Differing temporal patterns of *Chara hornemannii* cover correlate to alternate regimes of phytoplankton and submerged aquatic-vegetation dominance

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Abstract. Cover of the alga *Chara hornemannii* Wallman and water-quality parameters were measured over a 3-year period in adjacent mangrove subestuaries in Florida Bay, so as to describe temporal variability and infer relationships between *Chara* cover and water quality that will assist resource managers to restore *Chara* abundance to historically higher levels. A seasonal pattern of *Chara* cover was observed in the Alligator Creek subestuary that coincided with seasonal changes in water transparency in a relatively high-nutrient and phytoplankton environment. In contrast, higher *Chara* cover in the relatively low-nutrient and phytoplankton-abundance McCormick Creek subestuary did not exhibit a repeatable seasonal pattern, but was temporally negatively correlated with salinity and water depth. These observations suggest that water transparency may determine the importance of the salinity driver in these *Chara* communities. The present study demonstrates the differential importance of water quality and environmental drivers in estuaries distinguished by alternate regimes of phytoplankton and submerged aquatic-vegetation (SAV) dominance, and explains how differences in local estuarine geography may filter the response of SAV communities to environmental stressors.

Additional keywords: light, nutrients, salinity, SAV, water quality.

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Introduction

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 submerged aquatic vegetation (SAV) abundance that may be site-specific and non-seasonal (Cloern and Jassby 2008). *Chara* communities located within the mangrove estuaries and brackish 'lakes' located along the boundary between the freshwater Florida Everglades and salt-water Florida Bay exhibit signs of eutrophication (i.e. loss of cover, persistent algal blooms) (Frankovich *et al.* 2011) coincident with a mean sea-level rise of 2.2 mm year^{-1} over the past century (Maul and Martin 1993). Anecdotal reports (Tabb *et al.* 1962; Craighead 1971; Simmons and Ogden 1998) have indicated that historical *Chara* abundances (pre-1950s) were much higher than those observed recently (Morrison and Bean 1997). Large *Chara* beds once supported large populations of wading birds and wintering waterfowl within these areas (Tabb *et al.*

1962; Simmons and 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 mangrove zone (Light and Dineen 1994). Mean salinities in the mangrove zone 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 cover of the dominant alga *C. hornemannii* 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 and 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 *Chara* and suggested that a decline in water transparency, concurrent with increasing salinity, may have also contributed to the historical decline (Frankovich *et al.* 2011). The brackish estuaries along the south-western shores of
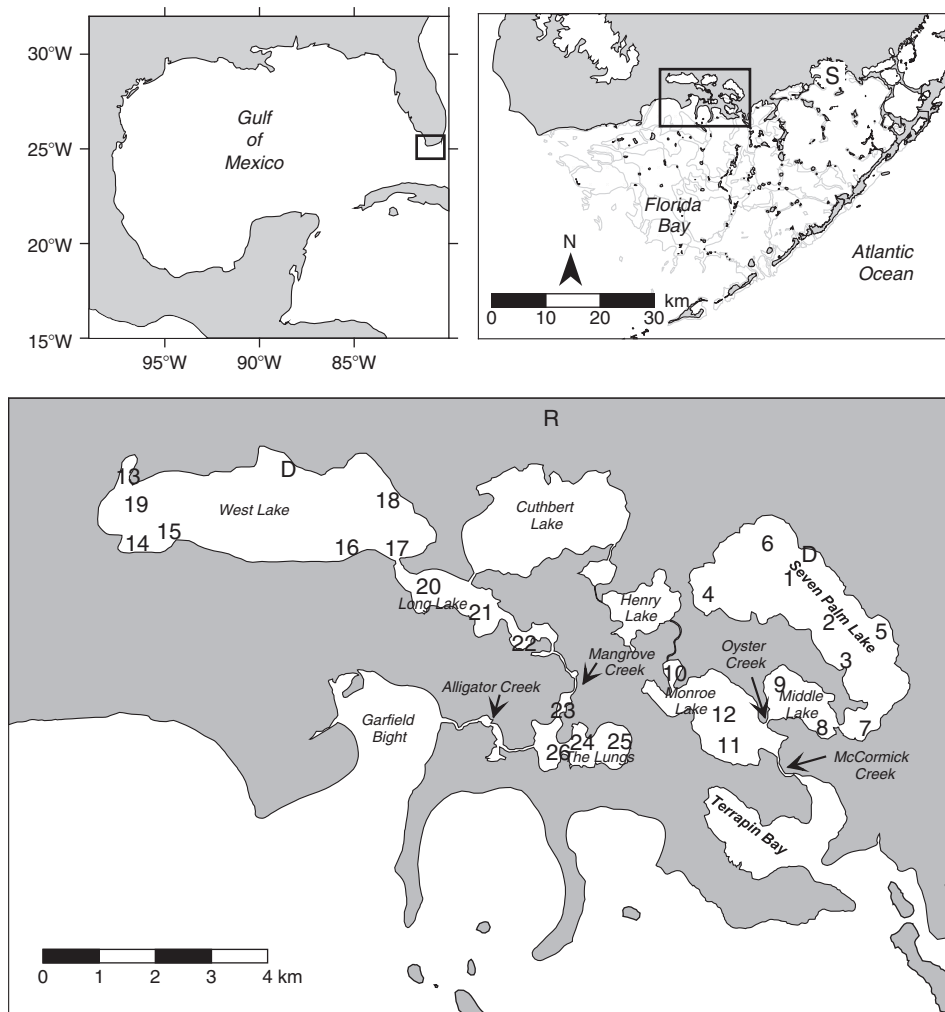
Fig. 1. Location map of study sites. S = Joe Bay solar insolation site. D = datasonde location. R = North Cuthbert Lake (NCL) rainfall-estimation location.

the Baltic Sea have experienced similar declines in SAV abundance, coincident with a similar deterioration of water quality over the same time period (Munkes 2005).

