

Light attenuation in estuarine mangrove lakes



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ABSTRACT

Submerged aquatic vegetation (SAV) cover has declined in brackish lakes in the southern Everglades characterized by low water transparencies, emphasizing the need to evaluate the suitability of the aquatic medium for SAV growth and to identify the light attenuating components that contribute most to light attenuation. Underwater attenuation of downwards irradiance of photosynthetically active radiation (PAR) was determined over a three year period at 42 sites in shallow (<2 m depth) mangrove-surrounded lakes in two sub-estuaries in the coastal Everglades, Florida USA. Turbidity, chromophoric dissolved organic matter (CDOM), and phytoplankton chlorophyll *a* (chl *a*) were measured concurrently and their respective contributions to the light attenuation rate were estimated. Light transmission to the benthos relative to literature estimates of minimum requirements for SAV growth indicated that the underwater light environment was often unsuitable for SAV. Light attenuation rates ($n = 417$) corrected for solar elevation angles ranged from 0.16 m^{-1} to 9.83 m^{-1} with a mean of 1.73 m^{-1} . High concentrations of CDOM with high specific light absorption contributed the most to light attenuation followed by turbidity and chl *a*. CDOM alone sufficiently reduces light transmission beyond the estimated limits for SAV growth, making it difficult for ecosystem managers to increase SAV abundance by management activities. Light limitation of SAV in these areas may be a persistent feature because of their proximity to CDOM source materials from the surrounding mangrove swamp. Increasing freshwater flow into these areas may dilute CDOM concentrations and improve the salinity and light climate for SAV communities.

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1. Introduction

Ecosystem managers have been seeking to restore freshwater flow to the Florida Everglades and increase submerged aquatic vegetation (SAV) coverage and associated fish and waterfowl densities in the coastal mangrove estuaries (USACE, 1999). SAV loss observed during the 20th century was associated with the encroachment of marine waters into the coastal Everglades as canals were constructed to drain the watershed. Increased salinities beyond the oligohaline to mesohaline preference range of the upstream *Chara hornemannii* algal communities were presumed to be the major factor causing SAV decline (Tabb et al., 1962; Craighead, 1971), but recent studies have identified low underwater light availability as a major contributor to continued low SAV cover

(Frankovich et al., 2011, 2012) and in need of further study.

Quantifying the underwater availability of photosynthetically available radiation (PAR, 400–700 nm) is fundamental for determining the suitability of aquatic environments for SAV. SAV is often limited to water depths receiving >5–40% of surface PAR irradiance (Duarte, 1991; Kenworthy and Fonseca, 1996; Middelboe and Markager, 1997; Manuel et al., 2013). Spatial and temporal distributions of underwater light availability often correlate with SAV abundance and community composition with large declines in SAV abundance associated with reduced light availability (Orth and Moore, 1983; Cambridge and McComb, 1984). Ecosystem resource managers may seek to restore SAV communities by increasing underwater light availability, but their actions are limited to indirect methods because light transmission cannot be directly regulated. SAV growth has been increased in shallow lakes by temporarily lowering water levels to allow greater light transmission to the lake bottom (Wallsten and Forsgren, 1989; Havens et al., 2004). Another management strategy is to decrease light attenuation by decreasing the concentrations of light-scattering and light-absorbing

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constituents in the water column such as suspended sediment, phytoplankton or organic matter. Successful implementation of this strategy ideally includes determination of the light attenuation coefficient with adjustments made for solar elevation angle [K_t (adj)], and identification of the constituents that contribute most to the light attenuation rate. The downwelling light attenuation coefficient for PAR is judged to be the best single parameter by which light availability may be compared among different water bodies (Smith, 1968).

The light attenuation coefficient, K_0 , is an apparent optical property that is affected by the solar elevation angle, the relative amounts of diffuse versus direct beam radiation (e.g., cloudiness), and the amounts and character of light-scattering and light-absorbing constituents in the water column (Kirk, 1994). Ideally, all of the factors influencing K_0 should be measured for the most complete and accurate determination of light attenuation specific to local water column characteristics. In practice, some of these factors are not often measured in the field and therefore these deficiencies must be considered when evaluating light attenuation rate determinations (McPherson and Miller, 1994). Inherent optical properties are affected only by light-scattering and light-absorbing constituents in the water column (Kirk, 1994); therefore, it is beneficial to adjust or make corrections to K_0 by subtracting the effects that contribute only to apparent light attenuation (e.g., solar elevation angle) so that the effects of water column parameters on light attenuation can be more accurately determined. A light attenuation component model can be used to express the adjusted light attenuation coefficient, K_t (adj), as the sum of partial light attenuation coefficients that correspond to a specific water column constituent (Kirk, 1994). The relative contributions of water column constituents can then be determined. Each partial coefficient is estimated by the product of the constituent concentration and a specific light attenuation coefficient for that constituent (Kirk, 1994). Specific light attenuation coefficients can be estimated either mechanistically through controlled laboratory experiments or statistically by regression of observed light attenuation coefficients versus the concentration of light attenuation constituents. The light attenuation component model has been successfully used to estimate the relative contributions of turbidity, chlorophyll a (chl a), chromophoric dissolved organic matter (CDOM), and water to light attenuation in estuarine waters (McPherson and Miller, 1987; 1994; Christian and Sheng, 2003; Kelble et al., 2005; Kostaglidis et al., 2005; Obrador and Pretus, 2008; Buzzelli et al., 2012).

The present study describes the underwater light climate in estuaries of the southern Everglades that are surrounded by extensive mangroves and characterized by persistent phytoplankton blooms and SAV decline (Frankovich et al., 2011). Measurements of underwater light availability are compared to estimates of SAV minimum light availability requirements. The light attenuation component model is used to estimate the contributions of water column light attenuation components to the downwelling light attenuation rate and to identify components of management concern. This study also compares results of the light attenuation component model using assumed regionally-relevant specific light attenuation coefficients obtained from the literature with that using coefficients determined from multiple regression of local field measurements of turbidity, chl a , and CDOM.

2. Materials and methods

2.1. Study area

This investigation was conducted at 42 sites in the estuarine mangrove-surrounded lakes and bays located along and adjacent to

the north shore of Florida Bay inside Everglades National Park (Fig. 1). These sites are located in two sub-estuaries of Florida Bay defined by separate freshwater flow paths that drain the southern Everglades via Alligator Creek and McCormick Creek. The western Alligator sub-estuary is comprised of West, Long, and Cuthbert Lakes, The Lungs, and Garfield Bight. The eastern McCormick sub-estuary is comprised of Seven Palm, Middle, and Monroe Lakes, and Terrapin Bay. Henry and Little Henry Lakes (not sampled due to inaccessibility) are located between the two sub-estuaries but connections between these and the surrounding lakes were not found. Water depths are <2 m. Large differences in water quality exist between the two sub-estuaries, with higher phytoplankton abundances and lower underwater light availabilities in the Alligator sub-estuary (Frankovich et al., 2011). SAV communities consisting of the green alga *Chara hornemannii* in the upstream lakes and the seagrass *Halodule wrightii* in the McCormick sub-estuary and Garfield Bight are organized along salinity and light availability gradients (Frankovich et al., 2011, 2012).

