundance (Figs. 2.4a and 2.4b). The censored Secchi depth data did not bias these relationships because there was no significant correlation between phytoplankton abundance (chlorophyll *a*) and water depths at the sites (Pearson $r = 0.026$, $P = 0.77$) that would suggest a systematic relationship.

Sediment depths to bedrock were spatially variable (Table 2.1), generally increasing from upstream "lakes" to the coastal embayments, and following the transition from upstream *Chara* communities to downstream *Halodule* communities (Fig. 2.3c). Sediment depths to bedrock ranged from zero in areas of exposed bedrock in Seven Palm Lake to depths exceeding one meter at most sites in Terrapin Bay and all sites in Garfield Bight (Table 2.1). Mean water depths ranged from 44 cm at site 38 in Garfield Bight to 157 cm at site 3 in Seven Palm Lake (Table 2.1). Deeper sites were generally in the middle of the most upstream lakes (Seven Palm Lake and West Lake) while the shallowest sites were located in Garfield Bight (Table 2.1).

Mean phytoplankton abundances, as estimated by chl *a* concentrations, ranged from 2.6 $\mu\text{g L}^{-1}$ in Middle Lake to 31.5 $\mu\text{g L}^{-1}$ in West Lake, with large differences between the West Lake and Seven Palm Lake drainage systems. Mean chl *a* concentrations at sites in the West Lake drainage system (range = 11.3 - 31.5 $\mu\text{g L}^{-1}$) were approximately an order of magnitude greater than those at sites in the Seven Palm Lake drainage system (range = 2.6 - 3.8 $\mu\text{g L}^{-1}$). West Lake exhibited the highest mean chl *a* concentration (31.5 $\mu\text{g L}^{-1}$). Linear regression revealed a significant relationship (Pearson $r = 0.77$, $P < 0.001$) between log phytoplankton abundance (chl *a*) and log water-column TP (Fig. 2.5).

The spatial variations in mean water column nutrient concentrations were similar to the spatial variation of chl *a* concentration with much higher concentrations in the West Lake drainage system than in the Seven Palm Lake drainage system. Mean TN concentrations in the West Lake system ranged from 81 - 105 μM , while in the Seven Palm Lake system, the range was 51 - 57 μM . Mean TP concentrations in the West Lake system ranged from 1.82 - 2.86 μM ,

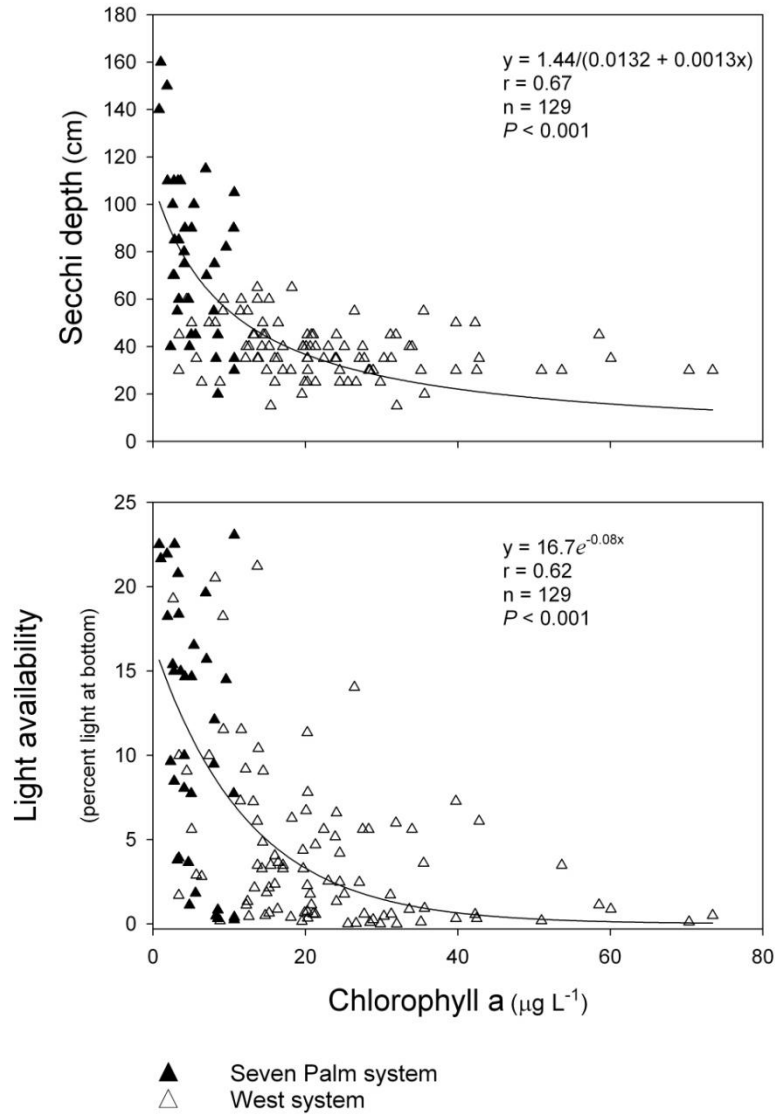


Figure 2.4 Fitted relationships of Secchi depth to phytoplankton abundance (water column chl *a* concentration) (a), and light availability (percent of light at bottom) to phytoplankton abundance (water column chl *a* concentration) (b). Regression equation in Fig. 5a is the inverse relation $Z_{SD} = a / (k_w + k_{chl} * \text{chlorophyll concentration})$, where Z_{SD} = Secchi depth, a = ratio estimate of the light attenuation coefficient (K_d) to Secchi depth (Z_{SD}) (Holmes, 1970), k_w = light attenuation coefficient for water and other attenuating constituents, and k_{chl} = light attenuation chlorophyll proportionality constant. Regression equation in Fig. 5b is an unconstrained 2-parameter exponential decay equation. Data points are individual sampling events conducted over the study period (May 2006 - April 2009) and are coded by drainage system location.

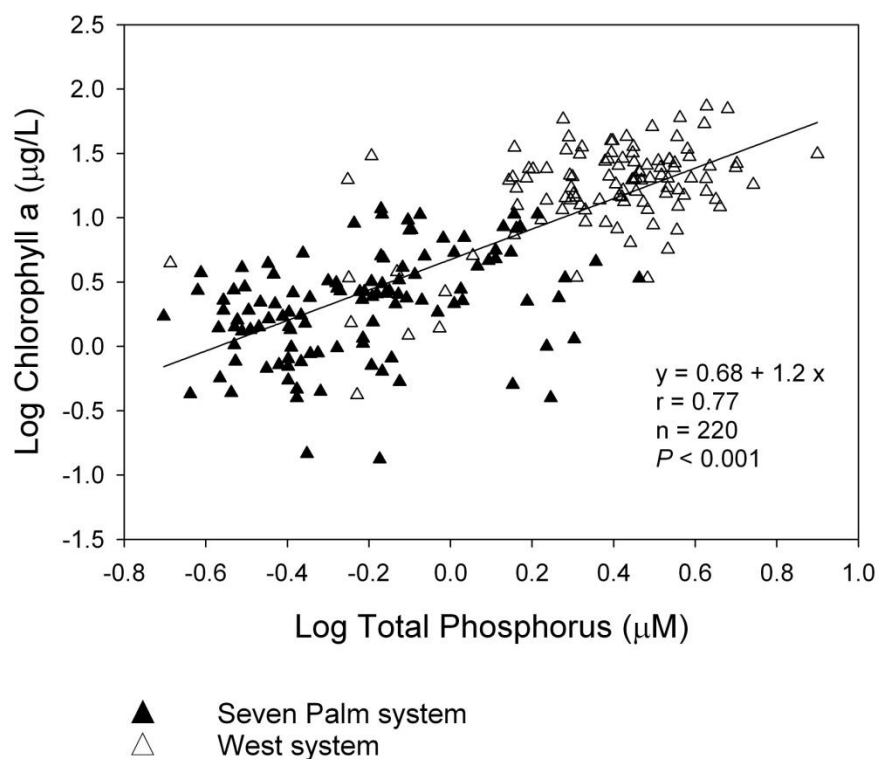


Figure 2.5 Relationship of water column chl *a* concentrations to water column TP concentrations. Data points are individual sampling events conducted over the study period (May 2006 - April 2009) at approximate monthly intervals and are coded by drainage system location.

while in the Seven Palm Lake system, the range was 0.67 - 0.83 μM . Mean N:P (TN to TP) ratios in the water column, ranging from 65 - 85:1 in the Seven Palm Lake system and from 37 - 44:1 in the West Lake system, are much higher than the Redfield Ratio (16:1) and indicate phosphorus (P) limiting conditions throughout, but also more severe limitation in the Seven Palm Lake system.

The constructed discriminant function models were limited to a maximum of three predictor variables because the total number of predictor variables must be less than the minimum number of cases (sites) in any particular SAV group to avoid overfitting (Tabachnick and Fidell 2007). A discriminant function model with only mean salinity as a predictor variable was able to correctly classify 78% of the sites according to SAV community group, much greater than the 43% by expected by chance based on prior probabilities. The addition of mean sediment depth to bedrock and median percent light at bottom improved the final model ($P \leq 0.10$, binomial test; Zar 1999) and increased classification accuracy to 90%. The final model was able to differentiate the SAV community groups along two dimensions (i.e., discriminant functions). The discriminant functions are separate linear combinations of the three predictor variables. The final model was accurate in predicting the occurrence of all three SAV groups (i.e., *Halodule* - 100% accuracy, *Chara* - 86% accuracy, and Low SAV coverage- 75% accuracy) (Figs. 2.6a, 2.6b). Only 4 of the 41 sites were misclassified with two *Chara* sites misclassified as Low SAV coverage sites (sites 26 and 28), one Low SAV coverage site misclassified as a *Chara* site (site 30), and one *Chara* site misclassified as a *Halodule* site (site 32).

The three predictor variables were correlated with the discriminant functions (Table 2.2). Median light availability was positively correlated with both discriminant functions, exhibiting its greatest correlation with discriminant function 2. Mean sediment depth to bedrock was only positively correlated with discriminant function 1. Mean salinity was positively correlated with discriminant function 1 and negatively correlated with discriminant function 2. Interpretation of the discriminant functions and the ordination plots in Figures 7a and 7b indicates increasing mean salinities, sediment depths to bedrock, and light availabilities from sites characterized by Low SAV coverage and *Chara* to sites characterized by *Halodule*.

Nine contrasts were performed to identify which predictors reliably separated the Low SAV coverage group from the others, the Low SAV coverage group from the *Chara* group, and

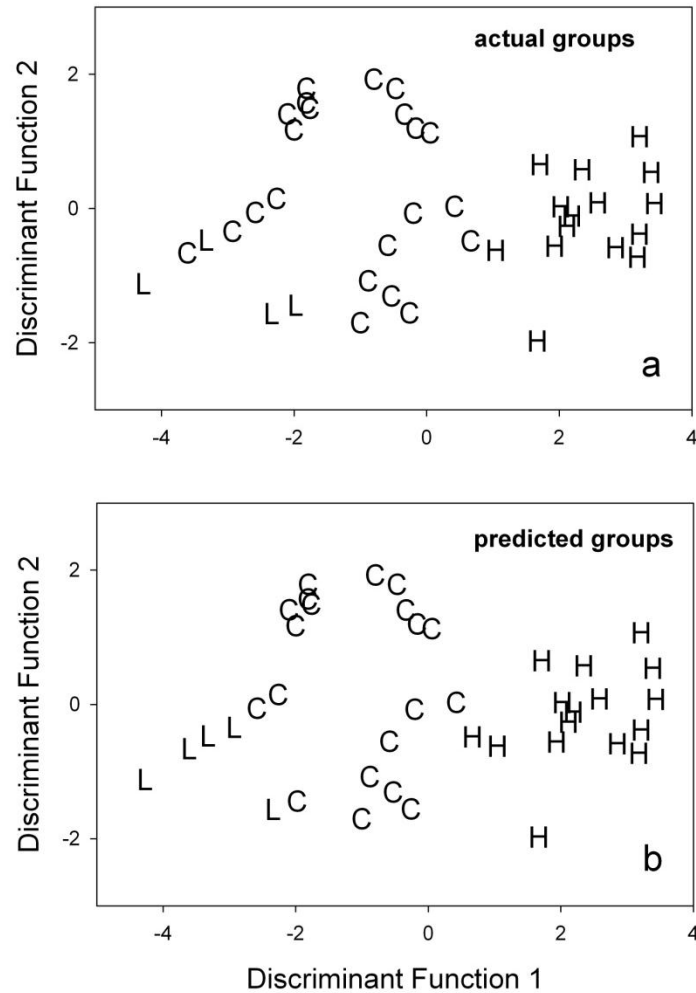


Figure 2.6 Discriminant function site scores generated using sediment depth to bedrock, light availability, and salinity predictor variables to distinguish among the identified SAV community groups. Site scores coded by actual group membership identified using cluster analysis (a). Site scores coded by predicted group membership using the discriminant function model (b).