The objectives of the present study were to describe spatial and temporal variability and to identify seasonal patterns, specifically wet season *versus* dry season differences, in *Chara* cover and water-quality parameters, including water transparency, in two of the mangrove subestuaries of Florida Bay. We also compare and contrast the local geographies between the two adjacent subestuaries, to evaluate whether these inherent system attributes may contribute to site-specific differences in SAV cover and water quality and to evaluate whether geographical differences may structure the ecosystem responses to reduced freshwater deliveries in both systems.

Materials and methods

Study location

We conducted our investigation in shallow (<1.8 m maximum depth) estuarine mangrove 'lakes' that drain portions of the southern Everglades (Fig. 1). Study sites were located in two

adjacent subestuaries located along the northern shore of Florida Bay (Fig. 1). The Alligator Creek subestuary includes West Lake, Long Lake and The Lungs. The McCormick Creek subestuary, located adjacent to the east, includes Seven Palm Lake, Middle Lake and Monroe Lake. The watershed that drains into these flow paths lies between the two main conduits for Everglades drainage, namely, Shark Slough to the north-west and Taylor Slough to the north-east. 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 characterised by distinct wet (May through October) and dry (November through April) seasons (Fig. 2). 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).

Field sampling

SAV abundance and water-quality parameters were measured at 26 sites (Fig. 1) from May 2006 through April 2009.
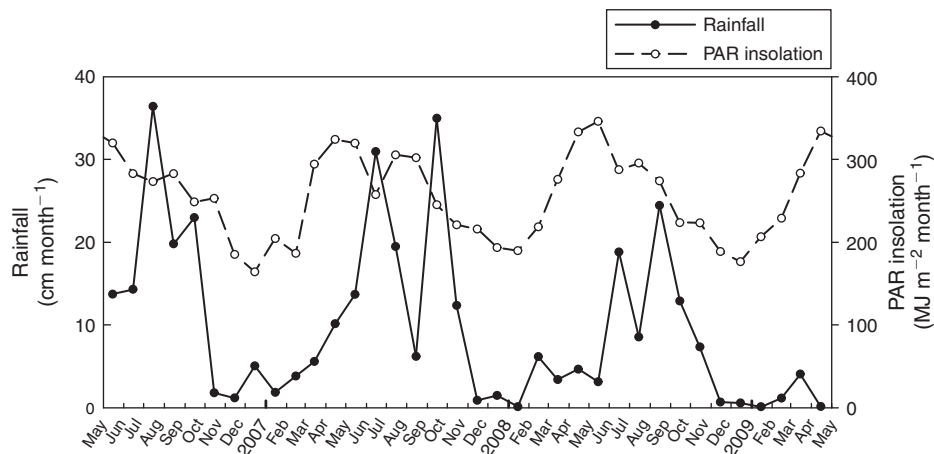
Fig. 2. Monthly rainfall and photosynthetically active radiation (PAR) from the nearest meteorological stations. Monthly rainfall amounts were summed from 15-min-interval next generation radar (NEXRAD) data from the USA National Weather Service. Data were downloaded from http://sofia.usgs.gov/eden/nexrad.php (accessed 3 June 2010). Total monthly PAR solar radiation was calculated from hourly broadband solar radiation.

SAV monitoring 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). SAV abundance at each site was surveyed by snorkeler at ~3-month intervals over the study period, a total of 12 times. Bottom coverage for each species present at each site was estimated at 15 haphazardly chosen plots located within a 10-m radius of the site location, by using a ¼-m² quadrat subdivided into 20 equal areas by using a string mesh that provided a visual reference to 5% area coverage. Bottom coverage was estimated to the nearest 5%. Sites were located using a GPS.

Spot measurements of salinity (based on the Practical Salinity Scale of 1978), water depth (Z), water temperature and water transparency (Secchi depth, $Z_{s.d.}$) were measured at each site at ~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, Yellow Springs, Ohio, USA). Measurements of water temperature, salinity and water level were also recorded continuously (hourly minimum rate) using YSI model 600 LS datasondes (Yellow Springs, Ohio, USA) at two additional sites in West Lake and Seven Palm Lake (Fig. 1). Daily means were calculated from these data and used in the analyses.

Using the continuous water-temperature, water-level and salinity data collected with datasondes and the spot data collected at each site, daily values of these parameters were reconstructed for each of the 26 vegetated sites. Daily values were modelled as linear combinations of data recorded from the datasonde sites. Time offsets that maximised the correlation coefficients between spot data and datasonde data were applied when autocorrelation was observed. The performance of the model was determined from the root mean squared error (RMSE) comparing measured values (spot site water temperatures, salinities and water depths) and modelled values (see Supplementary Material, available on the web). The reconstructed daily values were used to test for wet- *versus* dry-season

differences in temperature, salinity and water depth, as described in the section Statistical analysis.

