

Underwater Spectral Energy Distribution and Seagrass Depth Limits along an Optical Water Quality Gradient

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ABSTRACT. We measured in situ inherent optical properties and seagrass maximum depth distribution in widely differing optical water types, including turbid green waters of the Indian River Lagoon (IRL, Florida, USA), a mix of turbid and clear waters in Panama, and very clear waters in Belize. We used Hydrolight to model in situ spectral energy distributions and measured leaf absorbance spectra (*Thalassia testudinum*) to distinguish between photosynthetically available radiation (PAR) and photosynthetically usable radiation (PUR). Attenuation coefficients for PAR and PUR were nearly indistinguishable in Belize and Panama and differed only slightly in the IRL. Grass grew to depths of penetration of 33% of PAR in the IRL, 14% in Panama, and approximately 5% in Belize, although we expect the value for Belize is an underestimate because conditions more turbid than are typical were prevailing at the time of the measurements. Corresponding percentages for PUR were 27%, 12%, and 5% for IRL, Panama, and Belize, respectively. These regional differences in light requirements were striking, and less than half of the difference could be attributed to latitudinal variations in incident light. We conclude that factors other than spectral energy distribution that covary with water clarity control site-specific light requirements of seagrasses. Possibilities include epiphytes and sediment quality.

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INTRODUCTION

Seagrasses are important primary producers that play a role in the stability, nursery function, biogeochemical cycling, and trophodynamics of many coastal and estuarine ecosystems and as such are important for sustaining a broad spectrum of organisms (Hemminga and Duarte, 2000). Seagrasses are potentially sensitive indicators of declining water quality because of their high light requirements (11%–37% surface irradiance) compared to those of other aquatic primary producers with much lower light requirements (<1%) (Dennison et al., 1993; Zimmerman, 2003). Seagrass communities have declined in coastal regions worldwide (Orth et al., 2006), which is usually attributed to reductions in water clarity brought about, at least initially, by accelerated eutrophication in the coastal zone (Krause-Jensen et al., 2008).

Management efforts aimed at preserving and restoring seagrass systems generally focus on improving water clarity (Batiuk et al., 2000; Kenworthy and Haurert, 1991; Steward and Green, 2007), based on the high light requirements

of seagrasses and the reduction in light penetration associated with eutrophication (Ralph et al., 2007). Deciding on the extent of water quality improvements (or limit of allowable deterioration) requires more detailed knowledge of the wavelength-specific light requirements of seagrasses. Based on a survey of available literature, Carter et al. (2000) determined that mesohaline and polyhaline submerged grass communities in Chesapeake Bay require a long-term average of 22% of surface irradiance at the deep edge of the grass meadow for survival. Gallegos and Kenworthy (1996) determined a similar requirement for mixed beds of *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme* in the Indian River Lagoon (IRL) near Ft. Pierce, Florida. In contrast, Steward et al. (2005) found 20% to be near the minimum for the IRL, while the average light requirement was 33% of annual incident irradiance, similar to the wide range (24%–37%) reported for the southern Indian River Lagoon (Kenworthy and Fonseca, 1996). More recently, Duarte et al. (2007) analyzed 424 reports of seagrass colonization depths and light attenuation and found generally higher light requirements for plant communities growing in shallow, turbid waters than in clear, deep waters. The authors suggested that large differences in light requirements between shallow- and deep-growing seagrasses may be partially attributed to differences in the quality of light. Seagrasses may grow deeper in clear water because there is more high-energy blue light available for photosynthesis, whereas in shallow turbid water the shorter blue wavelengths are rapidly attenuated.

The wavelength specificity of light absorption by seagrasses has implications for setting water quality requirements needed to protect or restore these plants in eutrophic waters that are dominated by inefficient green wavelengths. The absorption of light by the complement of pigments (chlorophyll *a* and chlorophyll *b*) in seagrasses is highly wavelength selective, with absorption peaks in the blue (centered around 450 nm) and red (centered around 670 nm) regions of the visible spectrum, and a broad absorption minimum in the green between 500 and 600 nm (Drake et al., 2003; Zimmerman, 2003). Wavelengths of light that are poorly absorbed by the plant are relatively inefficient at driving photosynthesis (Drake et al., 2003; Falkowski and Raven, 2007).