Table 2.2 Pooled within-groups correlations (r) between discriminating predictor variables and discriminant functions. **Bold** indicates statistical significance at $P < 0.05$.

	Discriminant function	
	1	2
Light availability	0.386	0.666
Sediment depth to bedrock	0.463	-0.242
Salinity	0.579	-0.809

Table 2.3 Probabilities and 95% confidence limits of selected group contrasts for each predictor variable (adjusted for all others). Probabilities indicate Type I error rates for contrasts being significantly different from zero. **Bold** indicates statistical significance at comparison-wise error rate < 0.0055, calculated from an experiment-wise error rate of 0.05 and Bonferroni adjustment for 9 contrasts.

Contrast		Predictor variable (adjusted for all others)		
		Mean salinity	Median light availability	Mean sediment depth to bedrock
Low SAV coverage vs others	<i>P</i>	0.217	< 0.001	0.043
	95% CL	-2.1, 9.0	7.3, 24.2	-82.5, -1.3
Low SAV coverage vs <i>Chara</i>	<i>P</i>	0.785	< 0.001	0.014
	95% CL	-5.8, 4.4	6.8, 20.6	9.8, 82.2
<i>Chara</i> vs <i>Halodule</i>	<i>P</i>	0.001	< 0.001	0.005
	95% CL	-12.3, -3.3	-21.8, -8.2	-92.1, -21.7

the *Chara* group from the *Halodule* group after adjustment for the other predictors (Table 2.3). Mean salinity, median light availability, and mean sediment depth to bedrock were reliable predictors separating the *Chara* and *Halodule* groups. Median light availability was also a reliable predictor for separating the Low SAV coverage group from the others and the Low SAV coverage group from the *Chara* group.

Discussion

The SAV communities of the mangrove-lined estuaries are strongly controlled by salinity climate, sediment depth to bedrock, and light penetration through the water column. Any factor that changes these structuring variables is likely to result in a change in the distribution and abundance of SAV communities. The discriminant function model, in conjunction with the contrast analyses, identified the relative strengths of these structuring variables in differentiating the SAV community groups. Through analogy, the spatial analyses have also provided further insights into understanding the historical regime shift from SAV abundance and clear water-columns to phytoplankton abundance and the loss of SAV coverage that has occurred in the mangrove "lakes" of Florida Bay.

Our results provide targets for salinity, water clarity, and water-column TP concentration that, if achieved by ecosystem restoration, should see the return of the historical dense *Chara* communities in the upstream "lakes". Two SAV community groups were organized along a salinity gradient with *Chara hornemannii* dominant in the upstream "lakes" at mean annual salinities less than approximately 25 psu and *Halodule wrightii* dominant in the downstream marine embayments at greater mean annual salinities (Fig. 2.5a). The mean salinities at sites characterized by *Halodule* dominance (Fig. 2.5a) were all within the tolerance range (9 – 65 psu) for *H. wrightii* isolated in culture (McMahan 1968; Koch et al. 2007). The mean salinities at *Chara*-dominated sites (Fig. 2.5a) were also within the salinity range (0 – 41 psu) reported from field observations of *C. hornemannii* occurrence (Tabb et al. 1962; Morrison and Bean 1997). Within the "upstream lakes" where *Chara* occurred, were also sites where SAV presence was negligible (Fig. 2.2). These Low SAV coverage sites were characterized by low light availability caused by a combination of both greater phytoplankton abundance and greater water depth.

As indicated by the 78% accuracy rate for the prediction of community groups using only mean salinity, the discriminant function model justifies the use of salinity as a targeted performance measure for managing the distribution of SAV community types in estuaries. The model also indicated that median light availability and sediment depth to bedrock were valuable predictors of community types, whose addition increased model accuracy to 90%. Greater median light availability and greater sediment depth to bedrock characterized *Halodule* sites and further delimited the *Chara* and *Halodule* communities when they were added to the model. Differences in median light availability (Table 2.3) were uniquely valuable in identifying sites unsuitable for *Chara* occurrence (i.e., Low SAV coverage sites), even though mean salinities at those sites (i.e., sites 25, 27, 29, and 30 in the West Lake system) were within the approximate favorable range (<25).

The water column throughout the study area was P-limited as indicated by TN:TP ratios exceeding the Redfield ratio and a significant positive relationship between log phytoplankton abundance (chlorophyll *a*) and log water column TP concentration (Fig. 2.5). Lower TN:TP ratios in the West Lake system (37 - 44:1) relative to those in the Seven Palm Lake system (65 - 85:1) indicate less severe P-limitation in the western system, with greater phytoplankton concentrations in the West Lake system resulting from greater P availability. The observed P limitation and the east-west gradients in phytoplankton abundance and TN:TP ratios are consistent with larger regional patterns in productivity and P availability within the greater Everglades and Florida Bay ecosystems (Fourqurean et al. 1992; Chen and Twilley, 1999; Noe et al. 2001). The level of productivity and the P-limitation gradient reflect differences in proximity to a Gulf of Mexico P source (Fourqurean et al. 1992; Chen and Twilley 1999).

The observed pattern of increasing light availability from the *Chara* group to the *Halodule* group is consistent with the pattern of light requirements for algae and seagrasses. Seagrasses generally have higher light requirements than algae because photosynthesis in the seagrass leaves must provide greater energy per unit biomass to support non-photosynthetic roots and rhizomes (Fourqurean and Zieman 1991). Decreasing light availabilities may support only algae that have greater proportions of photosynthetic biomass. Ultimately, light availability decreases past the level to support any SAV.

Increasing sediment thickness (depth to bedrock) from the upstream "lakes" to the downstream coastal embayments reflect the progression of sea-level rise and associated marine carbonate sedimentation that created Florida Bay over the past 5000 years (Enos and Perkins 1979). Sediment depths to bedrock reliably separated the upstream *Chara* communities from the downstream *Halodule* communities when used a predictor variable in the discriminant function model (Table 2.3). The greater sediment depths to bedrock, which have the ability to store more nutrients, may favor the establishment of *Halodule* that can take up nutrients through its roots over *Chara* that predominantly takes up nutrients from the water column (Kufel and Kufel 2002).

Pre-drainage SAV data for the mangrove estuaries along the ecotone between Florida Bay and the freshwater Everglades are scarce, but anecdotal reports indicate that historical SAV abundances were much higher from those observed recently. Based on qualitative observations, Tabb et al. (1962) first described the disappearance of the *Chara-Ruppia-Batophora* community and associated waterfowl in Whitewater and Coot Bays (located to the adjacent west from present study area), following the construction of the Buttonwood Canal in 1956-57 that permitted the entry of saline water from Florida Bay. They also estimated that these SAV communities were in chronic decline starting in 1920 when Everglades drainage operations began south of Lake Okeechobee. During the time of their study, they also reported that the *Chara-Ruppia-Batophora* community in West Lake was less affected than areas further west and likely represented pre-drainage conditions. Shortly after their study, the conditions in West Lake deteriorated when a channel was cut between West and Long Lakes that permitted more saline water from Long Lake to enter West Lake causing another acute loss of the *Chara* communities (Craighead 1971). The decline of these communities since pre-drainage times is also associated with an estimated 20-30 psu increase in mean salinities along the north shore of Florida Bay (McIvor et al. 1994).

Though earlier investigators attributed historical *Chara* loss to increasing salinities (Tabb et al. 1962; Craighead 1971; Simmons and Ogden 1998), the unique ability of light availability to distinguish the Low SAV coverage group from the *Chara* and *Halodule* groups (Figure 4b, Table 3), suggests an additional mechanism for the loss of *Chara* communities. Decreased freshwater deliveries permit the intrusion of surface seawater from Florida Bay (Davis et al.

2003) and increase the discharge of brackish groundwater where fresh and saline groundwater meet (Price et al. 2006). Both Florida Bay seawater and brackish groundwater are enriched with P relative to upstream freshwater sources (Rudnick et al. 1999; Davis et al. 2003; Price et al. 2006); therefore, increased saltwater intrusion likely increased P loading to these estuaries. The clear relationships between P availability, phytoplankton abundance and light availability indicate that historic SAV communities will not be restored in the freshwater end of these estuarine systems unless water column TP concentrations are reduced, especially in the West Lake system. Though increased freshwater flow will decrease salinity and may also decrease P loading, the re-establishment of flourishing *Chara* communities in the estuaries of the southern Everglades may be inhibited by the long-term retention of P in P-limited carbonate ecosystems (Herbert and Fourqurean 2008). Because 75% of the sites characterized by *Chara* dominance exhibited median light at bottom exceeding 5% of surface light, and all sites characterized with Low SAV coverage were below this level of light availability (Fig. 2.3b), 5% light at bottom is a reasonable estimate for the maintenance of *Chara* communities. Using a light availability target of 5% of surface light at bottom and the regression equations relating light availability to chl *a* (Fig. 2.4b), and chl *a* to TP, we estimate that annual mean water column TP concentrations should be maintained at or below $2.2 \pm 1.1 \mu\text{M}$ (mean $\pm$ 95% confidence interval) to limit phytoplankton abundance and allow for the shift back to the *Chara*-dominated regime in the upstream "lakes". However, if the *Chara*-dominated and the phytoplankton-dominated regimes are distinct stable states characterized by hysteresis (Scheffer et al. 1993), a much lower TP concentration may be required.

This study has demonstrated how SAV distribution in the mangrove lakes and estuaries relates to salinity, light availability, and sediment depth to bedrock, and has also provided water quality restoration targets based upon these relationships. The study also suggests that in addition to salinity intrusion, decreased light availability facilitated by phytoplankton blooms that are fueled by increased nutrient availability, may have also contributed to a historical regime shift from SAV abundance to phytoplankton domination.

Chapter Three - Differential importance of water quality parameters and temporal patterns of submerged aquatic vegetation (SAV) cover in adjacent sub-estuaries distinguished by alternate regimes of phytoplankton and SAV dominance

Introduction

The current knowledge of seasonal patterns of submerged aquatic vegetation (SAV) abundance in tropical and sub-tropical coastal ecosystems is incomplete. This contrasts with canonical seasonal patterns of vegetation abundance in terrestrial systems (Goward et al., 1985) and for seagrass communities in temperate latitudes (Hemminga & Duarte, 2000). Greater solar radiation and higher temperatures in the tropics and sub-tropics allow for potential year round growth and create conditions conducive to seasonal growth limitation by other factors (e.g., nutrient limitation). Cloern & Jassby (2008) described the lack of consistent seasonal patterns of coastal phytoplankton abundances globally and attributed the large variability of observed seasonal patterns to the interactive and site-specific effects of local watershed geography, climatology, and coastal oceanography. Coastal SAV communities may exhibit the same level of complexity, but more determinations of SAV seasonal patterns in the tropics and sub-tropics are needed to test the analogy.

Solar insolation and temperature exhibit distinct seasonal cycles that are regulated by the changing amount of radiation received at the Earth's atmosphere that is determined primarily by the changing orientation of the Earth's axis of rotation in relation to the sun. Local climatology (e.g. seasonal cloudiness) further modulates temperatures and the amount of radiation that is seasonally available to vegetation. Aquatic plants are subject to further modulation of their environment by processes unique to their aquatic medium, such as changes in water clarity and, in the case of estuarine vegetation, seasonally changing salinities and water levels. The complexity of the estuarine environment and the direct and indirect effects of interacting factors (e.g., salinity, water level, nutrient availability) operating within the aquatic medium create temporal dynamics of SAV abundance that may be site-specific and non-seasonal.

Characteristics of local estuarine geography may favor the predominance of different structuring environmental factors resulting in different temporal or seasonal dynamics.

Differences in environmental factors caused by differing system attributes (e.g., local geographies) create different filters that modulate ecosystem response to global processes such as coastal eutrophication and sea-level rise (Cloern, 2001).

The vegetated state of shallow coastal ecosystems may also determine how these systems respond to a seasonally changing environment. Shallow lakes often exist in a state of alternative equilibria characterized by either a vegetated state with clear water or a turbid state with abundant phytoplankton (Scheffer, 2004). These alternate stable states are self-reinforcing and resistant to change because favorable environmental conditions are maintained by positive feedback mechanisms (Scheffer et al., 1993). An ecosystem in the clear-water, vegetated state maintains adequate light availability because turbidity is suppressed by mechanisms facilitated by the presence of benthic vegetation that limits sediment resuspension and promotes particle settling (Fonseca et al., 1983), and increases zooplankton grazing on phytoplankton (Timms & Moss, 1984). The maintenance of adequate light availability permits other environmental controls to exert greater influence on seasonal SAV abundance patterns. In contrast, low levels of light availability are maintained in shallow ecosystems characterized by low SAV abundance. Seasonal changes in light availability are expected to produce greater effects in these light-limited environments.