2.2. Measured parameters

Downwards irradiance of photosynthetically active radiation (PAR) was measured just below the water surface and at 25 cm below the upper measurement in order to calculate the downwelling light attenuation coefficient (K_0) at 42 sites (Fig. 1) at varying temporal frequencies ranging from 0.6 to 7.6 yr⁻¹ (mean = 3.0 yr⁻¹) during the period 2/9/2012 through 5/18/2015 (total K_0 estimates = 417). PAR measurements were made at both depths simultaneously using two Licor LI-192SA cosine-corrected sensors (flat irradiance collectors) and a Licor LI-1000 datalogger. Cosine-corrected sensors were used, as opposed to spherical scalar irradiance sensors, because inherent optical properties of the water column were compared. K_0 was calculated using the Lambert-Beer equation (Kirk, 1994):

$$I_z = I_0 \exp [-K_0(z)] \quad (1)$$

where I_z = PAR irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$) at depth, I_0 = PAR irradiance just below the water surface and z = distance (m) between light sensors. Because light attenuation calculations are affected by the solar elevation angle at the time and latitudinal location of light measurements (Moore and Goodman, 1983; Miller and McPherson, 1995) and because the primary focus of this study was relating properties of the aquatic medium to K_0 , adjustments were made for the effects of solar elevation angle (β). The adjusted light attenuation coefficient, K_t (adj), was calculated using the equations of McPherson and Miller (1994) and Miller and McPherson (1995):

$$\psi = (d - 1) 360/365.242 \quad (2)$$

$$\delta = 12 + 0.1236 \sin(\psi) - 0.0043 \cos(\psi) + 0.1538 \sin(2\psi) + 0.0608 \cos(2\psi) \quad (3)$$

$$Y = 15(\tau - \delta) - \lambda \quad (4)$$

$$\sigma = 279.9348 + \psi + 1.9148 \sin(\psi) - 0.0795 \cos(\psi) + 0.0199 \sin(2\psi) - 0.0016 \cos(2\psi) \quad (5)$$

$$\kappa = \arcsin [0.39785077 \sin(\sigma)] \quad (6)$$

$$\sin(\beta) = \sin(\gamma) \sin(\kappa) + \cos(\gamma) \cos(\kappa) \cos(Y) \quad (7)$$

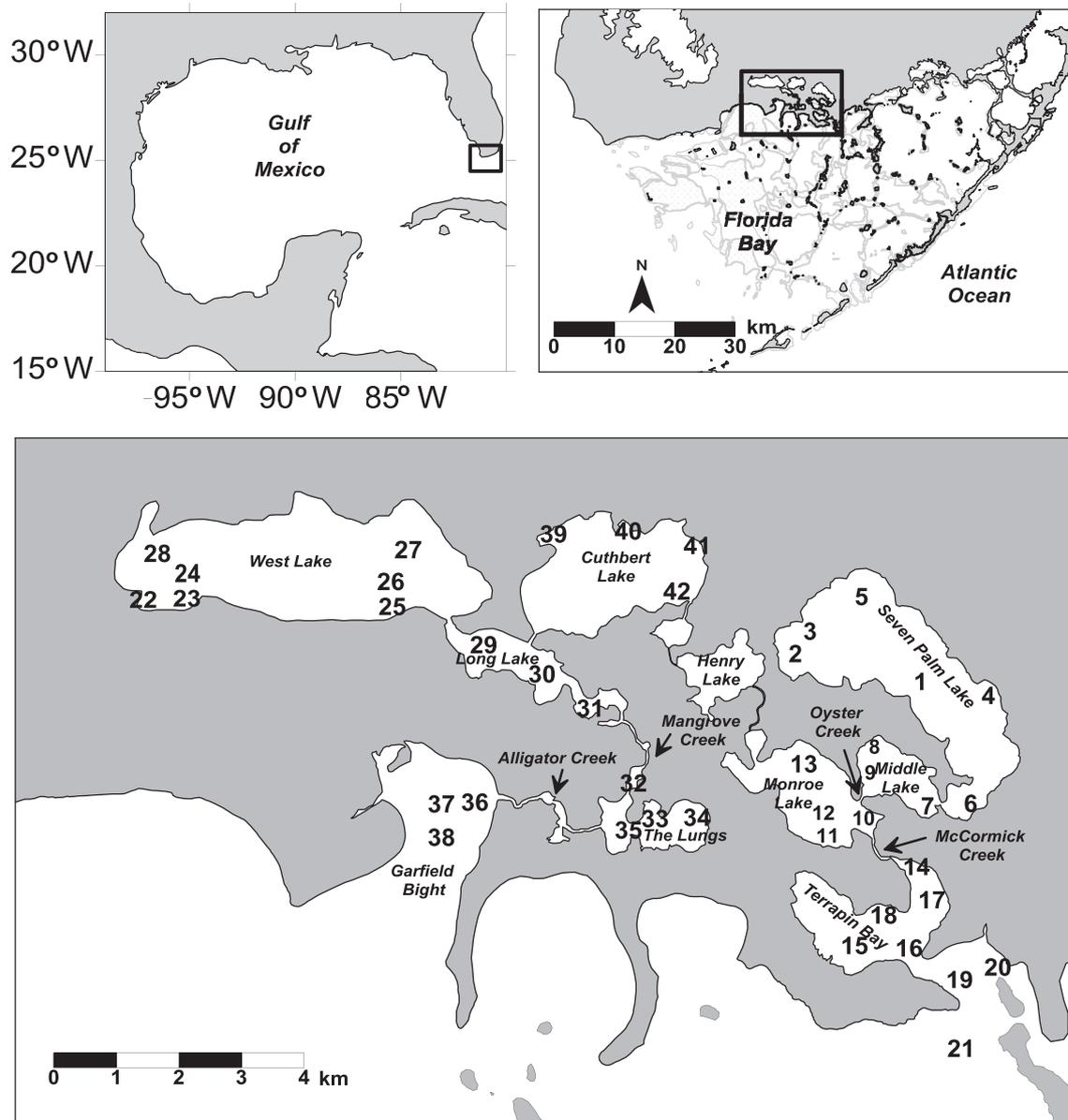


Fig. 1. Location map of study sites.

$$\theta = \arcsin(\sin(90^\circ - \beta)/1.33) \quad (8)$$

$$K_t(\text{adj}) = K_0[\cos(\theta)] \quad (9)$$

where ψ = the angular fraction of the year (degrees); d = Julian date; δ = true solar noon (hours); Y = the solar hour angle (degrees); τ = Greenwich Mean Time (hours); λ = longitude (degrees); σ = estimate of true longitude of sun (degrees); κ = solar declination (degrees); γ = latitude (degrees); θ = the average zenith angle of the refracted direct solar beam in water; β = solar elevation angle (degrees); K_0 = unadjusted light attenuation coefficient; and $K_t(\text{adj})$ = adjusted light attenuation coefficient.

Water depths, measured at each site during all sampling events and the calculated light attenuation coefficients were used in the Lambert-Beer equation to estimate the percent surface light available at the sediment surface. It was assumed that light attenuation in the top 25 cm of the water column of these shallow lakes was the

same as that throughout the entire water column. Because light transmission to the sediment surface depends on the inherent properties of the water column and the geometric structure of the light fields that pervade it (Kirk, 1994), the mean effect of sun angle was included in these calculations. The unadjusted light attenuation coefficient, K_0 , which does account for sun angle effects, was not used in these calculations because of site bias in K_0 calculations resulting from non-random differences in the time of day that each site was sampled (i.e., specific sites were routinely sampled at different times of the day based upon travel distances). Instead, the mean effect of sun angle on the light attenuation coefficient was determined from across all sampled sites and times (+13%, see Results) and was applied to the adjusted light attenuation coefficients, $K_t(\text{adj})$, to produce more accurate and unbiased estimates of light transmission to the sediment surface.