Light requirements of seagrasses that have been determined to date (Batiuk et al., 2000; Kenworthy and Fonseca, 1996) have been based on photosynthetically available radiation (PAR, 400–700 nm) because of the widespread availability of underwater quantum sensors. PAR measurements weight quanta of all visible wave-

lengths equally. By contrast, measurements of photosynthetically usable radiation (i.e., PUR; see Morel, 1978) weight quanta in proportion to the efficiency with which they are absorbed. There are no sensors for direct measurement of PUR; it must be calculated from the underwater spectrum (measured or modeled) weighted by the relative absorption spectrum of the plant of interest.

Using a bio-optical model of light penetration in the mesohaline Chesapeake Bay, Gallegos (1994) determined that the 22% surface PAR requirement for seagrasses occurred at the same depth as the penetration of 16% of surface PUR. The distinction is potentially important because the penetration of PUR is more sensitive to the concentration of phytoplankton chlorophyll (i.e., eutrophication) than is the penetration of PAR, for the reason that phytoplankton chlorophyll absorption selectively removes those same wavelengths most efficiently used in photosynthesis by seagrass. Thus, by basing light requirements on PUR rather than on PAR, we would predict greater restoration benefit from chlorophyll reduction, and greater seagrass losses from chlorophyll increases, than by light requirements based on PAR (Gallegos, 1994).

The objective of this work was to determine whether the distinction between PAR and PUR requirements could be determined from in situ depth distributions of seagrass communities. The distinction cannot be drawn from depth distributions at a single site such as Chesapeake Bay or the IRL, because within these systems the underwater spectrum is peaked in the green, and thus there is insufficient spectral variability in available light to differentiate between depth limits based on PAR compared with PUR. The gradient of optical water quality types across locations of the Smithsonian Marine Science Network, however, offers a potentially ideal scenario for making this determination. All three of the dominant seagrass species found in the IRL also occur in the tropical waters of Carrie Bow Cay, Belize, and Bocas del Toro, Panama. In optically clear waters, the underwater spectrum peaks in the blue, near an absorption peak of chlorophyll *a* or *b*. In blue water, therefore, PUR penetrates deeper than PAR, and plants should grow to relatively deeper depths in blue tropical waters if PUR rather than PAR is the determining factor. To investigate this distinction, we surveyed seagrass distributions and measured inherent optical properties (IOPs), from which we calculated underwater light spectra at the deep edges of grass beds, to test the hypothesis that across the optical water quality gradient seagrass would grow to a consistent depth of penetration of PUR but a variable percentage of PAR.

METHODS

STUDY SITES

Station locations are shown in Figure 1. We occupied stations in the clear tropical waters off Carrie Bow Cay, Belize (station Blue Ground Range, BGR), and in Bahia Almirante, Panama (station STRI [Smithsonian Tropical Research Institute]), a station receiving colored-water discharge from a nearby creek in Panama (station SN03), and the more eutrophic waters of the Indian River Lagoon, Florida (ICW194; see Figure 1). Detailed characteristics of these sites are given by Lang in the Introduction to this volume (Lang, 2009).

OPTICAL PROPERTIES

We measured in situ profiles of IOPs, the spectral absorption and beam attenuation coefficients, at nine wavelengths (412, 440, 488, 510, 532, 555, 650, and 715 nm)

using a WETLabs ac-9 instrument with a 0.1 m path-length, equipped with a pressure sensor to measure depth. A Seabird SBE-5T pump provided water flow to the ac-9 and a WETLabs MPAK unit that controlled pump and instruments and logged data.