The SAV communities located within the mangrove estuaries and brackish "lakes" located along the ecotone between the freshwater Florida Everglades and saltwater Florida Bay exhibit signs of eutrophication (i.e., loss of SAV cover, persistent algal blooms) (Chapter 2) coincident with a mean sea-level rise of 2.2 mm yr^{-1} over the last century (Maul & Martin, 1993). Anecdotal reports (Tabb et al., 1962; Craighead, 1971, Simmons & Ogden, 1998) indicate that historical SAV abundances (pre-1950s) were much higher than those observed recently (Morrison & Bean, 1997). Large SAV beds once supported large populations of wading birds and wintering waterfowl within these areas (Tabb et al., 1962; Simmons & Ogden, 1998). Extensive reduction of freshwater flows in the upstream Everglades over this time period has altered the amount and timing of delivery of freshwater and nutrients into the ecotone (Light & Dineen, 1994). Mean salinities along the Everglades/Florida Bay ecotone are estimated to have increased by 20-30 psu (McIvor et al., 1994). Because of the coincidence of increasing salinities with the decline of the dominant *Chara hornemannii* Wallman alga cover in the brackish "lakes"

and the lack of other historical water quality data, the temporal loss of *Chara* cover and seasonality of the *Chara* communities (Morrison & Bean, 1997) was attributed mostly to the assumed inability of the brackish *Chara* populations to tolerate elevated salinities, however, a recent spatial analysis of these communities revealed that differences in light availability could account for the presence or absence of SAV and suggested that a decline in water transparency concurrent with increasing salinity, may have also contributed to the historical decline (Chapter 2). During this historical time period, charophytes also declined in Sweden and in The Netherlands where losses were attributed to poor light conditions developing during nutrient enrichment (Van Dijk & Van Donk, 1991; Blindow, 1992).

The restoration of estuarine communities is one of the goals of the Comprehensive Everglades Restoration Plan (CERP) (USACE, 1999). Success will be assessed by comparison of future SAV patterns with established benchmarks. Establishing these benchmarks will require quantifying the spatial and temporal patterns of SAV abundance and an increased understanding of the processes governing the relationships between water quality and SAV abundances. The objectives of this study are to describe temporal variability and to identify any emerging seasonal patterns, specifically wet season versus dry season differences, in SAV cover and water quality parameters in two of the mangrove sub-estuaries of Florida Bay. We also compare and contrast the local geographies between the two adjacent sub-estuaries and evaluate how these inherent system attributes may have structured the ecosystem responses to reduced freshwater deliveries in both systems.

Study location

We conducted our investigation in the estuarine mangrove "lakes" and coastal embayments located along the north shore of Florida Bay. Study sites were located in two adjacent sub-estuaries that drain portions of the southern Everglades (Fig. 1.1). The West Lake sub-estuary system, referred hereafter as the West zone, runs from West Lake through Long Lake to "The Lungs" and finally out into central Florida Bay at Garfield Bight. The Seven Palm sub-estuary system, hereafter referred to as the East zone, runs from Seven Palm Lake to Middle Lake to Monroe Lake and out into Florida Bay through Terrapin Bay. The watershed that drains into these flowpaths lies between the two main conduits for Everglades drainage - Shark Slough to the northwest and Taylor Slough to the northeast. Surface water flows either into or out of

these mangrove-lined lakes depending on wind direction, Everglades water level and Florida Bay sea level.

The climate of the Everglades and Florida Bay is subtropical and characterized by distinct wet (May through October) and dry (November through April) seasons (Fig. 3.1). The wet season generates 67% to 82% of the annual rainfall (Thomas, 1974). The annual precipitation cycles drive similar periodicities in salinities, water levels, and water column nutrient concentrations (Boyer et al., 1999).

Materials and Methods

SAV abundance and water quality parameters were measured at 41 sites (Fig. 1) from May 2006 through April 2009. SAV monitoring sites were chosen from historic site locations that were previously sampled in short-term SAV monitoring studies (Morrison & Bean 1997; Richards & Fourqurean 2000). SAV abundance at each site was surveyed by snorkeler at approximate 3-month intervals over the study period, a total of 12 times. Mean percent bottom coverage ($n = 15$ surveys) for each species present was estimated using a $1/4 \text{ m}^2$ quadrat. Bottom coverage was estimated to the nearest 5%. During each sampling, the quadrat was arbitrarily placed on the benthos at 15 locations within a 30 m radius of the study site as located using GPS.

Spot measurements of salinity, water depth (Z), water temperature, and water transparency (Secchi depth, Z_{SD}) were measured at each site at approximate monthly intervals except when low water levels prevented access by boat. Surface temperature and salinity were measured using a combination temperature-conductivity-salinity probe (YSI model 30). Measurements of water temperature, salinity, and water level were also recorded continuously (hourly minimum rate) using YSI model 600LS datasondes at 4 additional sites in West Lake, Garfield Bight, Seven Palm Lake, and in Terrapin Bay (Figure 1). Daily means were calculated from these data and used in the analyses.

Using the continuous water temperature, water level and salinity data collected using datasondes and the spot data collected at each site, daily values of these parameters were reconstructed for each of the 41 vegetated sites. Daily values were modeled as linear combinations of data recorded from the datasonde sites. The performance of the model was determined from the root mean squared error (RMSE) comparing measured values (spot site

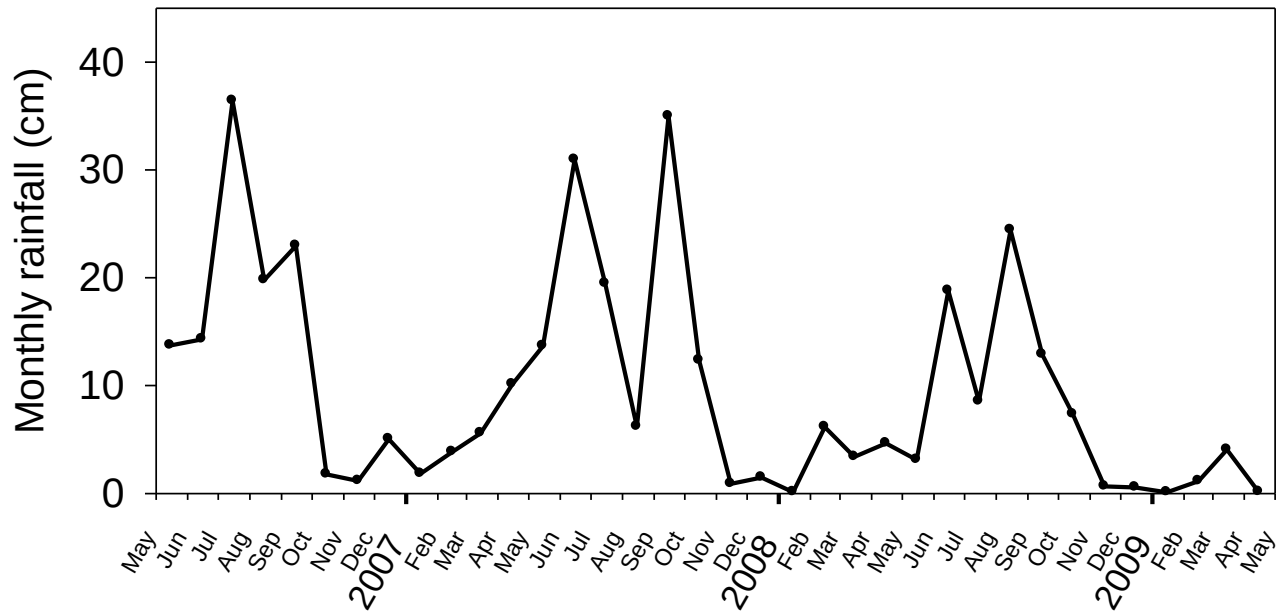


Figure 3.1 Monthly rainfall amounts for North Cuthbert Lake (NCL) summed from 15-minute interval Next Generation Radar (NEXRAD) data from the U.S. National Weather Service Data downloaded from <http://sofia.usgs.gov/eden/nexrad.php>.

water temperatures, salinities, and water depths) and modeled values (Online Resource 1). The reconstructed daily values were used to test for wet versus dry season differences in temperature, salinity and water depth and in lag correlation analyses described under Statistical Analysis.

Water transparency was measured to the nearest 5 cm using a 20 cm diameter Secchi disc. Underwater light availability to benthic macrophytes, expressed as percent light at bottom, was estimated from Secchi depth measurements and the daily water depth reconstructions using the approximate relations:

$$K_d = 1.44 / Z_{SD} \text{ (Holmes 1970)}$$

$$\text{Percent light at bottom} = 100e^{(-K_d Z)} \text{ (Kirk 1994)}$$

where K_d is the vertical attenuation coefficient for downwards irradiance of photosynthetically active radiation (PAR). When Secchi depths exceeded water depths (i.e., when the Secchi disk was visible on the bottom), light availability at the bottom was $\geq 23.7\%$, the maximum possible estimate using Secchi disc measurements and the equations listed above. Estimates of the percent light at bottom should be considered approximate because the relationship between K_d and Secchi depth has been shown to vary (Preisendorfer 1986) especially in more turbid waters where the relation $K_d = 1.44 / Z_{SD}$ would overestimate K_d (Kirk 1994).

Hourly integrated broad-band solar insolation data obtained from a meteorological station in Joe Bay (Fig. 1.1) and was used to estimate the seasonal amounts of light available at the water surface. Photosynthetically active radiation (PAR) insolation was estimated from the broadband data using the fraction of PAR to broadband solar radiation estimate of 0.45 (Jacovides et al., 2003). The time of day, time of year, and latitude were used to calculate hourly reflectance losses at the water surface using the reflectance equations provided in Kirk (1994). Wet and dry season estimates of bottom PAR insolation (MJ season^{-1}) were estimated from mean water depths, median PAR transmission values, and surface PAR insolutions corrected for reflectance.

Additionally, water column total nitrogen concentrations (TN), total phosphorus concentrations (TP), and phytoplankton abundances as water-column chlorophyll-a (chl *a*) were determined from water samples collected at selected sites within each water body (sites 2, 8, 13,

Table 3.1 Root mean squared errors (RMSE) comparing measured parameters (i.e., water temperature, salinity, and water level) and the modeled values that were used to reconstruct daily time series.

Site number	Water temperature (C)	Salinity (psu)	Water level (cm)
1	0.5	1.4	3.7
2	0.3	1.4	6.1
3	0.4	1.6	4.4
4	0.6	1.9	4.7
5	0.5	1.6	6.2
6	0.5	1.3	4.0
7	0.5	2.3	10.1
8	0.7	2.7	6.2
9	0.5	2.4	5.0
10	0.6	3.8	5.9
11	0.8	3.9	6.3
12	0.6	3.7	4.3
13	0.7	3.2	4.0
14	0.9	4.3	4.5
15	0.8	4.3	2.9
16	0.7	4.3	3.3
17	0.6	3.9	3.6
18	0.7	4.0	4.5
19	0.7	4.9	4.9
20	0.8	4.2	4.0
21	0.7	2.8	4.5
22	1.1	1.2	9.4
23	0.7	1.3	9.8
24	0.7	1.3	8.4
25	0.6	1.4	8.5
26	0.7	1.4	8.5
27	0.6	1.4	6.6
28	0.6	1.4	8.0
29	0.6	5.4	8.6
30	0.5	6.0	8.3
31	0.6	5.5	11.5
32	0.8	5.2	4.8
33	0.6	4.8	4.0
34	0.6	5.0	4.9
35	0.6	5.0	4.3
36	0.9	2.7	3.8
37	0.6	3.2	3.8

38	1.0	3.4	4.1
39	0.7	3.5	5.0
40	0.6	3.1	2.9
41	0.6	3.2	2.3

17, 28, 30, 35, and 40; see Fig. 1.1). Sampling was performed at the same times these sites were sampled for salinity, water depth, and water transparency. TN was measured by high temperature combustion using an ANTEK 7000N nitrogen analyzer. TP was determined using a dry ashing, acid hydrolysis technique (Solórzano & Sharp 1980). Chl *a* concentrations were determined by filtering water samples (25 mm glass-fiber GF/F) and extracting the pigment from the filter using 90% acetone. Extracts were analyzed for chl *a* using a Shimadzu RF-Mini 150 fluorometer equipped with low half-bandwidth (10 nm) filters (excitation = 439, emission = 671) to maximize sensitivity to chl *a* and minimize interference from phytin *a* (Welschmeyer 1994). The fluorometer was calibrated with a chl *a* standard (Sigma-Aldrich) whose concentration was established using a Shimadzu UV Mini 1240 spectrophotometer and the spectrophotometric equations of Jeffrey & Humphrey (1975).