Water transparency was measured to the nearest 5 cm with a 20-cm-diameter Secchi disc (Professional Secchi Disc, Ben Meadows Company, Janesville, WI, USA). Underwater light availability to benthic macrophytes, expressed as percentage light at bottom, was estimated from Secchi-depth measurements and the daily water-depth reconstructions by using the approximate relation for the vertical light-attenuation coefficient and Secchi depth, and the Lambert–Beer law, as follows:

$$K_d = 1.44/Z_{s.d.} \text{ (Holmes 1970) and}$$

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

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 ≥23.7%, the maximum possible estimate using Secchi disc measurements and the equations listed above. Estimates of the percentage light at the 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 $K_d = 1.44/Z_{s.d.}$ would overestimate K_d (Kirk 1994).

Hourly integrated broad-band solar insolation data obtained from a meteorological station in Joe Bay (Fig. 1) and were used to estimate the seasonal amounts of light available at the water surface. PAR insolation was estimated from the broadband data by 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 by 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 insolations corrected for reflectance.

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, 12, 19, 21 and 26; see Fig. 1). Sampling was performed at the same times as these sites were sampled for salinity, water depth and water transparency. TN was measured by high-temperature combustion using an ANTEK 7000N (Houston, Texas, USA) nitrogen (N) analyser. 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-fibre GF/F filter; Whatman International Ltd. Maidstone, England) and extracting the pigment from the filter with 90% acetone. Extracts were analysed for Chl *a* by using a Shimadzu RF-Mini 150 (Shimadzu, Tokyo, Japan) fluorometer equipped with low half-bandwidth (10 nm) filters (excitation = 439, emission = 671) to maximise sensitivity to Chl *a* and minimise interference from Phytin *a* (Welschmeyer 1994). The fluorometer was calibrated with a Chl *a* standard (Sigma-Aldrich, St Louis, MO, USA) the concentration of which was established using a Shimadzu UV Mini 1240 spectrophotometer (Shimadzu) and the spectrophotometric equations of Jeffrey and Humphrey (1975).

Statistical analysis

A principal components analysis (PCA) (SPSS 2001) was performed to define the independent underlying spatial pattern in the *Chara* cover and water-quality data. Data from Sites 2, 8, 12, 19, 21 and 26 included the entire suite of measured water-quality parameters (TN, TP, Chl *a*, temperature, salinity, depth and light availability) and were used in the PCA. Because the percentage light transmission data were truncated when Secchi depths exceeded water depths, the data were transformed to a constructed light availability index for use in the PCA. Percentage light transmissions were transformed to light availability index as follows: light transmission $<5\% = 1$, $5-10\% = 2$, $10-15\% = 3$, $15-20\% = 4$, $20-23.7 = 5$, and $>23.7 = 6$. All data were rank-transformed to satisfy the twin aims of a symmetrical distribution and linear relationships required for PCA (Clarke and Gorley 2006). Eigenvectors for each of the variables in the PCA were superimposed on the ordination plots, indicating the amount and direction of Spearman correlation with the principal components and samples.

Separate temporal analyses were performed according to subestuary (Alligator and McCormick Creek subestuaries) because spatial differences were distinct and dominant, as evidenced in the PCA ordination plots and also from previous statistical analyses that identified distinct differences in nutrient availability, phytoplankton abundance and water transparency between the two subestuaries (Frankovich *et al.* 2011). Because our goal was to identify temporal patterns of *Chara* cover and infer temporal relationships with water-quality parameters, the lack of vegetation at Sites 16, 18, 20 and 21 during all sampling times precluded these sites from the temporal analyses. We chose to analyse 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. 2) 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). Wilcoxon rank-sum tests (SPSS version 11.01; Zar 1999) were employed to detect wet-season *versus* dry-season differences in *Chara* cover, water temperature, salinity, TN, TP and Chl *a* and spatial differences among *Chara* cover, TN, TP and Chl *a*.

Chara cover may reflect temporal water-quality conditions that do not coincide directly with wet and dry seasons. To identify any additional temporal relationships, Spearman rank correlation (SPSS version 11.01; Zar 1999) was used to investigate any relationship between *Chara* cover and water temperature, salinity and water depth at the vegetated sites in each subestuary.

Results

Principal components analysis (PCA) identified distinct Alligator Creek and McCormick Creek subestuary site groups (Fig. 3*a*, *b*). Three principal components (PC1 through PC3) were extracted from the data that described 72% of the variation in the original set (Table 1). PC1 exhibited the greatest correlations with water-column chlorophyll and TP (both positive) and light availability index (negative), and accounted for 39% of the variation in the original dataset. This principal component was interpreted to be an indicator of phytoplankton abundance. PC2, interpreted as an indicator of *Chara* abundance, was highly positively correlated with *Chara* cover and negatively correlated with water depth, and accounted for 18% of the variation in the original dataset. PC3 was most correlated with temperature and salinity and accounted for an additional 15% of the variation in the original dataset. Inspection of the PCA ordination plots (Fig. 3*a*, *b*) revealed that sites in the Alligator Creek subestuary were characterised by higher water-column nutrient concentrations and phytoplankton abundance and lower light availability than were sites in the McCormick Creek subestuary. *Chara* cover was greater in shallower water in both subestuaries, as indicated by PC2. Greater temperatures and salinities were associated with decreased *Chara* cover, as indicated by PC3.