Measured absorption and beam attenuation coefficients were corrected for temperature according to the manufacturer's protocols. We corrected absorption coefficients for scattering errors (Kirk, 1992) by the Zaneveld et al. (1994) algorithm that subtracts a fraction of measured scattering coefficient from absorption (Equation 1):

$$a_{t-w}(\lambda) = a_m(\lambda) - \varepsilon(c_{t-w}(\lambda) - a_m(\lambda)) \quad (1)$$

where $a_{t-w}(\lambda)$ is the scattering-corrected absorption coefficient less pure water absorption at wavelength λ , a_m is the measured non-water absorption coefficient subject to scattering error, c_{t-w} is the measured non-water beam attenuation coefficient, and ε is a coefficient that accounts

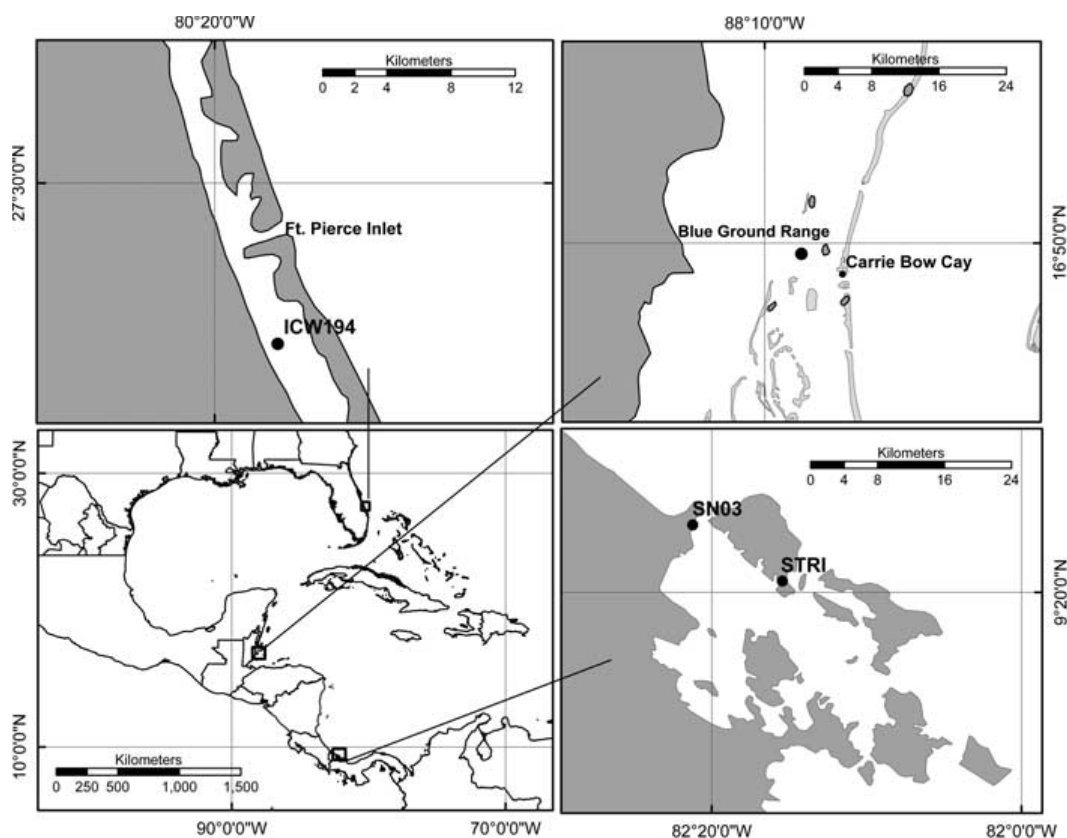


FIGURE 1. Locations of stations in the Indian River Lagoon, Florida (upper left), Belize (upper right), and Panama (lower right). Lower left panel shows overview of Caribbean. Light gray shading in Belize panel indicates coral reef habitat.

for overall errors with the reflective tube absorption meter of the ac-9 that result from a failure to collect all scattered light (Kirk, 1992). In this work we verified the assumption that non-water absorption at the longest ac-9 wavelength (715 nm) was not measurable in the laboratory (Tzortziou et al., 2006). Thus, we calculated ε by Equation 2:

$$\varepsilon = \frac{a_m(715)}{c_{t-w}(715) - a_m(715)} \quad (2)$$

We measured the absorption spectrum of *Thalassia testudinum* leaves in an integrating sphere (LICOR 1800-12S) interfaced to an Ocean Optics USB2000 spectrometer. A clean segment of leaf was placed on a microscope slide over the opening to the sphere and illuminated with a fiberoptic microscope light source. Black tape on the slide obscured the portion of the opening not covered by the leaf. Percent transmittance (%T) of the leaf was calculated referenced to the slide and tape without a leaf in place. Absorbance was calculated as $-\ln(\%T)$, and the spectrum was normalized to the value at the absorption peak at 675 nm. Measurements on eight leaves collected from the deep edge at the site in Belize were averaged. Similar measurements made in Panama had similar results.