Turbidity, and water column concentrations of chl *a* and CDOM were measured from water samples collected at the same time as light measurements. Water samples were kept on ice and

refrigerated prior to analyses. Turbidity (NTU) was measured using a Hach 2100Q Portable turbidimeter. Water samples were shaken to resuspend any settled particulates prior to measurement. Chl *a* concentrations ($\mu\text{g L}^{-1}$) were determined by filtering water samples (25-mm glass fiber GFF filters, pore size = 0.7 μm) 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 nm, emission = 671 nm) to maximize sensitivity to chl *a* and minimize interference from pheophytin *a* (Welschmeyer, 1994). The fluorometer was calibrated with a chl *a* standard (Sigma-Aldrich) whose concentration was established using a Shimadzu UV-1601 spectrophotometer and the spectrophotometric equations of Jeffrey and Humphrey (1975). CDOM concentrations (QSU) were determined from filtered (25-mm glass fiber GFF filters, pore size = 0.7 μm) water samples using a Turner Designs Trilogy filter fluorometer equipped with a CDOM optical kit (excitation = 350 nm, half-bandwidth = 80 nm; emission = 430 nm, half-bandwidth = 20 nm). Filtered water samples were diluted with 2 parts deionized water to 1 part sample prior to fluorescence measurement to avoid quench in higher absorbance samples and maintain linearity throughout the absorbance range of field samples (<http://www.turnerdesigns.com/t2/doc/appnotes/998-0050.pdf>). The fluorometer was calibrated with a 100 QSU quinine sulfate standard (1 QSU = 1 μg quinine sulfate L^{-1}) prepared in 0.1 N H_2SO_4 (Clark et al., 2002).

2.3. Estimating constituent contributions to light attenuation

Univariate relationships between K_t (adj), turbidity, chl *a*, and CDOM were analyzed using Pearson correlation (SPSS vers. 23). The contributions of turbidity, chl *a*, and CDOM to vertical light attenuation were estimated using a model that equates the light attenuation coefficient, K_t (adj), to the sum of partial attenuation coefficients determined for each component (Kirk, 1994; Christian and Sheng, 2003; Kelble et al., 2005):

$$K_t \text{ (adj)} = K_{\text{sw}} + K_{\text{turb}} + K_{\text{chl}} + K_{\text{CDOM}} \quad (10)$$

where K_{sw} = partial attenuation coefficient for seawater; K_{turb} = partial attenuation coefficient for turbidity; K_{chl} = partial attenuation coefficient for chl *a*; and K_{CDOM} = partial attenuation coefficient for CDOM. The partial attenuation coefficients for each component are assumed to be linear functions of the concentration of that component and may be expressed as the products of the measured concentrations/amounts of the light attenuation contributing components (c_x) and the specific light attenuation coefficients (lower case “k”) for each component (McPherson and Miller, 1994; Kelble et al., 2005):

$$K_t \text{ (adj)} = K_{\text{sw}} + k_{\text{turb}} (c_{\text{turb}}) + k_{\text{chl}} (c_{\text{chl } a}) + k_{\text{CDOM}} (c_{\text{CDOM}}) \quad (11)$$

where the values inside the parentheses are the measured concentrations/amounts of the light attenuation contributing components; k_{turb} = specific attenuation coefficient for turbidity; k_{chl} = specific attenuation coefficient for chl *a*; and k_{CDOM} = specific attenuation coefficient for CDOM. K_{sw} is not decomposed into a specific attenuation coefficient (k_w) and concentration because the differences in water concentrations are negligible. Measurements of turbidity, chl *a*, and CDOM, the adjusted light attenuation coefficients (K_t adj), and the following published and assumed regionally-relevant estimates for K_{sw} , k_{turb} , k_{chl} , and k_{CDOM} were used in the first version of the light attenuation component model to determine light attenuation component contributions:

$K_{\text{sw}} = 0.0384 \text{ m}^{-1}$ (Lorenzen, 1972), universal estimate.

$k_{\text{turb}} = 0.062 \text{ m}^{-1} \text{ NTU}^{-1}$ (McPherson and Miller, 1994), Tampa Bay and Charlotte Harbor, Florida USA.

$k_{\text{chl}} = 0.058 \text{ m}^2 \text{ mg}^{-1}$ (McPherson and Miller, 1994), Tampa Bay and Charlotte Harbor, Florida USA.

$k_{\text{CDOM}} = 0.000424 \text{ m}^{-1} \text{ QSU}^{-1}$ (Kelble et al., 2005), Florida Bay, Florida USA.

The second version of the light attenuation model used to estimate the contributions of turbidity, chl *a*, and CDOM to vertical light attenuation used values of the specific attenuation coefficients determined from multiple linear regression (SPSS vers. 23). K_t (adj) was regressed against turbidity, chl *a*, and CDOM to produce statistically-determined specific attenuation coefficients that may be specific for water quality characteristics in the study area. The percent contributions of turbidity, chl *a*, and CDOM were estimated from the recalculated partial attenuation coefficients and compared with the estimates produced using published specific attenuation coefficients.

Spatial differences between sub-estuaries and seasonal differences in K_t (adj), water depth, percent light at bottom, turbidity, chl *a*, CDOM, and partial light attenuation coefficients were examined by comparison of box plots summarizing the descriptive statistics of site means for each parameter. To compare seasonal differences, high and low water level time periods (July–December, January–June, respectively) corresponding to observed seasonal variation in water levels in the region (Frankovich et al., 2012; Wingard and Lorenz, 2014) were assigned to sampling events. Differences in measured and calculated parameters between sub-estuaries were tested using site means and the Mann-Whitney test (SPSS vers. 23, Zar, 1999). Differences between high and low water level time periods were analyzed using the Wilcoxon signed-rank test that tests for deviation from zero of the median of within-site differences (SPSS vers. 23, Zar, 1999).

3. Results

Using the equations to correct for variations of solar elevation angle (Miller and McPherson, 1995) reduced estimates of vertical light attenuation [K_t (adj)] relative to uncorrected determinations (K_0) (Fig. 2). K_0 estimates were <1–47% higher (mean = +13%) than K_t (adj). Estimates of K_t (adj) calculated from 417 measurements of light attenuation ranged from 0.16 m^{-1} at site 15 in the McCormick

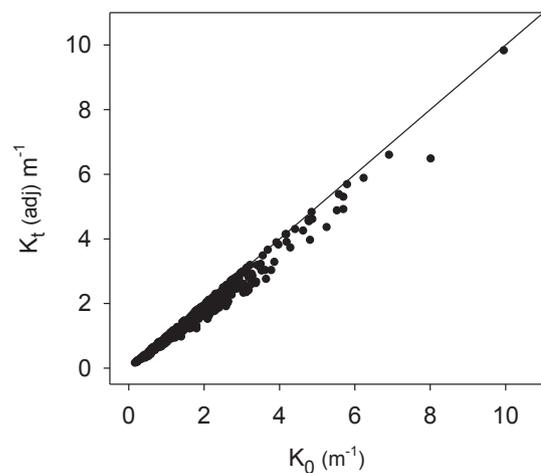


Fig. 2. Scatterplot of light attenuation coefficients adjusted for the effect of solar elevation angle, K_t (adj), versus unadjusted light attenuation coefficients, K_0 . The line represents a 1:1 relationship at a constant 90° solar elevation angle.

sub-estuary on May 12, 2015 to 9.83 m^{-1} at site 35 in the Alligator sub-estuary on June 11, 2013 with a mean of 1.73 m^{-1} (Table 1).

The light attenuation coefficient [K_t (adj)], turbidity, CDOM, and chl *a* were higher in the Alligator sub-estuary than in the McCormick sub-estuary ($P < 0.001$ for all, Mann-Whitney test) (Fig. 3a–d). Site means of K_t (adj) ranged from 0.42 to 1.86 m^{-1} with a mean of 1.03 m^{-1} in the McCormick sub-estuary and from 1.20 to 3.17 m^{-1} with a mean of 2.15 m^{-1} in the Alligator sub-estuary (Table 1). Site means of turbidity ranged from 2.3 to 11.8 NTU with a mean of 6.4 NTU in the McCormick sub-estuary and from 4.9 to 33.3 NTU with a mean of 16.8 NTU in the Alligator sub-estuary (Table 1). Site means of CDOM ranged from 63 to 147 QSU with a mean of 95 QSU in the McCormick sub-estuary and from 94 to 214 QSU with a mean of 137 QSU in the Alligator sub-estuary (Table 1). Site means of chl *a* ranged from 0.5 to $3.1 \mu\text{g L}^{-1}$ with a mean of $1.5 \mu\text{g L}^{-1}$ in the McCormick sub-estuary and from 3.1 to $30.3 \mu\text{g L}^{-1}$ with a mean of $12.1 \mu\text{g L}^{-1}$ in the Alligator sub-estuary (Table 1).