Percentage cover (mean ± standard error) of *Chara* in the McCormick Creek subestuary was almost twice that in the Alligator Creek subestuary, 41 ± 4 and 23 ± 3, respectively (Fig. 4) (Wilcoxon rank-sum test, $P = 0.003$). Seasonal differences in the percentage cover of *Chara* between wet and dry seasons were evident only in the Alligator Creek subestuary (Table 2). There, the percentage cover of *Chara* during the dry season (30 ± 4) was twice that during the wet season (16 ± 2) (Wilcoxon rank-sum test, $P = 0.05$, Table 2), whereas in the McCormick Creek subestuary, the cover was similar during dry and wet seasons (44 ± 8 and 37 ± 7, respectively) (Wilcoxon rank-sum test, $P = 0.51$, Table 2).

Seasonal cycles were observed in water temperature, salinity and water level (Fig. 5). Seasonal water-temperature profiles in Seven Palm Lake and West Lake were similar in timing of minimum and maximum values (Fig. 5*a*). 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
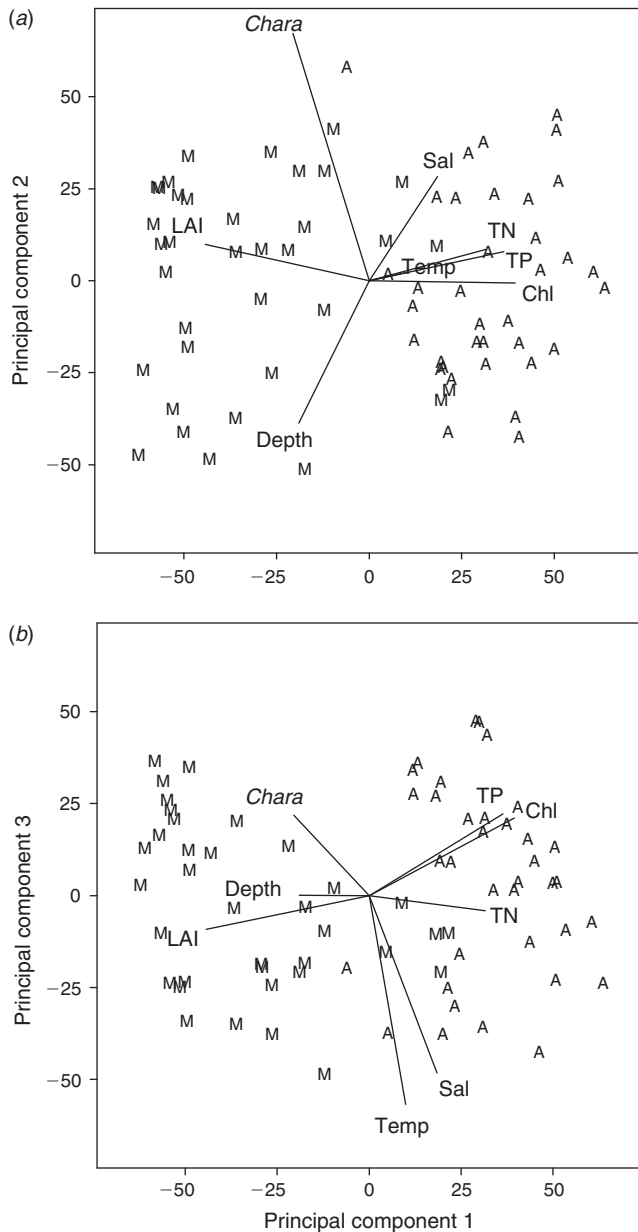
Fig. 3. Ordination-site scores and eigenvector plots for three principal components generated by principal components analysis (PCA) using the Euclidean distance metric of rank-transformed *Chara* cover and water-quality variables. (*a*) PC2 *v.* PC1. (*b*) PC3 *v.* PC1. Site scores are coded by subestuary, with A = Alligator Creek subestuary and M = McCormick Creek subestuary.