RADIATIVE TRANSFER MODELING

To calculate spectral diffuse attenuation coefficients and underwater light spectra, we used the commercially available radiative transfer model, Hydrolight 4.2, which is extensively documented by Mobley (1994). User input consists of specifications for IOPs, boundary conditions, and assumptions on inelastic scattering processes. We used the pure-water absorption coefficients of Pope and Fry (1997) and pure-water scattering coefficients for freshwater from Buiteveld et al. (1994). We used in situ estimates of absorption, attenuation, and scattering coefficients binned at 0.5 m intervals. Following Tzortziou et al. (2006), we used the Fournier-Forand scattering-phase function, the shape of which was shown by Mobley et al. (2002) to be well specified by the backscattering ratio. We omitted inelastic scattering processes because our interest is in downwelling irradiance, and these processes primarily affect only calculations of upwelling radiance. For incident irradiance and the distribution of total irradiance between direct and sky irradiance we used the built-in RADTRAN routine for the time, location, and estimate of approximate cloud cover.

From the simulations of spectral downwelling irradiance we calculated PAR according to its definition (Equation 3):

$$PAR(z) = \int_{400}^{700} Q(\lambda, z) d\lambda = \int_{400}^{700} \frac{E_d(\lambda, z)}{h\eta} d\lambda \quad (3)$$

where Q is the quantum flux, E_d is the spectral downwelling irradiance in energy units, h is Planck's constant, λ is the wavelength and $\eta = 2\pi c/\lambda$ is the frequency of light, and c is the speed of light in vacuum. PUR was calculated in an analogous manner, weighted by the plant absorption spectrum, measured at the deep edge of the Belize site:

$$PUR(z) = \int_{400}^{700} Q(\lambda, z) \tilde{a}_{Tb}(\lambda) d\lambda \quad (4)$$

where $\tilde{a}_{Tb}(\lambda)$ is the absorption spectrum of *T. testudinum* normalized to its peak at 675 nm and to unit sum. For comparison of attenuation rates, PAR and PUR were both normalized to their values at the surface.

SEAGRASS SURVEYS

At each sampling site a pair of scuba divers entered the water to visually confirm the seagrass bed (*T. testudinum*) deep edge, defined as the visible transition between vegetated and unvegetated bottom. Once the physical boundaries of the meadow edges were identified underwater, the divers laid out two 10 m long transects parallel to the edge of the seagrass bed. At 1.0 m intervals along each transect, the divers visually estimated seagrass cover in a 0.25 m² quadrat using the Braun-Blanquet scale (1965). The Braun-Blanquet cover abundance scale is a visual assessment technique for estimating the canopy cover. Values are 0.1 = solitary shoot, with small cover; 0.5 = few shoots, with small cover; 1 = numerous, but less than 5% cover, 2 = 5%–25% cover, 3 = 25%–50% cover, 4 = 50%–75% cover, and 5 = more than 75% cover.

At the same location each diver counted the number of seagrass short shoots in either a 0.25 m² or 0.0625 m² quadrat, depending on the shoot density. Short shoot counts were multiplied by the appropriate scaling factor and averaged for the 10 quadrats to obtain an estimate of the number of short shoots per square meter. For comparison of deep edge seagrass characteristics, we also surveyed relatively shallow sites at the Blue Ground Range station in Belize (2.4 m) and the STRI station in Panama (1.8 m). At SN03 in Panama we only surveyed at the deep

edge. Deep edge data for the IRL are from annual surveys by the South Florida Water Management District (http://my.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq_id=1797).