Temporal within-site variations in the light attenuation coefficient [K_t (adj)], water depth, percent light at bottom, turbidity, CDOM, and chl *a* were evident in the study area (Fig. 4a–f). The light attenuation coefficient [K_t (adj)] was higher during the high water level season in the McCormick sub-estuary ($P = 0.001$, Wilcoxon signed-rank test) but not in the Alligator sub-estuary ($P > 0.05$, Wilcoxon signed-rank test) (Fig. 4a). The seasonal

means of K_t (adj) in the McCormick sub-estuary were 0.89 m^{-1} and 1.15 m^{-1} during the high and low water periods, respectively. Mean water depths in both sub-estuaries were about 10–15 cm higher than during the high water level season than the low water level season ($P < 0.001$, Wilcoxon signed-rank tests) (Fig. 4b). The percent light reaching the bottom was higher during the low water level season in both sub-estuaries ($P \leq 0.001$, Wilcoxon signed-rank tests) (Fig. 4c). The high and low water level seasonal means of the percent light at bottom were 34% and 46%, respectively, in the McCormick sub-estuary, and 19% and 23%, respectively, in the Alligator sub-estuary. The increased light transmission during the low water level season was a result of both decreased water levels and decreased light attenuation coefficients (i.e., clearer water) in the McCormick sub-estuary, while in the Alligator sub-estuary; the increased light transmission was due only to decreased water levels. Turbidity was higher during the low water level season in the Alligator sub-estuary ($P < 0.001$, Wilcoxon signed-rank test) but not in the McCormick sub-estuary ($P > 0.05$, Wilcoxon signed-rank test) (Fig. 4d). The seasonal means of turbidity in the Alligator sub-estuary were 14.0 NTU and 19.8 NTU during the high and low water periods, respectively. CDOM and chl *a* in both sub-estuaries were higher during the high water level season ($P \leq 0.014$, Wilcoxon signed-rank tests) (Fig. 4e–f). The high and low water level seasonal means of CDOM were 111 QSU and 83 QSU during the high

Table 1

Summary of light transmission and light attenuation component characteristics (range, mean) at all study sites. * A correction factor of +13% was applied to the adjusted light attenuation coefficient, K_t (adj), to account for the effect of sun angle.

Site	K_t (adj) (m^{-1})	Turbidity (NTU)	CDOM (QSU)	Chl <i>a</i> ($\mu\text{g L}^{-1}$)	Depth (cm)	Percent light at bottom*	n
1	0.54–2.73, 1.66	2.4–11.6, 6.6	78–263, 147	0.5–5.5, 2.8	130–171, 154	1–38, 7	17
2	0.56–2.73, 1.66	2.6–25.4, 11.8	38–121, 82	0.8–1.7, 1.1	105–125, 113	6–48, 23	6
3	0.48–1.72, 0.95	2.1–8.5, 5.6	40–195, 111	0.7–2.6, 1.1	121–150, 131	4–43, 24	9
4	0.19–1.27, 0.77	1.1–6.5, 2.3	35–165, 106	0.4–1.8, 0.9	91–129, 111	14–79, 36	9
5	0.44–0.98, 0.76	2.3–7.1, 3.9	40–121, 81	0.4–0.6, 0.5	123–140, 132	16–45, 28	6
6	0.46–0.82, 0.70	1.5–9.1, 4.3	40–133, 83	0.7–2.2, 1.2	97–126, 109	32–51, 39	6
7	0.61–2.98, 1.31	1.1–14.8, 4.0	40–273, 130	0.9–6.7, 2.2	110–142, 126	1–41, 19	23
8	0.61–1.34, 0.92	3.2–10.0, 5.3	42–178, 108	0.7–3.0, 1.7	109–130, 120	10–43, 27	9
9	0.64–1.21, 0.86	4.3–14.8, 7.4	40–121, 76	1.0–2.4, 1.7	123–146, 136	12–35, 24	6
10	0.79–1.10, 0.97	4.1–15.1, 8.7	45–132, 74	0.9–3.1, 1.6	65–74, 71	33–52, 43	5
11	0.79–1.60, 1.12	4.7–10.5, 7.2	47–191, 107	1.0–6.0, 2.3	109–132, 119	10–31, 20	8
12	0.83–1.25, 1.05	6.9–11.8, 8.8	43–135, 75	1.0–2.5, 1.8	110–133, 123	11–32, 21	5
13	0.90–4.30, 1.86	3.9–15.1, 8.7	44–295, 134	1.1–5.9, 3.1	100–140, 122	<1–30, 11	22
14	0.60–1.83, 1.27	4.8–20.9, 10.9	41–143, 93	0.7–3.5, 1.7	43–80, 63	22–58, 39	8
15	0.16–1.72, 0.93	2.3–14.2, 6.3	36–142, 92	0.3–4.3, 1.2	70–95, 85	16–86, 42	8
16	0.35–1.40, 0.85	3.2–11.9, 6.6	42–133, 88	0.4–2.7, 0.9	77–104, 94	22–73, 39	8
17	0.28–3.48, 1.45	2.4–14.7, 6.9	37–278, 121	0.2–4.6, 2.3	65–98, 83	3–80, 31	25
18	0.26–1.65, 0.81	3.4–12.8, 6.7	39–143, 92	0.2–3.2, 1.0	70–100, 89	15–81, 45	8
19	0.25–1.12, 0.66	3.0–12.9, 5.4	36–130, 74	0.2–0.9, 0.6	60–87, 75	35–82, 55	8
20	0.21–0.99, 0.63	3.4–7.2, 5.1	34–104, 63	0.2–0.8, 0.5	50–88, 73	40–88, 57	8
21	0.20–0.82, 0.42	2.1–3.5, 2.6	26–120, 64	0.1–2.2, 0.5	111–138, 128	31–77, 53	8
22	1.39–2.50, 2.01	14.4–35.2, 21.5	56–121, 94	8.2–18.0, 12.0	70–126, 104	3–19, 9	7
23	0.74–2.92, 1.70	1.8–35.3, 16.9	70–160, 108	0.8–18.7, 10.7	71–135, 98	6–27, 14	10
24	1.58–3.11, 2.06	13.5–33.9, 21.6	66–120, 95	7.0–22.4, 13.1	92–121, 109	3–10, 7	6
25	1.01–2.95, 1.80	7.1–21.1, 14.2	63–216, 120	1.9–32.9, 12.6	102–153, 132	2–17, 6	11
26	1.54–3.09, 2.20	12.7–18.7, 16.4	63–151, 104	6.5–24.2, 13.2	120–150, 136	1–5, 3	7
27	1.28–2.64, 1.97	13.4–21.3, 18.0	70–125, 105	8.2–17.8, 12.3	135–160, 148	1–7, 4	7
28	1.14–3.13, 2.07	0.6–32.9, 14.9	62–255, 143	0.5–27.9, 12.9	118–160, 136	<1–13, 4	21
29	1.75–2.82, 2.31	13.3–28.6, 20.3	81–125, 107	6.5–22.4, 13.4	95–115, 107	3–7, 5	6
30	1.60–6.60, 2.80	8.8–29.1, 17.3	83–318, 168	4.4–38.4, 16.0	80–120, 103	<1–13, 5	22
31	1.24–2.92, 2.06	4.8–36.4, 17.6	72–276, 137	6.8–31.5, 14.2	66–107, 88	5–31, 12	10
32	1.97–3.82, 2.87	18.9–40.3, 29.3	83–183, 125	4.1–14.8, 10.2	30–60, 51	5–27, 18	6
33	2.05–4.57, 3.10	22.7–50.7, 33.3	86–213, 142	7.2–12.4, 10.0	59–85, 76	1–14, 6	6
34	1.04–6.49, 2.61	5.6–60.0, 23.4	81–294, 166	1.9–16.6, 9.5	50–82, 69	<1–40, 17	9
35	1.09–9.83, 2.67	2.4–44.3, 13.6	70–371, 204	1.7–51.6, 10.4	60–91, 80	<1–40, 14	21
36	0.75–1.65, 1.20	1.8–10.4, 6.1	129–149, 139	2.0–5.9, 4.0	57–58, 58	33–53, 43	2
37	0.69–4.92, 2.29	0.8–10.1, 5.1	71–369, 214	0.6–34.4, 12.2	46–65, 53	4–56, 31	8
38	0.91–1.75, 1.20	0.6–9.7, 4.9	131–186, 153	0.4–8.0, 3.1	50–71, 63	22–53, 39	3
39	1.12–3.11, 1.81	5.4–29.7, 14.4	65–138, 110	5.0–17.0, 12.0	40–80, 63	13–43, 28	6
40	1.15–5.88, 3.17	6.3–59.7, 22.2	66–246, 174	7.5–126.1, 30.3	45–95, 68	<1–35, 12	21
41	1.30–2.77, 1.90	5.8–21.7, 12.2	61–327, 160	5.0–47.1, 15.8	43–100, 71	4–39, 21	10
42	0.90–2.19, 1.44	3.6–20.5, 10.1	50–174, 106	3.1–9.2, 5.5	60–100, 81	13–35, 25	6