Table 1. Factor loadings for three principal components (PC1, phytoplankton abundance; PC2, *Chara* cover; PC3, temperature and salinity)
Loadings are the Spearman correlation between the ranked data with the principal components. Correlations >0.4 are highlighted in **bold** type. In total, the three principal components explained 72.2% of the variation in the original data
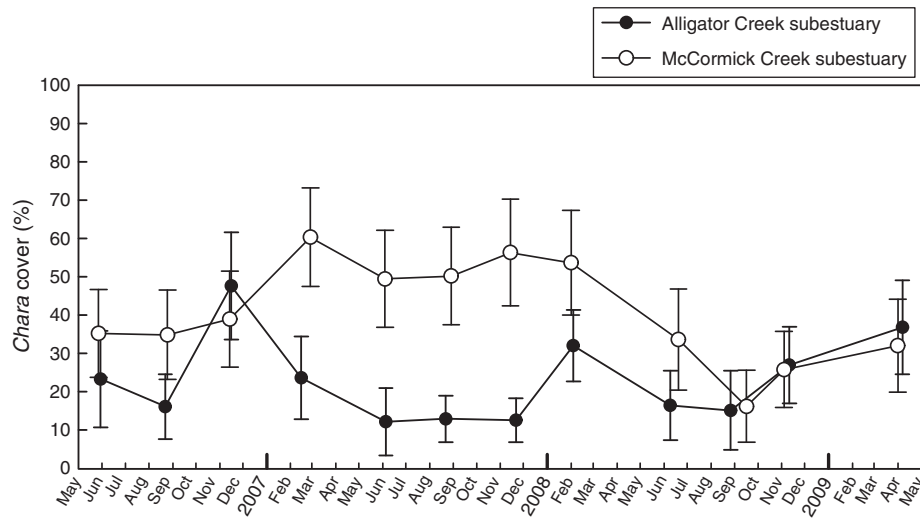
Original variable	PC1	PC2	PC3
Light availability	**−0.527**	0.117	−0.110
Chlorophyll	**0.469**	−0.007	0.250
TP	**0.433**	0.094	0.263
Chara	−0.244	**0.800**	0.259
Depth	−0.226	**−0.460**	0.001
Temperature	0.119	0.027	**−0.676**
Salinity	0.220	0.337	**−0.574**
TN	0.375	0.102	−0.050
Variance explained	39.0	18.1	15.2

to 17.3 in West Lake. Minimum daily salinities were observed during the fall (September–December), following the end of the wet season, whereas maximum salinities were observed at the end of the dry season and into the early wet season (April–August) (Fig. 5*b*). 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 2). Salinity ranges in Seven Palm Lake and West Lake ranged from 10.9 to 31.7 and from 4.1 to 30.8, respectively (Fig. 5*b*).

Seasonal water-level changes in Seven Palm Lake and West Lake were similar (Fig. 5*c*). Differences in the mean water depth were evident between wet and dry seasons (Table 3). Minimum water levels were observed during the latter half of the dry season (February–April), whereas maximum levels were observed during the middle of the wet season (August) (Fig. 5*c*). Maximum water-level differences of 63.2 cm and 71.0 cm were recorded in West Lake and Seven Palm Lake, respectively (Fig. 5*c*).

TN, TP and Chl *a* were ~2, 4 and 8 times higher (Wilcoxon rank-sum test, all $P \leq 0.001$), respectively, in the Alligator Creek subestuary than in the McCormick Creek subestuary (Fig. 6*a*–*c*). Mean TN : TP ratios indicated phosphorus (P)-limiting conditions in the water column throughout, ranging from 38–39 at the three sites in the Alligator Creek subestuary to 65–72 at those sites in the McCormick Creek subestuary (Frankovich *et al.* 2011).

There were no differences in TN, TP or Chl *a* between wet and dry seasons (Table 2). TN in the Alligator Creek subestuary (Sites 19, 21, 26) temporally ranged from 44 µM at Site 19 to 315 µM at Site 21 in August 2008 and October 2008, respectively (Fig. 6*a*), whereas TN in the McCormick Creek subestuary (Sites 2, 8, 12) temporally ranged from 33 µM at Site 2 to 99 µM at Site 8, in May 2007 and September 2008, respectively (Fig. 6*a*). TP in the Alligator Creek subestuary ranged from 0.21 µM to 7.93 µM, at Site 21 in August 2008 and August 2006, respectively (Fig. 6*b*), whereas TP in the McCormick Creek subestuary temporally ranged from 0.24 µM at Sites 2 and 8 in August 2008 to 2.90 µM at Site 12 in January 2009 (Fig. 6*b*).

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. Significant differences in the mean water temperature between wet and dry seasons were evident (Table 2).

Salinities were different in Seven Palm Lake and West Lake, but seasonal salinity dynamics were similar in the timing of minimum and maximum salinities (Fig. 5*b*). Mean daily salinities were mesohaline, ranging from 14.5 in Seven Palm Lake

Fig. 4. *Chara* percentage cover time series from Alligator Creek and McCormick Creek subestuary zones. Error bars designate standard error of the mean.

Table 2.   Comparison of wet-season *v.* dry-season *Chara* cover, water temperatures (Temp), salinities, total nitrogen (TN), total phosphorus (TP) and Chlorophyll *a* (Chl *a*) concentrations

Bold indicates statistically significant (Wilcoxon rank-sum test, $P = 0.05$) differences between wet and dry seasons. s.e. = standard error of the mean; n.a. = not applicable

Subestuary, season and *P*	*Chara* cover (%) (mean ± s.e.)	Temp (°C) (mean ± s.e.)	Salinity (mean ± s.e.)	TN (μM) (mean ± s.e.)	TP (μM) (mean ± s.e.)	Chl *a* (μg L^{-1}) (mean ± s.e.)
Alligator Creek subestuary						
Dry	**30 ± 4**	**23.8 ± 0.4**	21.0 ± 2.9	114 ± 5	2.86 ± 0.05	23.2 ± 5.2
Wet	**16 ± 2**	**29.9 ± 0.2**	22.2 ± 4.2	101 ± 23	2.65 ± 0.34	22.6 ± 1.8
P	**0.050**	**0.050**	0.827	0.513	0.513	0.513
McCormick Creek subestuary						
Dry	44 ± 8	**23.8 ± 0.4**	15.4 ± 2.7	50 ± 2	0.80 ± 0.25	3.1 ± 0.5
Wet	37 ± 7	**30.0 ± 0.2**	19.8 ± 4.1	56 ± 7	0.78 ± 0.21	3.4 ± 0.2
P	0.513	**0.050**	0.275	0.513	0.827	0.827