Statistical Analysis

Prior to analysis, vegetated sites were grouped according to SAV community type (dominated either by the alga *Chara hornemannii* or the seagrass *Halodule wrightii* Ascherson) and sub-estuary (West zone or East zone) as identified by differences in SAV and water quality in previous spatial analyses (Chapter 2). Accordingly, these SAV sub-estuary groups are referred to as *Chara* zones West and East, located in the upstream “lakes” and *Halodule* zones West and East, located in the coastal embayments of Florida Bay. *Chara* zone – West contained sites 22 – 24, 26, 28, and 31 – 35. *Chara* zone – East contained sites 1 - 9, and 11 – 13. *Halodule* zone – West was comprised of sites 36 – 41, and the *Halodule* zone – East was comprised of sites 10, and 14 – 21. Sites 25, 27, 29 and 30 were unvegetated (<1% mean total SAV cover) and were not included in these groups. Because one of our goals was to infer relationships between water quality parameters and temporal patterns of SAV cover, cover data from these unvegetated sites were not included in statistical analyses.

We chose to analyze for differences between the wet season (May through October) and dry season (November through April) because of the pronounced seasonal precipitation pattern in the study area (Fig. 3.1) and its widespread ecological effects (Sklar et al., 2001) and also because the timing and frequency of SAV sampling did not achieve minimum statistical replication for analysis at finer time scales (e.g., monthly analyses). T-tests (SPSS version 11.01; Zar, 1999) were employed to detect wet season versus dry season differences in *Chara* cover,

Halodule cover, water temperature, salinity, TN, TP and Chl *a* and spatial differences between *Chara* cover, *Halodule* cover, TN, TP and Chl *a*.

SAV cover may reflect antecedent environmental conditions better than concurrent conditions and cover changes may lag behind changes in water quality parameters; therefore, we used the reconstructed daily time series of water temperature, salinity, and water depth at each vegetated site in Pearson correlation analyses. Mean values of water temperature, salinity, and water depth at each vegetated site from four antecedent periods (30, 60, 90, and 180 days] and single measurements at the time of sampling were analyzed for the strength of correlation with sampling time estimates of mean SAV cover for each SAV sub-estuary group.

Results

SAV cover

Chara percent cover (mean $\pm$ standard error) was almost twice as abundant in *Chara* zone – East compared to *Chara* zone – West, 41 ± 4 and 23 ± 3 , respectively (Figs. 3.2b and 3.2a) ($t = 3.5$, $P = 0.002$, t-test). In contrast, *Halodule* percent cover was similar in both zones - 32 ± 5 in *Halodule* zone - West and 22 ± 2 in *Halodule* zone – East (Figs. 3.2c and 3.2d) ($t = 1.9$, $P = 0.08$, t-test).

Seasonal differences in SAV percent cover between wet and dry seasons were only evident in *Chara* zone – West (Table 3.2). *Chara* percent cover in *Chara* zone - West was twice as abundant during the dry season (30 ± 4) than during the wet season (16 ± 2) (t-test $P = 0.027$, Table 3.2), while in *Chara* zone - East *Chara* percent covers were similar during dry and wet seasons (44 ± 8 and 37 ± 7 , respectively) (t-test, $P = 0.502$, Table 3.2). Temporally, *Chara* percent cover in *Chara* zone - West ranged from 12 ± 8 in June 2007 to 48 ± 13 in November 2006 (Fig. 3.2a), while that in *Chara* zone - East ranged from 16 ± 9 in September 2008 to 60 ± 13 in February 2007 (Fig. 3.2b).

Halodule percent cover in *Halodule* zone - West ranged from 14 ± 6 in November 2008 to 66 ± 13 in August 2007 (Fig. 3.2c), while that in *Halodule* zone - East ranged from 11 ± 2 in April 2009 to 37 ± 6 in November 2007 (Fig. 3.2d). *Halodule* percent covers were similar (t-tests, $P > 0.05$) during dry and wet seasons for both *Halodule* zones. *Halodule* mean percent

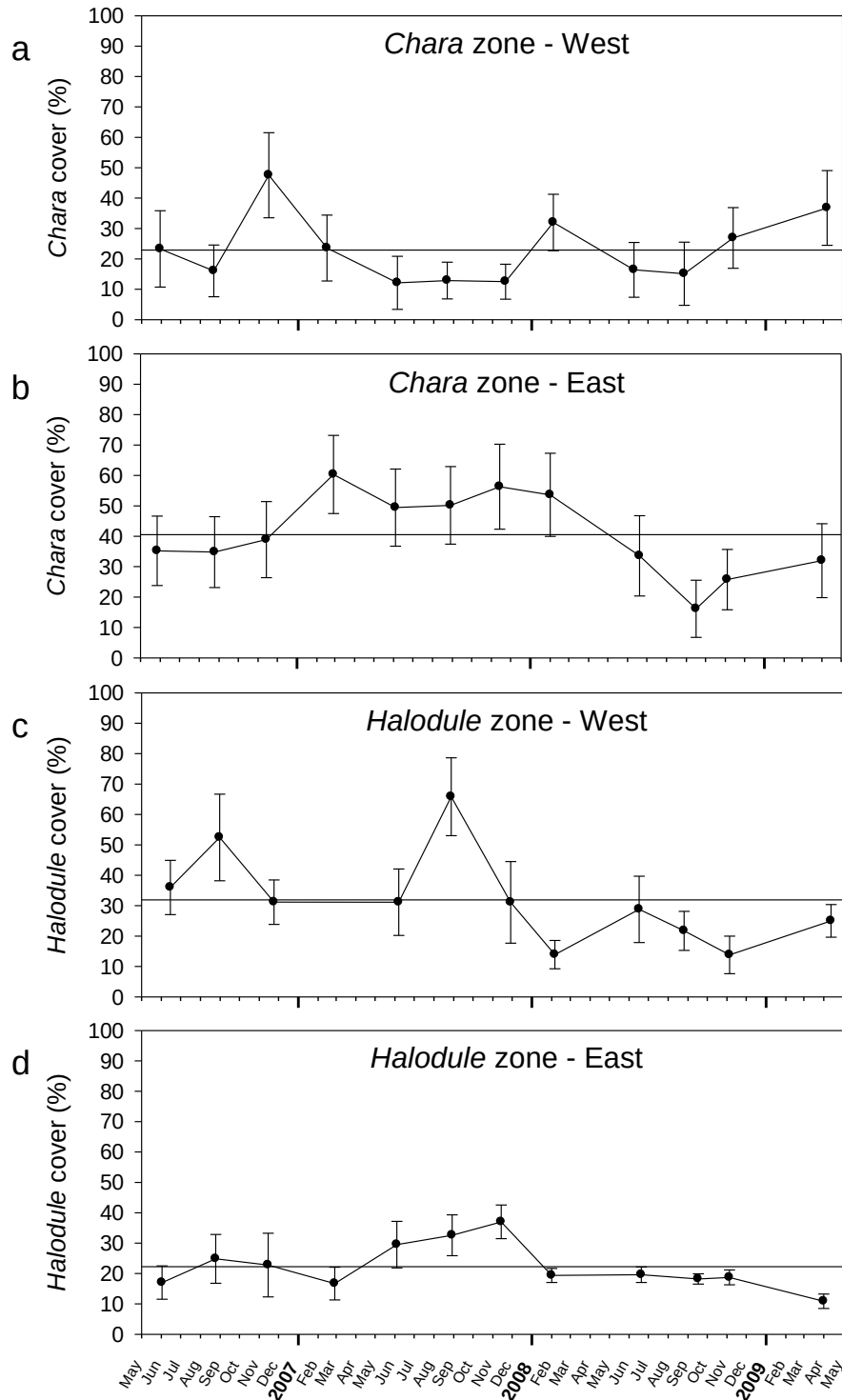


Figure 3.2 SAV (*Chara*, *Halodule*) percent cover time series from *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d) sub-estuary zones. Error bars designate standard error of the mean calculated from $n = 10$ (a), 12 (b), 6 (c), and 9 (d) sites. Horizontal reference lines designate the grand means calculated from 12 sampling periods for each sub-estuary zone.

Table 3.2 Comparison of wet season versus dry season SAV coverage (*Chara* and *Halodule*) water temperatures (Temp), salinities, total nitrogen (TN), total phosphorus (TP), and chlorophyll *a* (Chl *a*) concentrations. **Bold** indicates statistically significant (t-test, $P < 0.05$) differences between wet and dry seasons. se = standard error of the mean; na = not applicable.

	<i>Chara</i> cover (%) (mean $\pm$ se)	<i>Halodule</i> cover (%) (mean $\pm$ se)	Temp (C) (mean $\pm$ se)	Salinity (psu) (mean $\pm$ se)	TN (μ M) (mean $\pm$ se)	TP (μ M) (mean $\pm$ se)	Chl <i>a</i> (μ g L ⁻¹) (mean $\pm$ se)
<i>Chara</i> zone - West							
Dry	30 $\pm$ 4	0	23.8 $\pm$ 0.4	21.0 $\pm$ 2.9	114 $\pm$ 5	2.86 $\pm$ 0.05	23.2 $\pm$ 5.2
Wet	16 $\pm$ 2	0	29.9 $\pm$ 0.2	22.2 $\pm$ 4.2	101 $\pm$ 23	2.65 $\pm$ 0.34	22.6 $\pm$ 1.8
<i>P</i>	0.027	na	< 0.001	0.381	0.640	0.610	0.907
<i>Chara</i> zone - East							
Dry	44 $\pm$ 8	< 1	23.8 $\pm$ 0.4	15.4 $\pm$ 2.7	50 $\pm$ 2	0.80 $\pm$ 0.25	3.1 $\pm$ 0.5
Wet	37 $\pm$ 7	< 1	30.0 $\pm$ 0.2	19.8 $\pm$ 4.1	56 $\pm$ 7	0.78 $\pm$ 0.21	3.4 $\pm$ 0.2
<i>P</i>	0.502	na	< 0.001	0.433	0.479	0.970	0.954
<i>Halodule</i> zone - West							
Dry	0	23 $\pm$ 5	23.9 $\pm$ 0.3	33.0 $\pm$ 2.3	91 $\pm$ 2	2.1 $\pm$ 0.5	13.6 $\pm$ 4.7
Wet	0	37 $\pm$ 6	29.8 $\pm$ 0.1	28.4 $\pm$ 5.8	75 $\pm$ 4	1.8 $\pm$ 0.4	11.7 $\pm$ 5.2
<i>P</i>	na	0.150	< 0.001	0.505	0.016	0.593	0.806
<i>Halodule</i> zone - East							
Dry	0	21 $\pm$ 4	23.8 $\pm$ 0.4	29.6 $\pm$ 2.1	55 $\pm$ 3	0.52 $\pm$ 0.04	3.4 $\pm$ 1.8
Wet	0	24 $\pm$ 4	30.0 $\pm$ 0.2	30.2 $\pm$ 4.0	58 $\pm$ 6	0.72 $\pm$ 0.17	2.7 $\pm$ 1.5
<i>P</i>	na	0.642	< 0.001	0.903	0.749	0.324	0.778

covers in the *Halodule* zone - West for the dry and wet seasons were 23 ± 5 and 37 ± 6 , respectively, while in *Halodule* zone - East they were 21 ± 4 and 24 ± 4 , respectively (Table 3.2).

Seasonal cycles were observed in water temperature, salinity and water level (Figs. 3.3 – 3.5). Seasonal water temperature profiles at the four datasonde monitored sites were similar in timing of minimum and maximum values but showed slight differences in temperature ranges (Fig. 3.3a-d). Maximum water temperatures ranging from 33.4 C to 36.0 C were recorded during the start of the wet season in the summer months of July and August. Minimum water temperatures ranging from 11.6 C to 14.3 C were observed during the middle of the dry season in the winter months of January and February when periodic cold fronts traversed the area. Differences in mean water temperature between wet and dry seasons were evident (Table 3.1). Seasonal and daily water temperature ranges were greater in the shallower *Halodule* zone – West (overall temperature range = 22.4 C degrees, average depth approx. 50 cm) and *Halodule* zone – East (overall temperature range = 24.4 C degrees, average depth approx. 80 cm) than in the deeper upstream lakes of *Chara* zone – West (overall temperature range = 19.0 C degrees, average depth approx. 110 cm) and *Chara* zone – East (overall temperature range = 19.7 C degrees, average depth approx. 130 cm) (Fig. 3.3 a-d, depths from Chapter 2).