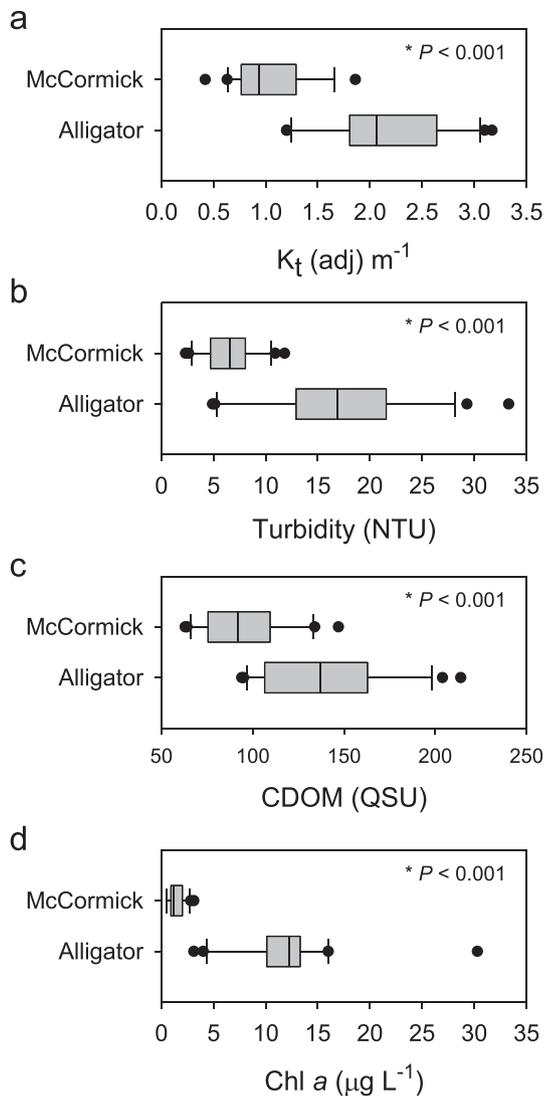


Fig. 3. Descriptive statistics of time-averaged site means of adjusted light attenuation coefficient, K_t (adj), (a), turbidity (b), CDOM (c), and chl a (d) at sites in McCormick and Alligator sub-estuaries. Boxes indicate the 25th and 75th percentiles of the site means, error bars indicate 10th and 90th percentiles of the site means, vertical lines indicate median of the site means, and dots are outliers. * indicates significant differences (Mann-Whitney test) between sub-estuaries. P indicates statistical significance.

and low water periods, respectively, in the McCormick sub-estuary, and 146 QSU and 127 QSU during the high and low water periods, respectively, in the Alligator sub-estuary. The high and low water level seasonal means of chl a were $1.9 \mu\text{g L}^{-1}$ and $1.1 \mu\text{g L}^{-1}$ during the high and low water periods, respectively, in the McCormick sub-estuary, and $13.0 \mu\text{g L}^{-1}$ and $11.1 \mu\text{g L}^{-1}$ during the high and low water periods, respectively, in the Alligator sub-estuary.

Turbidity, chl a , and CDOM were correlated with K_t (adj) (Table 2), suggesting that these variables contributed to water column light attenuation. The light attenuation component model using the measured water quality parameters and specific light attenuation coefficients obtained from the published literature for water (Lorenzen, 1972), turbidity (McPherson and Miller, 1994), CDOM (Kelble et al., 2005) and chl a (McPherson and Miller, 1994) predicted light attenuation coefficients with an $r^2 = 0.58$ and an RMSE = 0.77 m^{-1} (Fig. 5a). The RMSE of this model was 8% and 45% of the observed maximum (9.83 m^{-1}) and mean (1.73 m^{-1}) K_t (adj), respectively. The multiple linear regression relating the measured

quantities of turbidity, CDOM, and chl a to observed total light attenuation coefficients, K_t (adj), explained a greater proportion of the variance in K_t (adj) (Fig. 5b) relative to the model using published specific light attenuation coefficients and was therefore used to estimate the relative contributions of the component parameters to the total light attenuation coefficient. The multiple linear regression was statistically significant ($F_{3, 416} = 360$, $P < 0.001$) with an $r^2 = 0.72$ and RMSE = 0.60 m^{-1} (SPSS vers. 23). The RMSE of the multiple regression model was 6% and 35% of the observed maximum (9.83 m^{-1}) and mean (1.73 m^{-1}) K_t (adj), respectively. The coefficients determined for turbidity, CDOM, and chl a were significantly different from zero in the multiple regression model ($P < 0.001$ for each). The statistically-determined specific light attenuation coefficient \pm standard error for turbidity, k_{turb} , was $0.059 \pm 0.004 \text{ m}^{-1} \text{ NTU}^{-1}$ and compared very well with the coefficient of $0.062 \text{ m}^{-1} \text{ NTU}^{-1}$ as determined by McPherson and Miller 1994 and employed in the literature coefficient model. The statistically-determined specific light attenuation coefficient \pm standard error for CDOM, k_{CDOM} , was $0.008 \pm 0.001 \text{ m}^{-1} \text{ QSU}^{-1}$ and was ca. 20 \times higher than the literature value ($0.000424 \text{ m}^{-1} \text{ QSU}^{-1}$, Kelble et al., 2005) used in the literature coefficient model. The statistically-determined specific light attenuation coefficient \pm standard error for chl a , k_{chl} , was $0.024 \pm 0.004 \text{ m}^2 \text{ mg}^{-1}$ and was ca. 60% less than the literature value ($0.058 \text{ m}^2 \text{ mg}^{-1}$, McPherson and Miller, 1994) used in the literature coefficient model, but 71% greater than the mean ($0.014 \text{ m}^2 \text{ mg}^{-1}$) of experimentally-determined coefficients of Atlas and Bannister 1980. Confident interpretation of multiple regression coefficients is supported by the relatively low standard errors of the specific light attenuation coefficients and the high tolerances (tolerance = $1 - \text{multiple } r^2$) among the independent variables that exceeds the default value (tolerance = 0.1) in most statistical programs (Tabachnick and Fidell, 2007), including SPSS vers. 23.