In the Alligator Creek subestuary, Chl *a* temporally ranged from 1.5 μg L^{-1} at Site 26 to 73.4 μg L^{-1} at Site 19, in May 2008 and September 2008, respectively (Fig. 6*c*), whereas in the McCormick Creek subestuary, Chl *a* temporally ranged from 0.1 μg L^{-1} at Site 12 in May 2007 to 10.7 μg L^{-1} at Sites 2 and 12 in July 2006 (Fig. 6*c*).

Water transparency (Secchi depth, $Z_{s.d.}$) exceeded water depth at most sites and times in the McCormick Creek subestuary. In contrast, median Secchi depths were less than water depth most of the time in the Alligator Creek subestuary. 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. 2). Light penetration to the sediment surface in the Alligator Creek subestuary during the wet season was estimated to be less than 1%, whereas during the dry season, light penetration was estimated to be ~5% (Table 3). Light availability (estimated PAR bottom insolation) was about five times greater in the McCormick Creek subestuary than in the Alligator Creek subestuary (Table 3). Light availability was

about five times greater during the dry season than during the wet season in the Alligator Creek subestuary (Table 3).

Significant correlations (Spearman rank correlation, $P < 0.05$) between *Chara* cover and environmental variables were evident only in the McCormick Creek subestuary (Table 4). *Chara* cover in the McCormick Creek subestuary was negatively correlated with salinity and water depth.

Discussion

When light is not limiting, as in the McCormick Creek subestuary, *Chara* cover was temporally negatively correlated with salinity, suggesting that these communities may grow faster during periods of lower salinity. Seasonality of the *Chara* cover was not evident in this area, but cover decreased and remained lower than the long-term mean during the 2008 wet season and the following wet season (Fig. 4). This decline in cover is coincident with elevated salinities mostly above the long-term mean, with maximum salinities approaching 30 during the same period (Fig. 5*b*). This decline may reflect the exceeding of a salinity maximum threshold for *Chara hornemannii* growth.
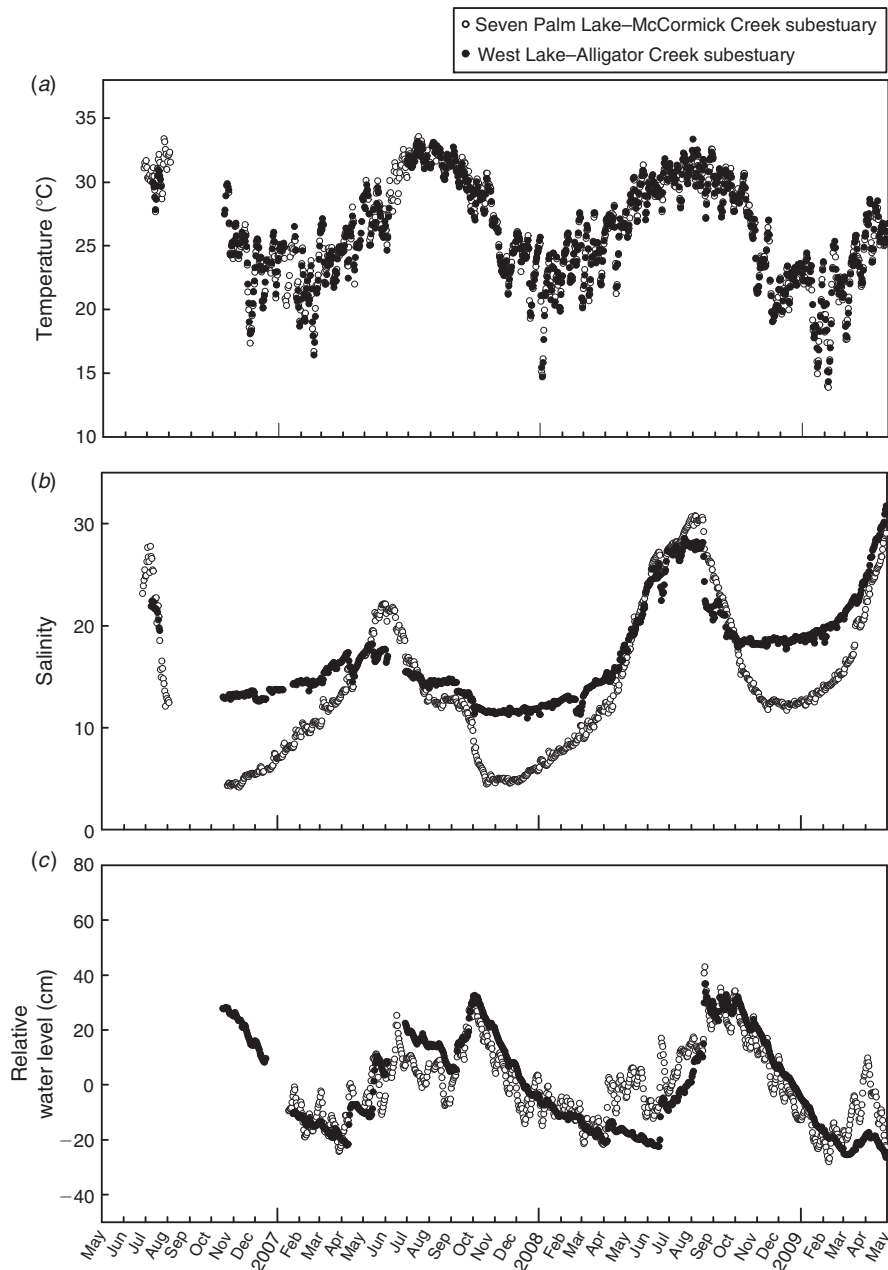
Fig. 5. (*a*) Water temperature, (*b*) salinity and (*c*) relative water-level time series from datasondes deployed in West Lake–Alligator Creek and Seven Palm Lake–McCormick Creek subestuaries.