Salinity levels were different at the four datasonde monitored sites but seasonal salinity profiles were similar in the timing of minimum and maximum levels (Fig. 3.4 a-d). Mean daily salinities were mesohaline in the upstream lakes, ranging from 14.5 psu in Seven Palm Lake (*Chara* zone – East) to 17.3 psu in West Lake (*Chara* zone – West), while they were polyhaline in the coastal embayments, ranging from 28.2 psu in Terrapin Bay (*Halodule* zone – East) to 33.6 psu in Garfield Bight (*Halodule* zone – West). Minimum daily salinities were observed during the fall (September – December) following the end of the wet season, while maximum salinities were observed at the end of the dry season and into the early wet season (April – August) (Fig. 3.4 a-d). Because the salinity extremes occurred during the transition periods between wet and dry seasons, differences between mean wet and mean dry season salinities were not evident (Table 3.2). Salinity ranges were much greater in Terrapin Bay and Garfield Bight than in Seven Palm Lake and West Lake. Daily salinities in Terrapin Bay and Garfield Bight ranged from 5.2 psu to 49.7 psu, and 11.4 psu to 61.1 psu, respectively; while that in Seven Palm

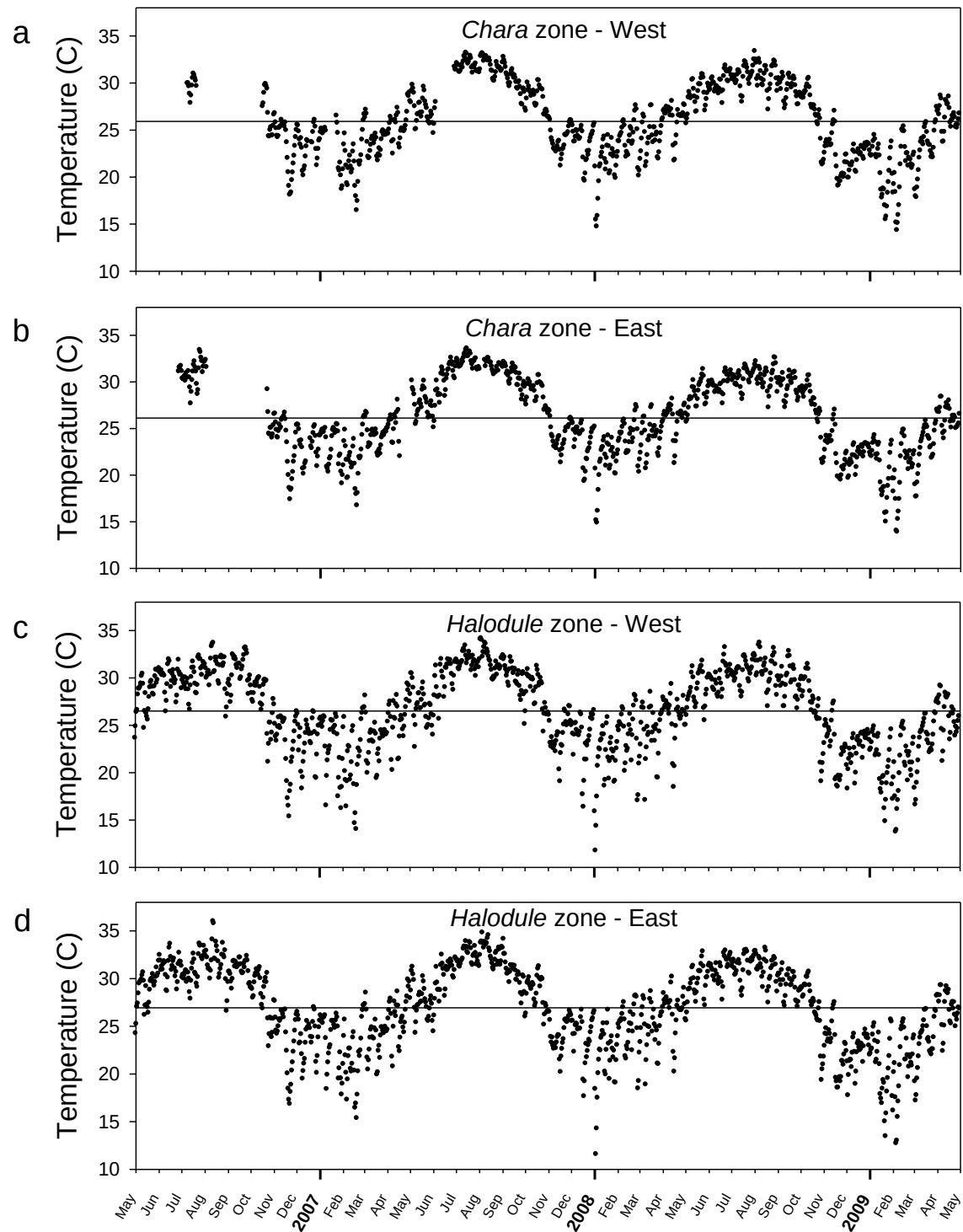


Figure 3.3 Water temperature time series from datasondes deployed in *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d). Horizontal reference lines designate the mean.

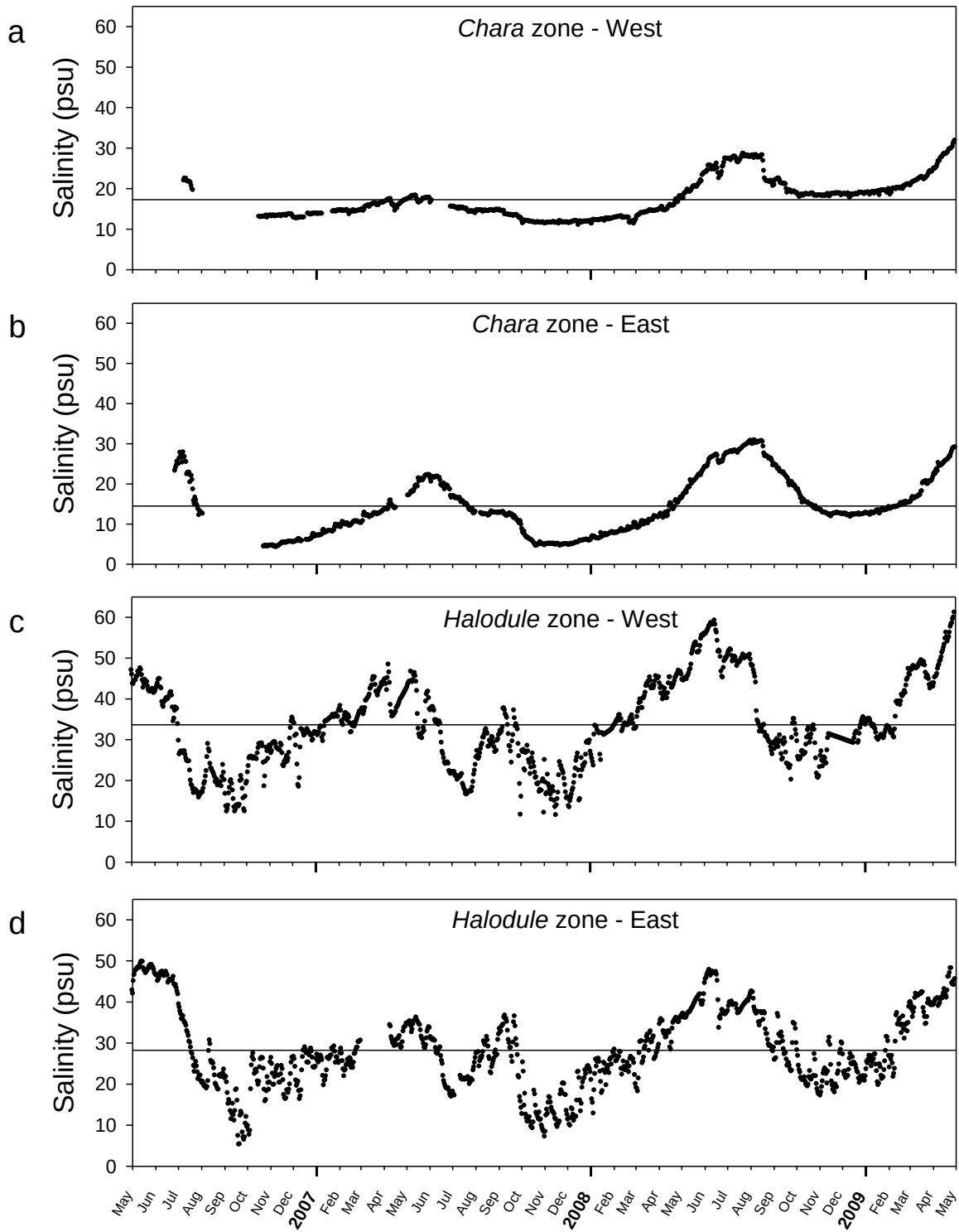


Figure 3.4 Salinity time series from datasondes deployed in *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d). Horizontal reference lines designate the mean.

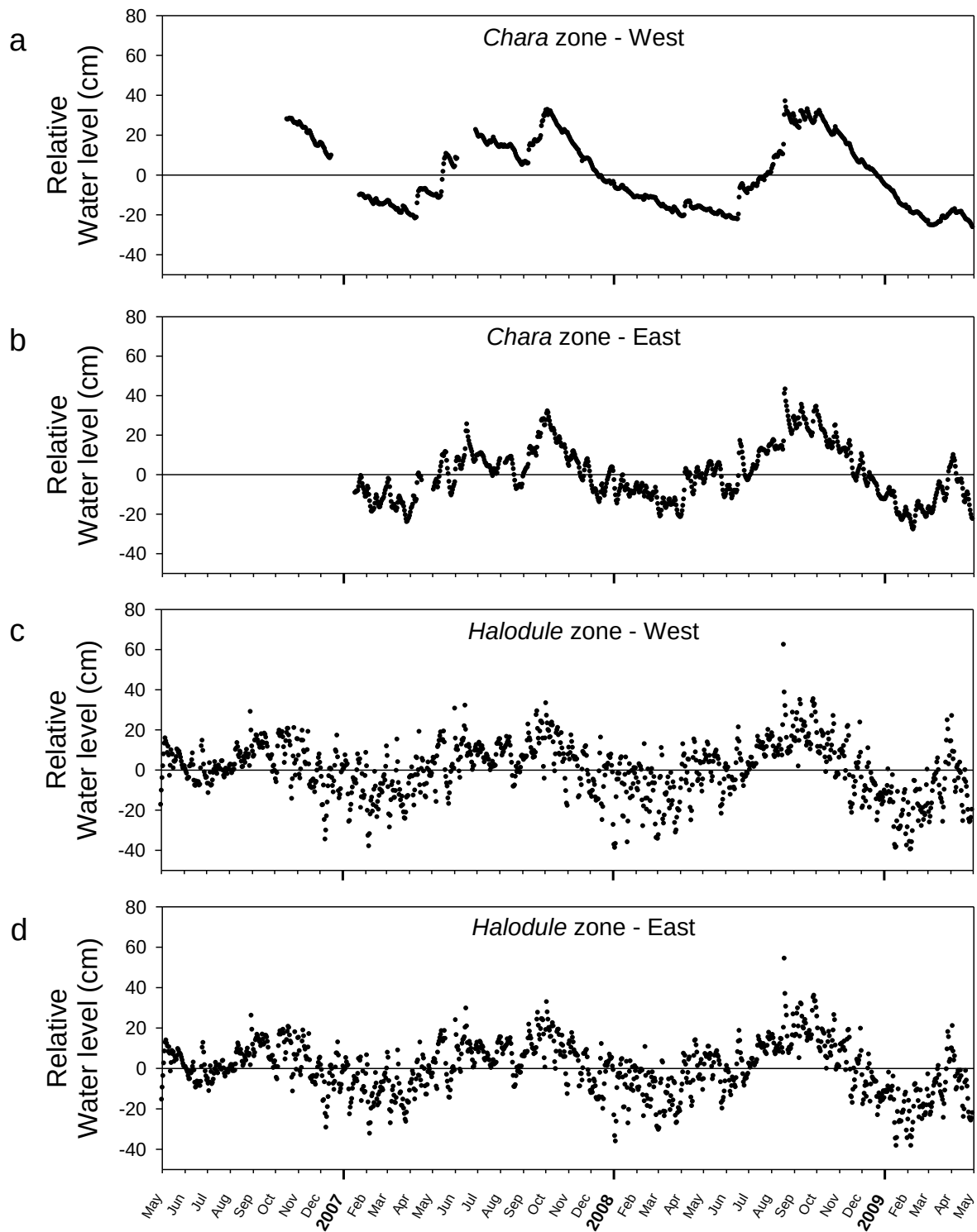


Figure 3.5 Water level time series, as differences from mean, from datasondes deployed in *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d). Horizontal reference lines designate the mean.