The results of the multiple regression model indicated that K_{CDOM} contributed the most to light attenuation in both sub-estuaries with 63% and 45% contributions to K_t (adj) in the McCormick and Alligator sub-estuaries, respectively (Fig. 6a–b, Table 3). K_{turb} was the second largest contributor to light attenuation in both sub-estuaries with 31% and 41% contributions to K_t (adj) in the McCormick and Alligator sub-estuaries, respectively (Fig. 6a–b, Table 3). K_{chl} contributed 3% and 12% to light attenuation in the McCormick and Alligator sub-estuaries, respectively (Fig. 6a–b, Table 3). K_w contributed only 2–3% to light attenuation in both sub-estuaries (Fig. 6a–b, Table 3). The relative contributions of K_w and K_{chl} to light attenuation were little changed between high and low water level seasons in both sub-estuaries (Fig. 6a–b). The relative contributions of K_{CDOM} to light attenuation were ca. 10% greater in both sub-estuaries during the high water level season. The relative contributions of K_{turb} to light attenuation were 8% and 12% higher in the low water level season in the McCormick and Alligator sub-estuaries, respectively.

4. Discussion

This study's estimates of downwelling light transmission to the benthos of the mangrove lakes and bays relative to literature estimates of SAV minimum requirements of >5–40% of surface PAR at depth (Duarte, 1991; Kenworthy and Fonseca, 1996; Middelboe and Markager, 1997; Manuel et al., 2013) indicate that the underwater light environment may often be unsuitable for submerged aquatic vegetation (Table 1). 100% and 50% of the study sites experienced $\leq 40\%$ and $\leq 5\%$ of surface PAR light transmission to the bottom, respectively, at least once during the study period (Table 1). 83% and 12% of the study sites had mean levels of $\leq 40\%$ and $\leq 5\%$ of surface PAR light transmission to the bottom, respectively. Though

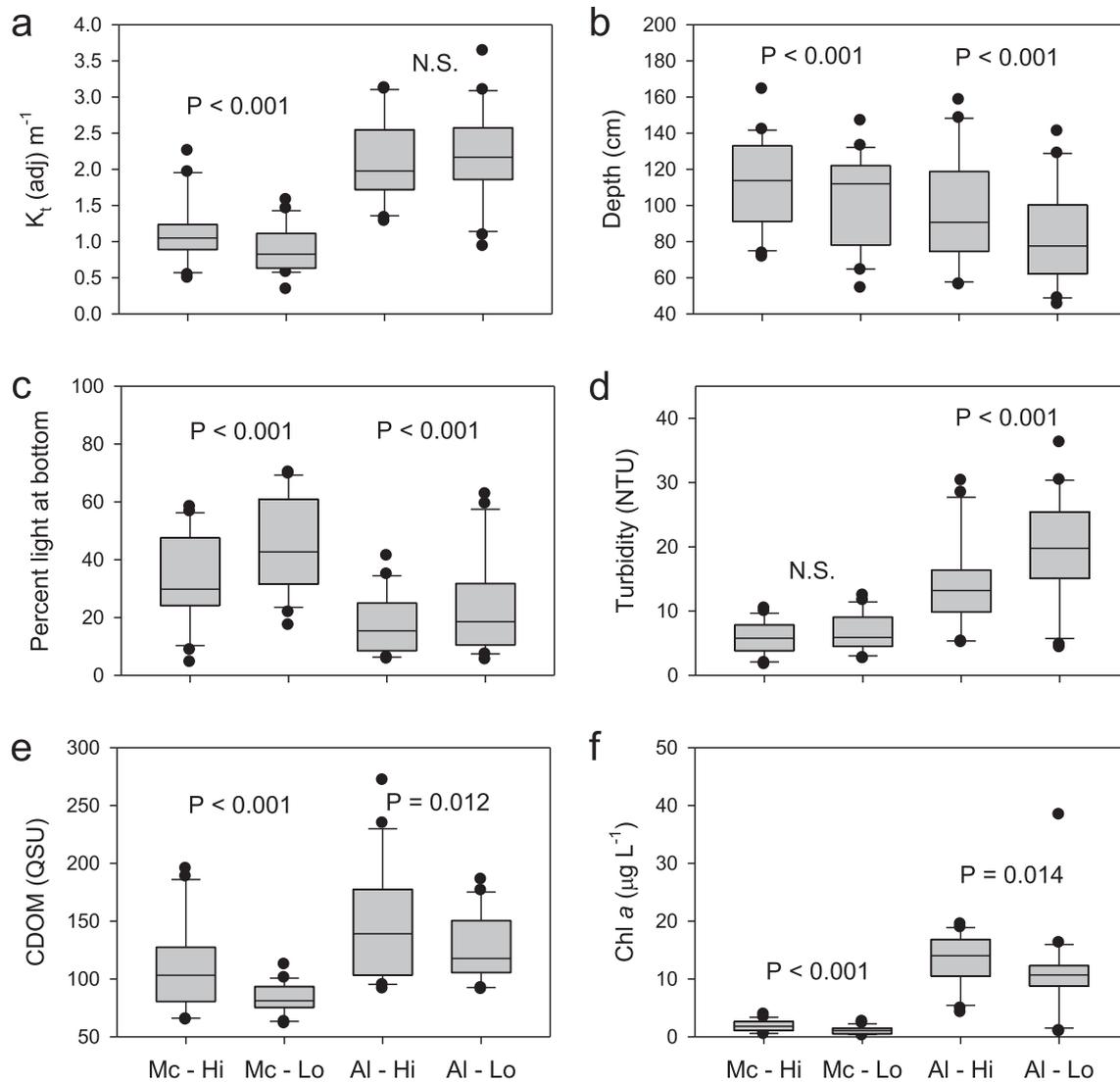


Fig. 4. Descriptive statistics of mean adjusted light attenuation coefficient, K_t (adj), (a), mean water depth (b), mean percent light at bottom (c), turbidity (d), CDOM (e), and chl *a* (f) between high and low water level seasons at sites in the McCormick and Alligator sub-estuaries. Boxes indicate the 25th and 75th percentiles of the site means, error bars indicate 10th and 90th percentiles of the site means, horizontal lines indicate median of the site means, and dots are outliers. *P* indicates statistical significance of Wilcoxon signed-rank tests examining within-site differences of the measured/calculated parameters between high and low water level seasons for the McCormick and Alligator sub-estuaries. N.S. indicates no statistical difference.

Table 2

Pearson correlation coefficient matrix for K_t (adj), turbidity, chl *a*, and CDOM variables. Below the diagonal are the correlation coefficients (*r*) for the correlation between the variables. Above the diagonal are the statistical significances of the correlations (*P*). **Boldface** type indicates correlations significant at $P < 0.05$.

	K_t (adj)	Turbidity	Chl <i>a</i>	CDOM
K_t (adj)		<0.01	<0.01	<0.01
Turbidity	0.65		<0.01	0.14
Chl <i>a</i>	0.67	0.53		<0.01
CDOM	0.56	0.05	0.39	

estimates of downwelling light attenuation may be best for comparing inherent optical properties of the water column (Smith, 1968), and corrections for sun angle were performed, the use of these estimates to determine light availability for SAV growth does not account for light reflected from sediment surfaces, differences in the amount of diffuse versus direct solar radiation in the atmosphere (e.g., cloudiness) that affect light transmission, differences

in SAV architecture (e.g., growth form and canopy height), and the ability of SAV to store photosynthate and survive short-periods of sub-optimal light availability (Lobban and Harrison, 1994; Alcoverro et al., 2001). In addition, the temporal frequency of light attenuation measurements of the present study was insufficient to estimate the duration of sub-optimal light availabilities. For all of these reasons, the estimates of light transmission to the benthos relative to the wide range of reported SAV minimum light requirements should be interpreted with caution. Light availability for both the *Chara* and *Halodule* communities in the study area may also be higher than that suggested from downwelling light transmission estimates alone because *Chara* grows tall in the study area with canopy heights often reaching the water surface and because of exposed light-colored carbonate sediments that reflect light upward in the *Halodule* communities (unpublished data).