The negative temporal correlation of water depth with *Chara* cover in the McCormick Creek subestuary may indicate small changes in light availability in this area also, that may have been undetected by Secchi depth measurements. Small changes in light attenuation in the relatively clear water of the McCormick Creek subestuary may go undetected when Secchi depth (transparency) remains greater than water depth. An increase in light attenuation may result from the deeper water column itself or from increased chromophoric dissolved organic matter (CDOM) associated with Everglades freshwater runoff during the wet season when water levels are higher (Clark *et al.* 2004).

Wet *versus* dry seasonality of *Chara* cover was evident only in the Alligator Creek subestuary. During the dry season (November through April), 4–26 times greater light availability was associated with almost two times greater *Chara* cover. As median light availability in the Alligator Creek subestuary ranged from <1% during the wet season to ~5% during the dry season, the *Chara* communities there experienced low light levels. The low light availability was due to high phytoplankton abundances fuelled by greater availability of P in the Alligator Creek subestuary (Fig. 3*a*, *b*; Frankovich *et al.* 2011). The lack of seasonality in phytoplankton abundances may suggest that

Table 3.   Comparison of wet-season *v.* 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 insolations

Bottom insolations are the products of percentage light at the bottom estimates and surface PAR insolation. **Bold** indicates statistically significant (Wilcoxon rank-sum test, $P = 0.05$) differences in mean water depth between wet and dry seasons; s.e. = standard error of the mean. Seasonal differences in Secchi depths and calculated light-transmission estimates were not statistically tested because of truncated nature of transparency data when Secchi depths exceed water depths

Estuary and season	Secchi depth ($Z_{s.d.}$, median) (cm)	K_d	Water depth (Z, mean) (cm)	Percentage light at bottom (%)	Surface insolation (PAR, mean $\pm$ s.e.) (MJ m^{-2} season^{-1})	Bottom insolation (PAR, mean) (MJ m^{-2} season^{-1})
Alligator Creek subestuary						
Wet	30	4.8	**99**	0.9	1377 ± 39	12
Dry	40	3.6	**84**	4.9	1170 ± 17	57
McCormick Creek subestuary						
Wet	>Bottom depth	<1.4	**128**	>23.7	1377 ± 39	>326
Dry	>Bottom depth	<1.4	**112**	>23.7	1170 ± 17	>277

the shallower water depths during the dry seasons were responsible for the greater light penetrations in the Alligator Creek subestuary; however, the lack of any correlation of *Chara* cover with water depth suggests the possible importance of other unmeasured components of light attenuation such as tripton or CDOM, rather than the water itself. CDOM is higher in the wet season (Clark *et al.* 2004), whereas 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 the Alligator Creek subestuary during the dry season; however, seasonal water temperatures were similar in both subestuaries, suggesting that higher water temperatures did not suppress *Chara* growth.

Differences in watershed geography between the McCormick Creek and Alligator Creek subestuaries 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 Alligator Creek subestuary changed from a *Chara*-dominated clear-water state to a turbid phytoplankton state, whereas the adjacent eastern McCormick Creek subestuary 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 developed only in the adjacent Alligator Creek subestuary. The mangrove 'lakes' in the Alligator Creek subestuary are connected to each other and to central Florida Bay at Garfield Bight 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 McCormick Creek subestuary 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 may allow greater flushing and lower water-residence times in the McCormick Creek subestuary, thereby constraining the development of persistent algal blooms (Søballe and Kimmel 1987). These local geographies are 'system-specific filter attributes' (Cloern 2001) that modulate the response of the adjacent subestuaries to the change

in freshwater delivery. Long water-residence times in the Alligator Creek subestuary (Kelly *et al.* 2011) will also hinder restoration efforts to flush the excess P retained in the system.