Lake and West Lake ranged from 4.1 psu to 30.8 psu, and 10.9 psu to 31.7 psu, respectively (Fig. 3.4 a-d).

Seasonal water level changes at the four datasonde monitored sites were similar in timing but differed in magnitude (Fig. 3.5 a-d). Differences in mean water depth were evident between wet and dry seasons (Table 3.3). Minimum water levels were observed during the latter half of the dry season (February – April) while maximum levels were observed during the middle of the wet season (August) (Fig. 3.5 a-d). Seasonal and shorter period (days) water level changes were greater in Terrapin Bay and Garfield Bight (overall water level ranges = 92.6 cm and 102.0 cm, respectively) than that in Seven Palm Lake and West Lake (overall water level ranges = 71.0 cm and 63.2 cm, respectively) (Fig. 3.5 a-d).

Nutrients and phytoplankton abundance

TN, TP and chl *a* were approximately 2, 3, and 7 times higher ($t = 9.7, 15.4, \text{ and } 13.9$, respectively, all $P \leq 0.001$, t-test), in the West sub-estuary than in the East sub-estuary (Figs. 3.6 a-d to 3.8 a-d). Mean TN, TP and Chl *a* concentrations for the whole West sub-estuary (sites 28, 30, 35, and 40) were $107 \pm 5 \mu\text{M}$, $2.57 \pm 0.1 \mu\text{M}$, and $21.6 \pm 1.3 \mu\text{g L}^{-1}$, respectively, while that for the whole East sub-estuary (sites 2, 8, 13, and 17) were $54 \pm 2 \mu\text{M}$, $0.75 \pm .05 \mu\text{M}$, and $3.1 \pm 0.3 \mu\text{g L}^{-1}$. Mean TN/TP ratios indicated phosphorus (P)-limiting conditions in the water column throughout, ranging from 37 to 44 at the four sites in the West sub-estuary to 65 to 85 at those sites in the East sub-estuary (see Chapter 2). A significant positive relationship between chl *a* and TP also indicated P-limitation (see Chapter 2 for statistical analysis).

With the exception of TN in *Halodule* zone – West, there were no differences in TN, TP, or chl *a* between wet and dry seasons (Table 3.2)., TN in *Chara* zone - West (sites 28, 30, 35) temporally ranged from $44 \mu\text{M}$ at site 28 to $315 \mu\text{M}$ at site 30 in August 2008 and October 2008, respectively (Fig. 3.6a), while TN in *Chara* zone – East (sites 2, 8, 13) temporally ranged from $33 \mu\text{M}$ at site 2 to $99 \mu\text{M}$ at site 8, in May 2007 and September 2008, respectively (Fig. 3.6b). In *Halodule* zone - West (site 40), TN temporally ranged from $29 \mu\text{M}$ to $135 \mu\text{M}$, in July 2008 and October 2008, respectively (Fig. 3.6c), while TN in *Halodule* zone - East (site 17) temporally ranged from $32 \mu\text{M}$ to $94 \mu\text{M}$, in August 2008 and June 2008, respectively (Fig. 3.6d). TN in

Table 3.3 Comparison of wet season versus dry season water transparencies (Secchi depths), vertical attenuation coefficients for downwards irradiance of photosynthetically active radiation (K_d), water depths, light transmission estimates and solar PAR insulations for *Chara*- and *Halodule*-dominant zones in the Seven Palm and West Lake drainage systems. Bottom insulations are the products of percent light at bottom estimates and surface PAR insolation. **Bold** indicates statistically significant (t-test, $P \leq 0.002$) differences in mean water depth between wet and dry seasons; se = standard error of the mean. Seasonal differences in Secchi depths and calculated light transmission estimates were not statistically tested due to truncated nature of transparency data when Secchi depths exceed water depths.

		Secchi depth, (Z_{SD} , median) (cm)	K_d	Water depth (Z, mean) (cm)	Percent light at bottom (%)	Surface insolation (PAR, mean $\pm$ se) (MJ m ⁻² season ⁻¹)	Bottom insolation (PAR, mean) (MJ m ⁻² season ⁻¹)
<i>Chara</i> zone - West	Wet	30	4.8	99	0.9	1377 $\pm$ 39	12
	Dry	40	3.6	84	4.9	1170 $\pm$ 17	57
<i>Chara</i> zone - East	Wet	> bottom depth	<1.4	128	>23.7	1377 $\pm$ 39	>326
	Dry	> bottom depth	<1.4	112	>23.7	1170 $\pm$ 17	>277
<i>Halodule</i> zone - East	Wet	> bottom depth	<1.4	84	>23.7	1377 $\pm$ 39	>326
	Dry	> bottom depth	<1.4	68	>23.7	1170 $\pm$ 17	>277
<i>Halodule</i> zone - West	Wet	> bottom depth	<1.4	49	>23.7	1377 $\pm$ 39	>326
	Dry	> bottom depth	<1.4	32	>23.7	1170 $\pm$ 17	>277

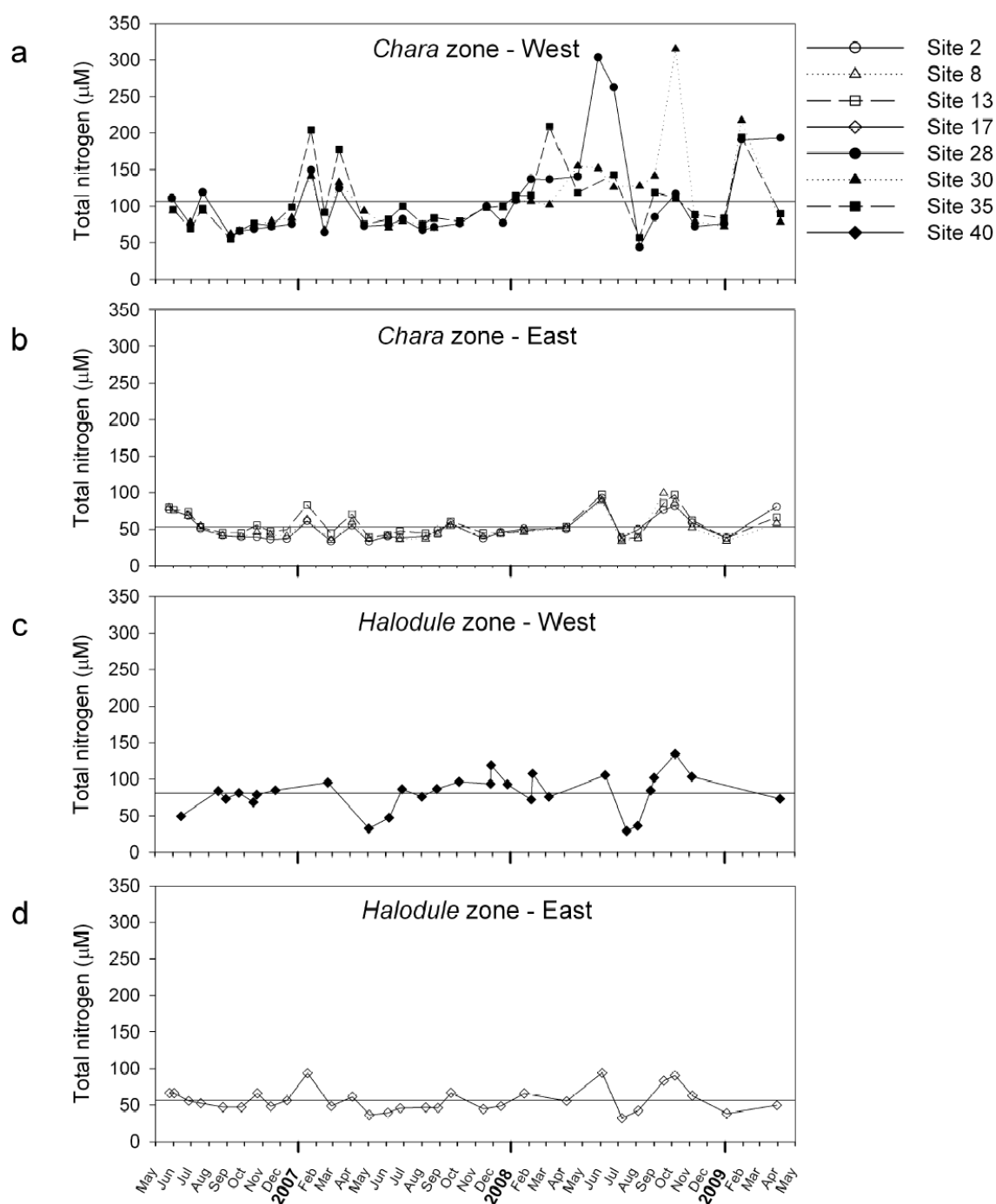


Figure 3.6 Water column total nitrogen concentration time series from sites in *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d) sub-estuary zones. Horizontal reference lines designate the grand means calculated from all measurements in each sub-estuary zone.

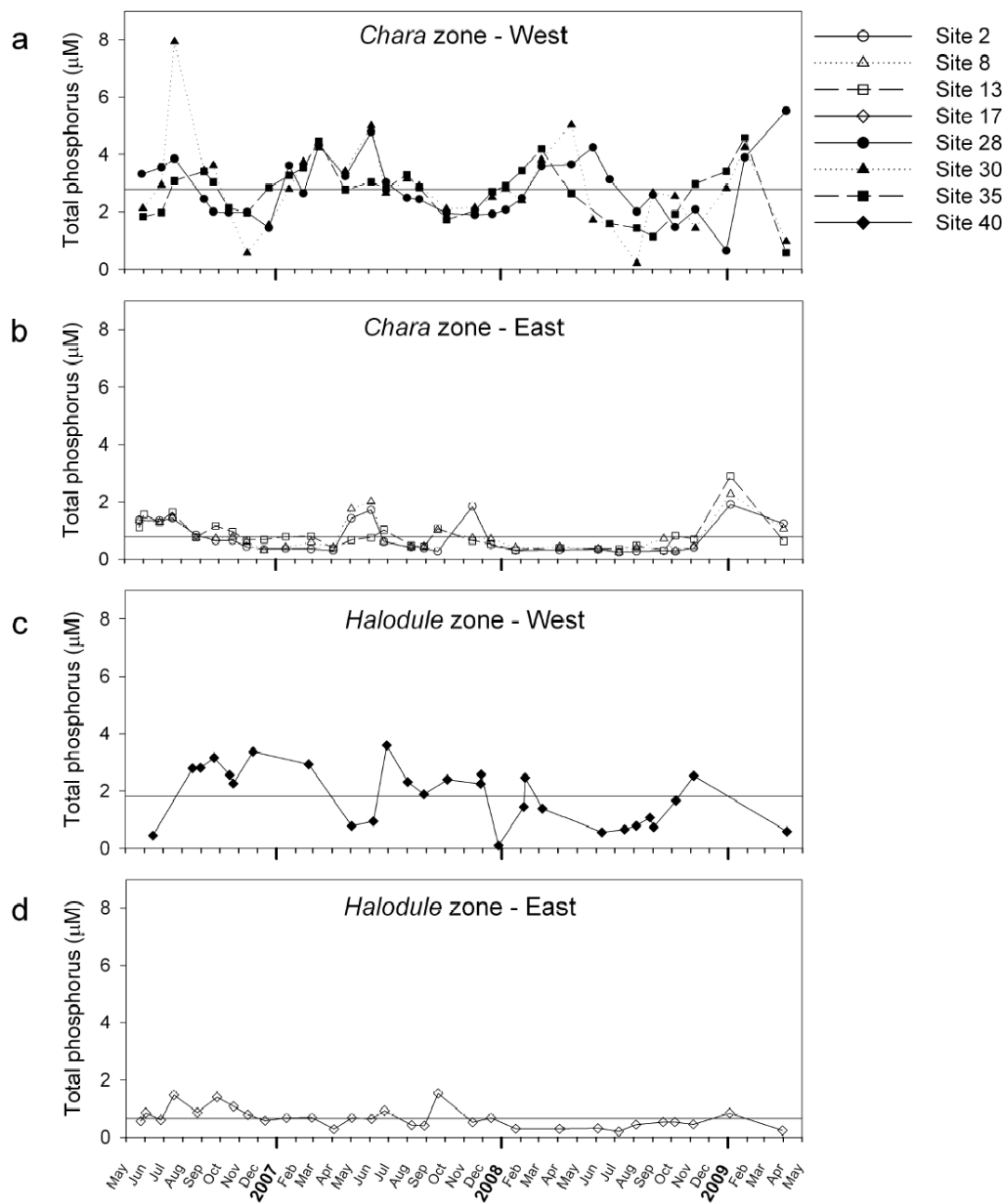


Figure 3.7 Water column total phosphorus concentration time series from sites in *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d) sub-estuary zones. Horizontal reference lines designate the grand means calculated from all measurements in each sub-estuary zone.