Increasing SAV abundance by increasing light availability beyond estimated minimum SAV requirements may be difficult in these sub-estuaries because of the majority influence of CDOM on vertical light attenuation, a variable insensitive to direct

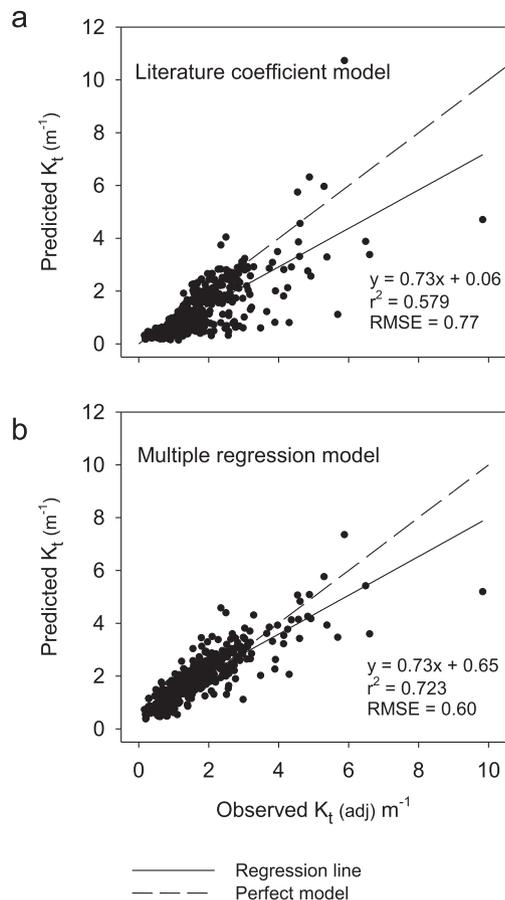


Fig. 5. Scatterplots of light attenuation coefficient, K_t , predicted from light attenuation coefficient partitioning models versus observed adjusted light attenuation coefficient, K_t (adj). Model using experimentally-determined specific attenuation coefficients from the literature (a) and model using coefficients determined from multiple linear regression (b).

management control. In order to achieve light transmission to the benthos >40% at 1-m depth, the light attenuation rate must be < 0.92 m^{-1} . The mean partial light attenuation coefficients for CDOM ranged from 0.72 m^{-1} in the McCormick sub-estuary to 1.05 m^{-1} in the Alligator sub-estuary (calculated from Table 3), suggesting that attenuation due to CDOM alone reduces light transmission to the bottom sufficiently to decrease the suitability of the benthos for SAV. The dominance of CDOM is similar to that observed in Albufera des Grau, Balearic Islands, Spain (Obrador and Pretus, 2008) and the Swan River estuary, Australia (Kostaglidis et al., 2005) (Table 3). In the Albufera des Grau, dissolved organic carbon (measured as a proxy for CDOM) exhibited temporal variation associated with the decomposition of SAV, suggesting an autochthonous source of CDOM (Obrador and Pretus, 2008). In contrast to the Albufera des Grau, but more similar to mangrove lakes of the present study, the elevated CDOM in the Swan River estuary appears to be a consequence of “catchment characteristics” and allochthonous input of decomposing material from surrounding coastal wetlands and swamps during seasonal (winter) rains (Kostaglidis et al., 2005). Similarly, CDOM concentrations in the study area increase during high water level periods when the surrounding mangroves are flooded during the wet season (Clark et al., 2002) releasing freshly leached CDOM from the decomposition of mangrove leaves and wood (Jaffe et al., 2004; Bergamaschi et al., 2012).

The greater contributions of CDOM to light attenuation in the

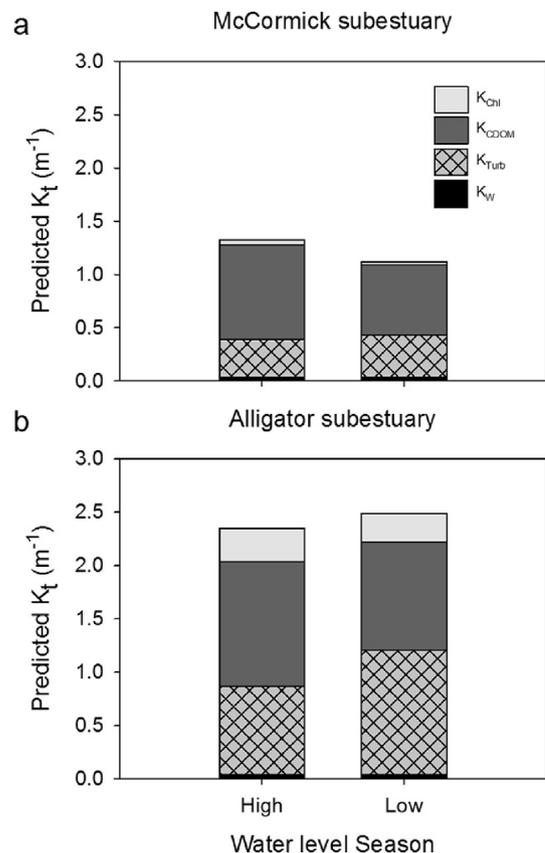


Fig. 6. Stacked bar chart depicting the contributions of chl *a*, CDOM, turbidity, and water to the total light attenuation coefficient during high and low water level seasons in the McCormick sub-estuary (a) and the Alligator sub-estuary (b). Component light attenuation coefficients were derived from time-averaged site means produced from the light attenuation coefficient partitioning model using specific attenuation coefficients determined from multiple linear regression.

studied mangrove lakes relative to the more downstream and open estuaries of Florida Bay, Tampa Bay, Charlotte Harbor, and the Indian River Lagoon (Table 3) are hypothesized to be the result of differences in both CDOM concentration and CDOM composition. Allochthonous CDOM originating from the surrounding mangrove swamp is reduced in concentration towards the lower estuary because of conservative mixing with marine waters (Clark et al., 2002; Jaffe et al., 2004). The 20-fold difference between the determined CDOM specific light attenuation coefficient for the study area ($k_{\text{CDOM}} = 0.008 \text{ m}^{-1}$) and that previously determined for downstream Florida Bay ($k_{\text{CDOM}} = 0.0004 \text{ m}^{-1}$, Kelble et al., 2005) also indicates that upstream or mangrove-derived CDOM has a much greater specific light absorption than CDOM in the lower estuary. These differences in the specific light absorption characteristics of CDOM suggest differing CDOM compositions between the upstream mangrove lakes and downstream Florida Bay. CDOM composition is determined by the organic matter sources (e.g., freshwater marsh vegetation, mangroves, submerged aquatic vegetation, phytoplankton, etc.), photolytic exposure and diagenetic decomposition histories (see Mostafa et al., 2013 for review). CDOM in the mangrove sub-estuaries of Florida Bay is predominantly mangrove-derived while that in downstream Florida Bay is characterized by greater proportions of seagrass-derived CDOM (Jaffe et al., 2004). CDOM in the downstream Everglades estuaries and Florida Bay is further altered by photo bleaching (Jaffe et al., 2004), while CDOM in the lakes and bays of the present study is more likely to be freshly leached from nearby mangroves and

Table 3

Comparison of mean light attenuation coefficient $\overline{K_t}$, and the mean percent contribution of light attenuation components for Florida and other estuaries. Component contributions of the present study determined from the multiple regression model.