The mangrove 'lakes' of the Florida Everglades 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 and, to a lesser extent, the ecosystem observed in the McCormick Creek subestuary, whereas the turbid phytoplankton-dominated state is represented by the observed conditions in the Alligator Creek subestuary. Restoring greater *Chara* coverage by lowering salinities and increasing light availability may be achieved by increasing freshwater flow into the region. The mangrove estuaries 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 P 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. Even if it were possible to greatly reduce external P loading into these systems, restoration of the *Chara* communities may be problematic because of internal loading and release of P already in the system, enhanced by site-specific effects of local watershed geography. Despite 40–50% decrease in N and P concentrations in the Greifswalder Bodden, Baltic Sea, internal nutrient recycling has maintained phytoplankton dominance, hindering SAV recovery there (Munkes 2005).

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 cover. The present study compared seasonal patterns of *Chara* cover in subtropical estuaries in Florida Bay and demonstrated the importance of different water-quality parameters in structuring temporal variation in adjacent subestuaries. The identification of the temporal patterns of *Chara* cover, the associated water-quality conditions and
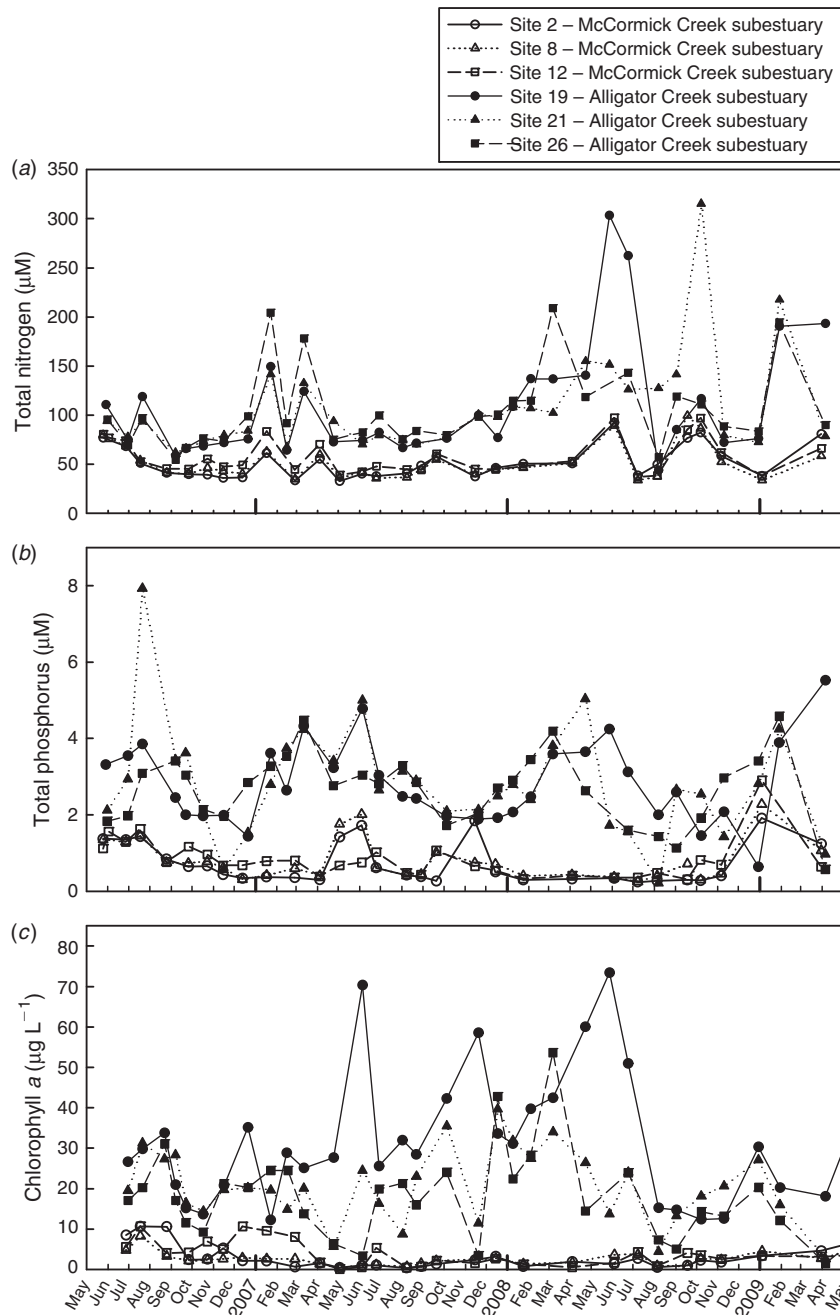
Fig. 6. Water column (*a*) total nitrogen, (*b*) total phosphorus and (*c*) Chlorophyll *a* concentration time series from sites in the Alligator Creek and the Seven Palm Lake subestuaries.

Table 4.   Correlation matrix of *Chara* coverage *v.* temperature, salinity and water depth

r_s = Spearman rank correlation coefficient. P = 2-tailed statistical significance. $n = 12$. **Bold** indicates significant correlation at $P = 0.05$

Correlation	Variable	Alligator Creek subestuary	McCormick Creek subestuary
Chara cover *v.* temperature	r_s	−0.48	−0.34
	P	0.11	0.27
Chara cover *v.* salinity	r_s	−0.02	**−0.57**
	P	0.95	**0.05**
Chara cover *v.* depth	r_s	−0.15	**−0.69**
	P	0.64	**<0.01**

system-specific geography attributes will guide ecosystem restoration efforts in the Everglades and Florida Bay.

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