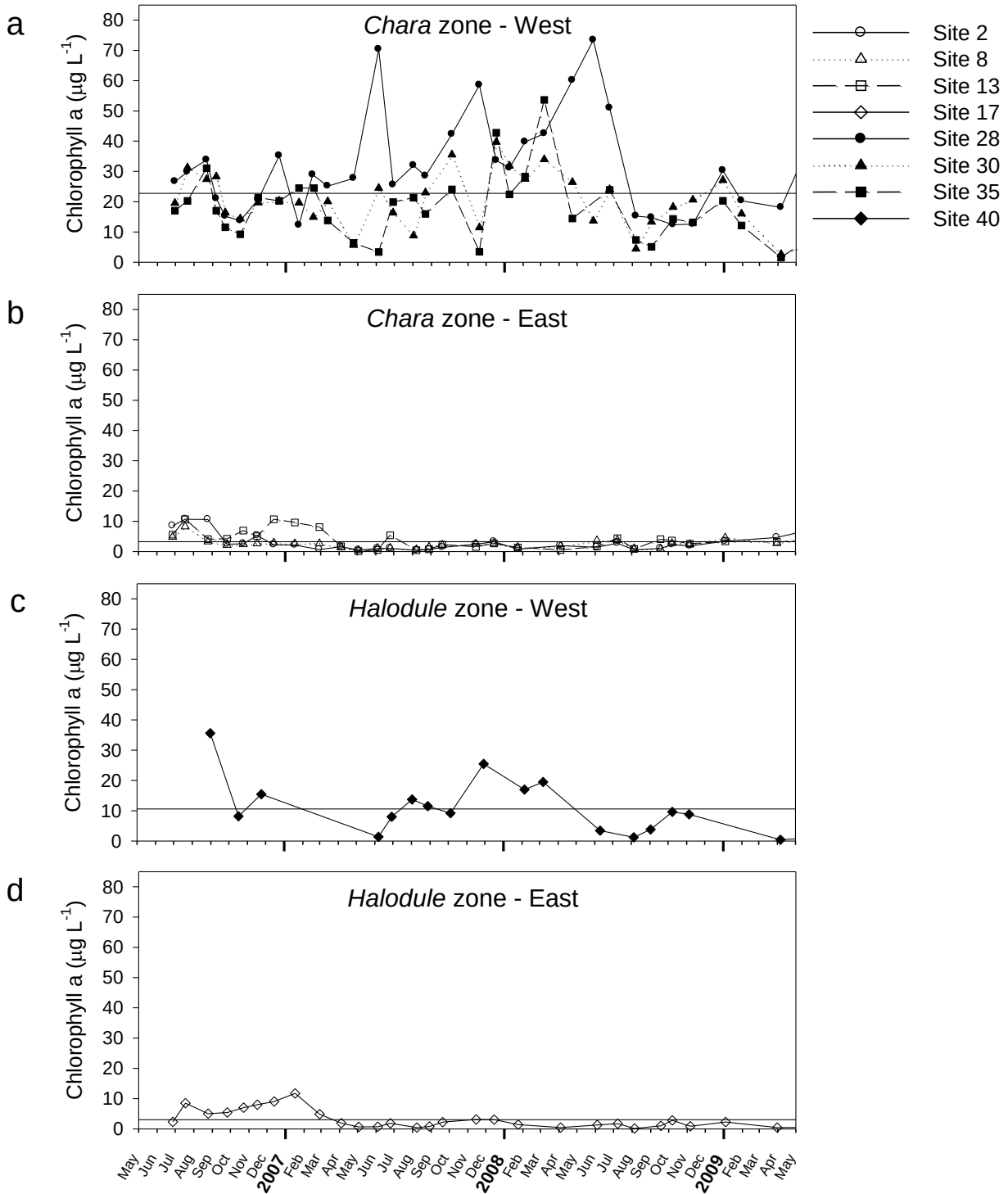


Figure 3.8 Water column chlorophyll *a* concentration time series from sites in *Chara* zone – West (a), *Chara* zone – East (b), *Halodule* zone – West (c), and *Halodule* zone – East (d) sub-estuary zones. Horizontal reference lines designate the grand means calculated from all measurements in each sub-estuary zone.

Halodule zone - West was approximately 20% higher during the dry season ($91 \pm 2 \mu\text{M}$) than during the wet season ($75 \pm 4 \mu\text{M}$) (Table 3.2).

TP in *Chara* zone – West ranged from $0.21 \mu\text{M}$ to $7.93 \mu\text{M}$, at site 30 in August 2008 and August 2006, respectively (Fig. 3.7a), while TP in *Chara* zone - East temporally ranged from $0.24 \mu\text{M}$ at sites 2 and 8 in August 2008 to $2.90 \mu\text{M}$ at site 13 in January 2009 (Fig. 3.7b). In *Halodule* zone - West, TP temporally ranged from $0.09 \mu\text{M}$ to $3.59 \mu\text{M}$, in December 2007 and June 2007, respectively (Fig. 3.7c), while TP in *Halodule* zone – East temporally ranged from $0.20 \mu\text{M}$ to $1.54 \mu\text{M}$, in August 2008 and September 2007, respectively (Fig. 3.7d).

In *Chara* zone - West, Chl *a* temporally ranged from $1.52 \mu\text{g L}^{-1}$ at site 35 to $73.41 \mu\text{g L}^{-1}$ at site 28, in May 2008 and September 2008, respectively (Fig. 3.8a), while in *Chara* zone - East Chl *a* temporally ranged from $0.13 \mu\text{g L}^{-1}$ at site 13 in May 2007 to $10.66 \mu\text{g L}^{-1}$ at sites 2 and 13 in July 2006 (Fig. 3.8b). Chl *a* in *Halodule* zone - West temporally ranged from $0.42 \mu\text{g L}^{-1}$ to $35.62 \mu\text{g L}^{-1}$, in April 2009 and August 2006, respectively (Fig. 3.8c), while in *Halodule* zone - East Chl *a* temporally ranged from $0.15 \mu\text{g L}^{-1}$ to $11.72 \mu\text{g L}^{-1}$, in August 2008 and November 2007, respectively (Fig. 3.8d).

Water transparency (Secchi depth, Z_{SD}) exceeded water depth at most sites and times in *Chara* zone – East, *Halodule* zone – East, and *Halodule* zone – West, indicating sufficient light availability ($> 23.7\%$ light penetration to the bottom) for SAV growth. Only in *Chara* zone – West were median Secchi depths less than water depth most of the time. PAR insolation at the water surface was seasonal with maximum insolation occurring during the end of the dry season in April or May and minimum levels during the start of the dry season in December or January (Fig. 3.9). Light penetration to the sediment surface in the *Chara* zone – West during the wet season was estimated to be less than 1%, while during the dry season, light penetration was approximately 5% (Table 3.3). Light availability (PAR bottom insolation) was approximately 5 times greater in the *Chara* zone – East, *Halodule* zone – East, and *Halodule* zone – West than in the *Chara* zone – West (Table 3.3). Light availability was approximately 5 times greater during the dry season than during the wet season in the *Chara* zone – West (Table 3.3).

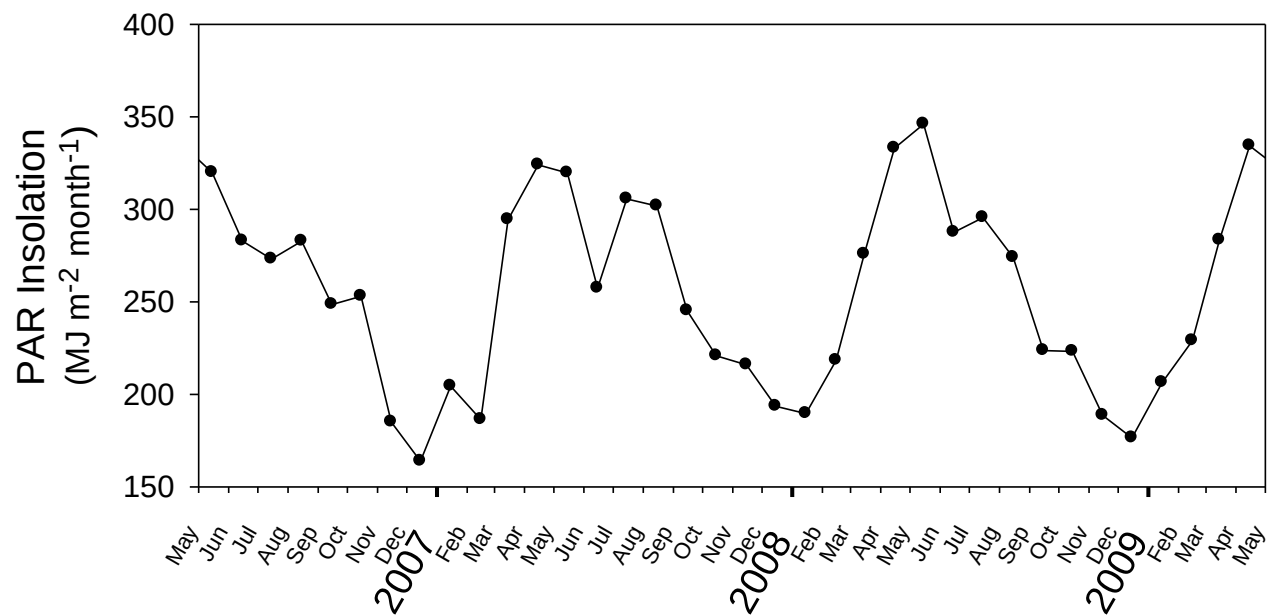


Figure 3.9 Total monthly PAR solar insolation from Joe Bay meteorological station.

Correlations between SAV cover and temperature, salinity and depth at various antecedent time periods and at the time of sampling were evident (Table 3.4). Significant correlations ($P \leq 0.05$) were limited to *Chara* cover in *Chara* zone – East and *Halodule* cover in *Halodule* zone – West. *Chara* cover in *Chara* zone – East was negatively correlated with salinity at 60-, 90-, and 180-day time periods and with time of sampling water depth. *Halodule* cover in *Halodule* zone – West was positively correlated with water temperature at 30- and 60-day antecedent time periods. (Table 3.4)

Discussion

Previous descriptions of temporal dynamics of *Chara hornemannii* communities and the presumed predominant importance of the salinity driver (Morrison & Bean, 1997; Richards & Fourqurean, 2000) were incomplete. This study demonstrated how water clarity may determine the importance of the salinity driver in these communities. The salinity driver appeared to be more important when light availability is higher. Wet versus dry seasonality of SAV cover was only evident in the *Chara* zone - West where almost 4 to 26 times greater light availability was associated with almost 2 times greater *Chara* cover during the dry season (November through April). Previous spatial analyses indicated that 75% of the sites characterized by *Chara* dominance in both *Chara* zones (West and East) exhibited median light at the lake bottom exceeding 5% of surface light with all unvegetated sites below this level of light availability (Chapter 2). As median light availability in *Chara* zone – West ranged from <1% during the wet season to approximately 5% during the dry season, the *Chara* communities there were light-limited and close to disappearance under those light conditions. The low levels of light availability in *Chara* zone – West were due to high phytoplankton abundances fueled by greater availability of phosphorus in the West Lake sub-estuary system (Chapter 2). Sufficient light availability, as indicated by median Secchi depths exceeding water depths further downstream in *Halodule* zone – West, were likely due to shallower water depths despite high phytoplankton abundance in the West Lake sub-estuary system. The lack of seasonality in phytoplankton abundances may suggest that the shallower water depths during the dry seasons were responsible for the greater light penetrations in the *Chara* zone – West, but the lack of any correlation of *Chara* cover with any antecedent period mean of water depth suggests the possible importance of other unmeasured components of light attenuation such as tripton or chromophoric

Table 3.4 Correlation matrix of predominant SAV coverage (*Chara* or *Halodule*) versus antecedent period means of temperature, salinity, and water depth. r = Pearson correlation coefficient. P = 2-tailed statistical significance. n = 12, 11, 11, 10, and 9 for the 0, 30, 60, 90, and 180 day antecedent periods, respectively. **Bold** indicates significant correlation at $P \leq 0.05$.