Estuary	$\overline{K_t}$ (m ⁻¹)	Turbidity/Tripton (%)	CDOM/Color (%)	Chl <i>a</i> (%)	Water (%)	Reference
Mangrove Lakes (all)	1.73 ^a	38 ^b	51 ^c	9	2	Present study
McCormick sub-estuary	1.15 ^a	31 ^b	63 ^c	3	3	Present study
Alligator sub-estuary	2.33 ^a	41 ^b	45 ^c	12	2	Present study
Florida Bay, USA	0.59 ^d	89 ^e	1 ^c	2	8	Kelble et al., 2005
Florida Bay, USA	1.36 ^d	75 ^f	7 ^g	14	4	Phlips et al., 1995
Charlotte Harbor, USA	0.79 ^a	55 ^b	22 ^g	16	7	McPherson and Miller 1994
Tampa Bay, USA	0.73 ^a	54 ^b	13 ^g	27	6	McPherson and Miller 1994
Indian River Lagoon, USA	0.1–4.6 ^d	78 ^e	5 ^g	16	1	Christian and Sheng 2003
Indian River Lagoon, USA	0.77 ^h	42 ^b	25 ⁱ	25	7	Buzzelli et al., 2012
Swan River, Australia	1.47	8 ^e	66 ^j	NI	NI	Kostaglidis et al., 2005
Albufera des Grau, Spain	1.42	6 ^e	47 ^k	44	3	Obrador and Pretus 2008

NI = variable not included in results of stepwise multiple regression.

^a K_t adjusted for effects of solar elevation angle.

^b Turbidity measured in NTU.

^c CDOM measured in QSU.

^d No adjustments made for solar elevation angle.

^e Tripton measured as total suspended solids.

^f Tripton determined as total suspended solids minus estimated dry weight of phytoplankton.

^g Color measured in Pt-Co units.

^h K_t calculated as sum of light attenuation component coefficients.

ⁱ Color calculated from salinity using negative exponential function.

^j CDOM measured as absorption coefficient at 440 nm.

^k CDOM estimated as DOC.

therefore of different composition.

Higher CDOM concentrations in the Alligator sub-estuary relative to the McCormick sub-estuary may be explained by differences in watershed geography between the McCormick and Alligator sub-estuaries (Frankovich et al., 2012). The mangrove lakes of the Alligator sub-estuary are effectively separated from each other and from downstream Florida Bay by long, shallow, and tenuous creeks. In contrast, the shorter and wider creeks between the lakes of the McCormick sub-estuary and Florida Bay permit a greater exchange of upstream and downstream waters (Kelly et al., 2011) and therefore, dilution of CDOM concentrations.

It appears that alleviation of light limitation may be more possible in the McCormick sub-estuary if turbidity, the second largest contributor to light attenuation, can be reduced, but this is also unlikely. The mangrove-surrounded lakes and bays of the study area are lagoonal estuaries with no riverine influences that might supply suspended sediments; turbidity here and in other shallow water bodies originates from in-situ wave-resuspended sediments and is likely to be little affected by any upstream management control (Bachmann et al., 1999). Turbidity was higher at the shallower sites in the Alligator sub-estuary (mean depth = 90 cm) than at those in the McCormick sub-estuary (mean depth = 107 cm) and during low water level periods, possibly due to greater sediment resuspension from wave action in shallower water depths (Bachmann et al., 1999). Greater wind speeds in the study area during winter and spring increase sediment resuspension (Boyer et al., 1999) and were also likely to increase turbidity during the low water level periods. However, if salinity is reduced through increased freshwater flow, the oligohaline to mesohaline *Chara* communities may expand and decrease turbidity by decreasing sediment resuspension (Van den Berg et al., 1997).

Chl *a* contributed only 12% to light attenuation in the Alligator sub-estuary (Table 3) despite high phytoplankton abundance compared to that found in the more open Florida Bay to the immediate south (Fourqurean et al., 1993). Management reduction of phytoplankton abundance (chl *a*) through control of nutrient loading of upstream water sources is also an unlikely option to increase light availability because of the already low phosphorous concentrations in the P-limited upstream Everglades (Noe et al.,

2001).

This study also demonstrates the advantages of correcting calculated light attenuation coefficients for variations of solar elevation angle and of using location-specific statistically-determined specific light attenuation coefficients rather than using estimates determined from assumed similar estuaries. Uncorrected K_0 estimates were on average 13% higher than those that were corrected for variations in sun angle (Fig. 2), but overestimates were as high as 47% at times when sun angles were low. The observed overestimate range of <1–47% is very similar to that reported for nearby Tampa Bay and will bias temporal and spatial comparisons if sun angle corrections are not performed (Miller and McPherson, 1995). Measurements of chl *a*, CDOM, and turbidity were better fit to adjusted light attenuation coefficients using a multiple regression model to determine the component specific light attenuation coefficients rather than using assumed regionally relevant specific light attenuation coefficients (Fig. 5). As shown for k_{CDOM} in the present study, the determined values of specific light attenuation coefficients from different estuaries can be expected to differ because of possible likely differences in the composition of phytoplankton, CDOM, and particulates among estuaries. The varying compositions likely have different absorptive and scattering characteristics that will result in different specific light attenuation coefficients demonstrated herein. For example, k_{chl} determined from the phytoplankton in the mangrove lakes of the present study was 60% lower than that determined from Tampa Bay and Charlotte Harbor (McPherson and Miller, 1994) and was probably due to differences in phytoplankton community composition and the techniques used for chl *a* determination, both of which affect k_{chl} determinations (Kirk, 1994). The high performance liquid chromatography separation of phytoplankton pigments used by McPherson and Miller 1994 results in lower measured chl *a* concentrations relative to a given amount of light attenuation and therefore a higher value of k_{chl} (McPherson and Miller, 1994).

The relative importance of changes in salinity and light climate to the historical decline of SAV in the study area is still largely unknown because of the lack of water quality data when SAV loss was first observed in the middle of the 20th century. Seasonal patterns of *Chara* abundance in the mangrove lakes are negatively

correlated with salinity in the McCormick sub-estuary and positively correlated with light availability in the Alligator sub-estuary (Frankovich et al., 2012). This suggests that the poor light climate and increased salinity are both currently negatively affecting SAV abundance. Light limitation of SAV may be expected to be a persistent feature of the studied mangrove lakes. Saltwater intrusion resulting from diversions of freshwater flow from the Everglades not only increased nearshore salinities, but has also greatly expanded the coverage of mangroves around the study area since pre-drainage times (Smith et al., 2013) likely increasing CDOM deliveries. Reversing the expansion of mangrove forests is unlikely given present sea-level rise (Smith et al., 2013). Management actions to increase freshwater flow may dilute CDOM concentrations and change the relative contributions of CDOM sources and their associated optical properties. It may be premature to judge the effects of increased freshwater flow on CDOM contributions to light attenuation without knowing more about the optical properties and diagenesis of different CDOM source materials and their relative contributions to the CDOM pool. The efficacy of such an effort will depend upon the CDOM concentration that is the net product of CDOM production from mangroves and the increased dilution of this CDOM with increased water flow in the mangrove estuaries. Increased freshwater may also decrease phytoplankton concentrations by increasing cell export and decreasing estuarine residence time (Dickman, 1969), and by decreasing the relatively higher nutrient inputs associated with saltwater intrusion (Rudnick et al., 1999) and groundwater discharge (Price et al., 2006). Reduced salinities may also reduce osmotic stress and increase light use efficiency of brackish algal populations (French and Moore, 2003) enabling *Chara* growth at lower light levels. The combination of these possible benefits of increased freshwater deliveries may decrease light attenuation and increase the ability of SAV to grow under present low light conditions.

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