			Antecedent period (days)				
			0	30	60	90	180
<i>Chara</i> cover - West versus:							
Temperature	r		-.52	-.52	-.49	-.38	-.12
	P		.08	.11	.13	.29	.75
Salinity	r		0	.01	-.15	-.29	-.10
	P		.99	.97	.67	.41	.80
Depth	r		0	-.05	-.11	.01	.21
	P		.99	.89	.76	.99	.60
<i>Chara</i> cover - East versus:							
Temperature	r		-.38	-.43	-.38	-.33	.04
	P		.22	.18	.25	.36	.92
Salinity	r		-.47	-.58	-.73	-.77	-.88
	P		.13	.06	.01	.01	<.01
Depth	r		-.79	-.57	-.40	-.39	-.07
	P		<.01	.07	.23	.27	.85
<i>Halodule</i> cover - West versus:							
Temperature	r		.36	.63	.66	.49	.06
	P		.27	.05	.04	.18	.89
Salinity	r		-.21	-.31	-.38	-.18	-.13
	P		.54	.39	.28	.64	.76
Depth	r		-.08	.10	.01	.09	-.16
	P		.83	.79	.99	.83	.70
<i>Halodule</i> cover - East versus:							
Temperature	r		.09	.45	.55	.58	.39
	P		.79	.16	.08	.08	.30
Salinity	r		-.57	-.51	-.46	-.33	-.20
	P		.06	.11	.15	.36	.61
Depth	r		-.08	.34	.43	.43	.27
	P		.81	.31	.19	.21	.48

dissolved organic matter (CDOM) rather than the water itself. CDOM may be particularly important because of its seasonally high concentration from Everglades freshwater runoff during the rainy season (Clark et al., 2004). In contrast, tripton levels are highest during the dry season when wind speeds are highest (Boyer et al., 1999). Lower water temperatures were also associated with greater *Chara* cover in *Chara* zone – West during the dry season, but seasonal water temperatures were similar across all vegetation zones, suggesting that higher water temperatures did not suppress *Chara* growth.

Chara cover in *Chara* zone - East was inversely correlated with 60, 90, and 180-day antecedent period means of salinity, suggesting that these communities may grow faster during periods of lower salinity. *Chara* cover seasonality was not evident in this zone, but cover decreased and remained lower than the long-term mean during the 2008 wet season and the following wet season (Fig. 3b). This decline in cover is coincident with elevated salinities mostly above the long-term mean with maximum salinities approaching 30 psu during the same period (Fig. 5b). This decline may reflect the exceeding of a salinity maximum threshold for *Chara hornemannii* growth. Spatial analysis of the *Chara* and *Halodule* communities indicated that these community groups were organized along the salinity gradient with the dividing line between the two communities at approximately 25 psu mean annual salinity (Chapter 2). This 25 psu upper salinity limit is similar to that observed for *Chara aspera* in the Baltic Sea and along the Swedish coast (Blindow et al., 2003).

The negative correlation of sampling time water depth with *Chara* cover in *Chara* zone – East may suggest the importance of temporal changes in light availability in this zone also, despite light availability being at least 4 to 26 times greater in *Chara* zone – East than that in *Chara* zone – West and the inability of Secchi depth measurements to measure light availability differences when visibility exceeds water depth. With lower phytoplankton abundances, greater water depths, and Secchi depths exceeding water depths most of the time in *Chara* zone - East, the important light attenuation components influencing temporal variation in *Chara* cover were more likely to be water or CDOM rather than phytoplankton abundance or turbidity.

Inspection of the *Halodule* cover time series in both West and East zones (Figs. 3C and D) shows cover generally rising during the wet season in summer and fall and decreasing during the dry season in the winter. However, *Halodule* cover did not exhibit wet versus dry season

differences because a seasonal pattern appears to be masked by interannual variability. *Halodule* cover in the West zone exhibited positive correlations with water temperature at 30 and 60-day antecedent mean periods suggesting greater growth with higher temperatures, but this relationship was not as strong in the East zone suggesting the influence of other unmeasured factors.

Successful restoration of the mangrove “lakes” estuaries to a clear water state with higher SAV coverage that persists throughout the year requires not only the knowledge of identifying the water quality factors associated with increased SAV coverage, but also an understanding that restoration towards a clear-water state may require greater changes in reversing water quality conditions than those changes that initiated SAV loss. These mangrove “lakes” may function similarly to shallow freshwater lakes that alternate between a clear-water SAV-dominated stable state and a turbid phytoplankton-dominated stable state (Scheffer, 2004). The clear-water SAV-dominated state represents the historical conditions of the Everglades mangrove lakes and to a lesser extent the ecosystem observed in *Chara* zone - East, while the turbid phytoplankton-dominated state is represented by the observed conditions in *Chara* zone - West. Because the historical loss of SAV cover was associated with a 20-30 psu increase in salinity (McIvor et al. 1994), it might be expected that a managed decrease in salinity of similar magnitude would restore SAV to its previous abundances, but our analyses indicated that SAV cover in the degraded *Chara* zone -West may currently be more responsive to seasonal changes in light availability than changes in salinity. Maintaining SAV coverage in *Chara* zone – East with lower salinities, and increasing SAV coverage in *Chara* zone – West by increasing light availability may both be achieved by increasing freshwater flow into the region. The mangrove estuaries on the north shore of Florida Bay are “upside-down”, meaning that the coastal ocean (i.e., Gulf of Mexico), as opposed to the upstream oligotrophic Everglades, is the source of limiting phosphorus to these systems (Davis et al., 2005). Increasing freshwater delivery from the Everglades will displace the relatively P-rich marine water, decreasing P concentrations and phytoplankton abundance, and therefore increasing light availability, in addition to decreasing salinity. Increased freshwater delivery was successful in the restoration of Lake Veluwe, The Netherlands, by reducing P loading and phytoplankton abundance and increasing water transparency (Hosper, 1985). If the SAV-dominated regime and the phytoplankton-dominated regime are separate stable states defined by hysteresis (Scheffer et al., 1993), water column P

concentrations may need to be decreased to levels much lower than that prior to the start of phytoplankton domination because the water clearing effect of SAV is no longer present. Even if it is possible to greatly reduce P loading into these systems, restoration of the SAV communities may be problematic due to site-specific effects of local watershed geography.

Differences in watershed geography between the East and West sub-estuaries likely enabled different ecosystem responses to hydrologic changes (reduction in freshwater delivery and sea-level rise) in each system. Following the reduction of freshwater delivery into these systems and the subsequent increase in salinities since pre-drainage times (McIvor et al. 1994), the western sub-estuary changed from a SAV-dominated clear water state to a turbid phytoplankton state while the adjacent eastern sub-estuary remained in the SAV-dominated clear water state. The reduction in freshwater flow permitted relatively nutrient-rich marine water to enter both systems, yet persistent phytoplankton blooms only developed in the adjacent western system. The mangrove “lakes” in the western system are connected to each other and to Florida Bay over a distance of 7.9 km via long, tenuous, mangrove creeks (Mangrove Creek and Alligator Creek, 3.1 km total length) with small, shallow (< 50 cm) ponds within them (Fig. 1) that effectively separate the lakes and limit water exchange. In contrast, the “lakes” of the eastern sub-estuary are more directly connected with each other through shorter and wider creeks (0.7 km total length) and to central Florida Bay over a shorter distance of 5.9 km. These differences in local geography allow greater flushing and lower water residence times in the eastern sub-estuary, thereby constraining the development of persistent algal blooms (Søballe & Kimmel, 1987). The local geographies are “system-specific filter attributes” (Cloern, 2001) that modulate the response of the adjacent sub-estuaries to the change in freshwater delivery. The longer water residence times in the western sub-estuary will also hinder restoration efforts to flush the excess phosphorus retained in the system.

This study has described a lack of consistent seasonal patterns of SAV cover in subtropical mangrove estuaries in Florida Bay and demonstrated the differential importance of water quality parameters in structuring temporal variation in adjacent sub-estuaries distinguished by alternate regimes of phytoplankton and SAV dominance. The identification of SAV temporal patterns, the associated water quality conditions, and system-specific geography attributes will guide ecosystem restoration efforts in the Everglades and Florida Bay.

Chapter Four – Conclusions

Spatial and temporal variability of submerged aquatic vegetation (SAV) has been described and both spatial and temporal relationships between SAV and water quality have been identified. These descriptions and identifications will assist resource managers in establishing Everglades restoration targets in the Florida Bay mangrove estuaries. Statistical modeling tools have been also been developed that can be used to predict ecosystem change from proposed management actions that are aimed at restoring SAV communities to historically greater abundances.

Three distinct SAV communities (i.e., *Chara hornemannii* alga group, *Halodule wrightii* seagrass group, and a Low SAV coverage group) were identified along the Everglades - Florida Bay ecotone. These communities were differentiated along salinity and nutrient availability gradients and were structured spatially by annual mean salinity, light availability, and sediment depth to bedrock. *Chara* communities were located in the lower salinity (mean annual salinity < 25 psu) upstream “lakes”, while *Halodule* communities were located in the more marine coastal embayments. SAV cover, particularly in the *Chara* communities, varied according to water quality differences observed between two adjacent sub-estuaries (i.e., West Lake to Garfield Bight sub-estuary and the Seven Palm Lake to Terrapin Bay sub-estuary). These sub-estuaries were characterized by alternate states of water quality and SAV abundance. The West Lake sub-estuary was turbid, dominated by persistent algal blooms and high nutrient concentrations, and suffered from low SAV abundance. In contrast, the Seven Palm Lake sub-estuary was characterized by clear water, higher SAV cover that persisted throughout the year, and low nutrient and phytoplankton concentrations. The SAV community groups were related to water quality using a discriminant function model that predicted the type of plant community at a given site from salinity, light availability and sediment depth to bedrock. Mean salinity alone was able to correctly classify 78% of the sites and reliably separated the *Chara* group from the *Halodule* group. The addition of light availability and sediment depth to bedrock increased model accuracy to 90% and further distinguished the *Chara* group from the *Halodule* group. Light availability was uniquely valuable in separating the *Chara* group from the Low SAV coverage group. Regression analyses identified significant relationships between phosphorus concentration, phytoplankton abundance and light availability, and suggest that a decline in water transparency,

associated with increasing salinity, may have also contributed to the historical decline of *Chara* communities in the region.

Repeatable seasonal patterns were not evident in most SAV communities with the exception of light-limited brackish alga *Chara hornemannii* Wallman communities that experienced seasonal changes in light availability in a turbid environment. In contrast, *Chara* cover in clear water SAV-dominated environments was temporally negatively correlated with salinity and water depth. These observations suggest that water clarity may determine the importance of the salinity driver in these *Chara* communities. Cover of the more marine seagrass *Halodule wrightii* exhibited some temporal variation that was positively correlated with water temperature. This study demonstrated the differential importance of water quality and environmental drivers in estuaries distinguished by alternate regimes of phytoplankton and SAV dominance, and explains how differences in local estuarine geography may filter the response of SAV communities to environmental stressors.

The clear relationships between P availability, phytoplankton abundance and light availability indicate that historic SAV communities will not be restored in the freshwater end of these estuarine systems unless water column TP concentrations are reduced, especially in the West Lake system. Though increased freshwater flow will decrease salinity and may also decrease P loading, the re-establishment of flourishing *Chara* communities in the estuaries of the southern Everglades may be inhibited by the long-term retention of P in P-limited carbonate ecosystems (Herbert and Fourqurean 2008). Because 75% of the sites characterized by *Chara* dominance exhibited median light at bottom exceeding 5% of surface light, and all sites characterized with Low SAV coverage were below this level of light availability, 5% light at bottom is a reasonable estimate for the maintenance of *Chara* communities. Using a light availability target of 5% of surface light at bottom and the regression equations relating light availability to chl *a*, and chl *a* to TP, we estimate that annual mean water column TP concentrations should be maintained at or below $2.2 \pm 1.1 \mu\text{M}$ (mean $\pm$ 95% confidence interval) to limit phytoplankton abundance and allow for the shift back to the *Chara*-dominated regime in the upstream "lakes". However, if the *Chara*-dominated and the phytoplankton-dominated regimes are distinct stable states characterized by hysteresis (Scheffer et al. 1993), a much lower TP concentration may be required.

Restoring higher levels of freshwater flow to the mangrove estuaries of Florida Bay may promote the spatial and temporal expansion of SAV communities if the quality of the freshwater, as indicated by low nutrient and phytoplankton content, is sufficient. Increased freshwater flow will decrease salinities and possibly decrease water column nutrient concentrations by displacing relatively phosphorus rich marine water. Decreased nutrients should increase light availability to benthic macrophytes by alleviating persistent algal blooms that are currently affecting much of the mangrove lake estuaries.

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