RESULTS

SEAGRASS DEPTH LIMITS

At the Blue Ground Range station in Belize, the deep edge of the *Thalassia testudinum* meadow was located at 10–11 m. The deep edge was a distinct transition from a sparse cover of *T. testudinum* to unvegetated, fine carbonate mud. Recently germinated seedlings of the small opportunistic species *Halophila decipiens* were observed just outside of the deep edge of the *T. testudinum* meadow. Braun-Blanquet cover values ranged from 0.5 (a few individual short shoots) to 1 (<5%). *Thalassia testudinum* short shoot densities ranged from 0 to 48 shoots m⁻², averaging 22.4 shoots m⁻². At the shallow Blue Ground Range transect, *T. testudinum* Braun-Blanquet scores ranged from 3 to 4, indicating that cover generally varied from 25% to 75%, while densities ranged from 176 to 416 shoots m⁻², averaging 310 shoots m⁻². At the shallow station *T. testudinum* was 14 times more dense than at the deep edge. No other seagrass species were observed at this station.

At the STRI station in Panama we located the deep edge of the *T. testudinum* at 8.5 m. The transition edge of the *T. testudinum* meadow was distinct; however, there was considerably more *H. decipiens* just downslope of the edge than there was at the Blue Ground Station in Belize. *Thalassia testudinum* short shoot densities ranged from 0 to 56 shoots m⁻², averaging 18 shoots m⁻², similar to the deep edge at the Blue Ground Range Station in Belize. Braun-Blanquet values ranged from 0 to 1, indicating that cover was generally less than 5%. We also observed three quadrats with a relatively sparse cover of *Halodule wrightii*. At the shallow STRI station (1.8 m), *T. testudinum* densities ranged from 160 to 528 shoots m⁻² with an average of 465, 25 times the density at the deep edge and more dense than the shallow station at Blue Ground Range in Belize. Braun-Blanquet values ranged from 3 to 4, similar to the shallow station at Blue Ground Range (BGR) in Belize.

At the SN03 site in Panama, the deep edge of the *T. testudinum* bed was located at 2.4 m. Short shoot densities ranged from 0 to 288 m⁻², with a mean value of 114. The deep edge of the *T. testudinum* meadow was marked

by a transition from *T. testudinum* to unvegetated sediment. Braun-Blanquet scores ranged from 0 to 3, indicating cover values less than 50%.

Seagrass depth limits in the IRL at the site where optical measurements were made in 2001 were reported as 0.92 m for beds described as continuous and dense, with a lower limit of 50% to 60% cover.

OPTICAL PROPERTIES

A wide range of optical properties was observed among the four sites (Figure 2a). Based on absorption spectra, Belize had the clearest water while the most turbid water occurred in the IRL. The two sites in Panama were intermediate. The rank order of sites was different for scattering coefficients (Figure 2b), with scattering coefficients at the Panama shallow site (SN03) being the highest and the Panama deep site (STRI) the lowest.

ABSORPTION SPECTRUM

Normalized absorption by *T. testudinum* was similar to measurements by other investigators (Zimmerman, 2003), having peaks in the red wavelengths (~680 nm), a broad maximum at blue wavelengths (400–490 nm), and a trough at green wavelengths (~525–625 nm) (Figure 3, solid line). This spectrum was used to calculate PUR from simulated downwelling spectral irradiance according to Equation 4. However, even at the local minimum at 555 nm, measured absorption was still 37% of the red peak. On considering that *T. testudinum* has no chlorophyll pigments that absorb green wavelengths (Zimmerman, 2003), we also constructed a hypothetical photosynthetic action spectrum based on chlorophyll absorption alone, consisting of Gaussian curves with peaks at 410, 430, 455, 642, and 680 nm for an alternate calculation of PUR (see Figure 3, dashed line). The hypothetical action spectrum is expected to produce the maximal separation between PAR and PUR, especially in turbid green water, because the trough in the hypothetical chlorophyll absorption spectrum at green wavelengths is much more pronounced compared with the measured absorption spectrum, which includes an unquantified contribution by photosynthetic carotenoids. This hypothetical chlorophyll-based action spectrum serves as a site-independent sensitivity test for the greatest possible difference between PAR and PUR for a higher plant. We did not measure absorption spectra in the IRL, so they are unknown. The hypothetical spectrum allows a comparison among sites in the absence of measurements at all sites.

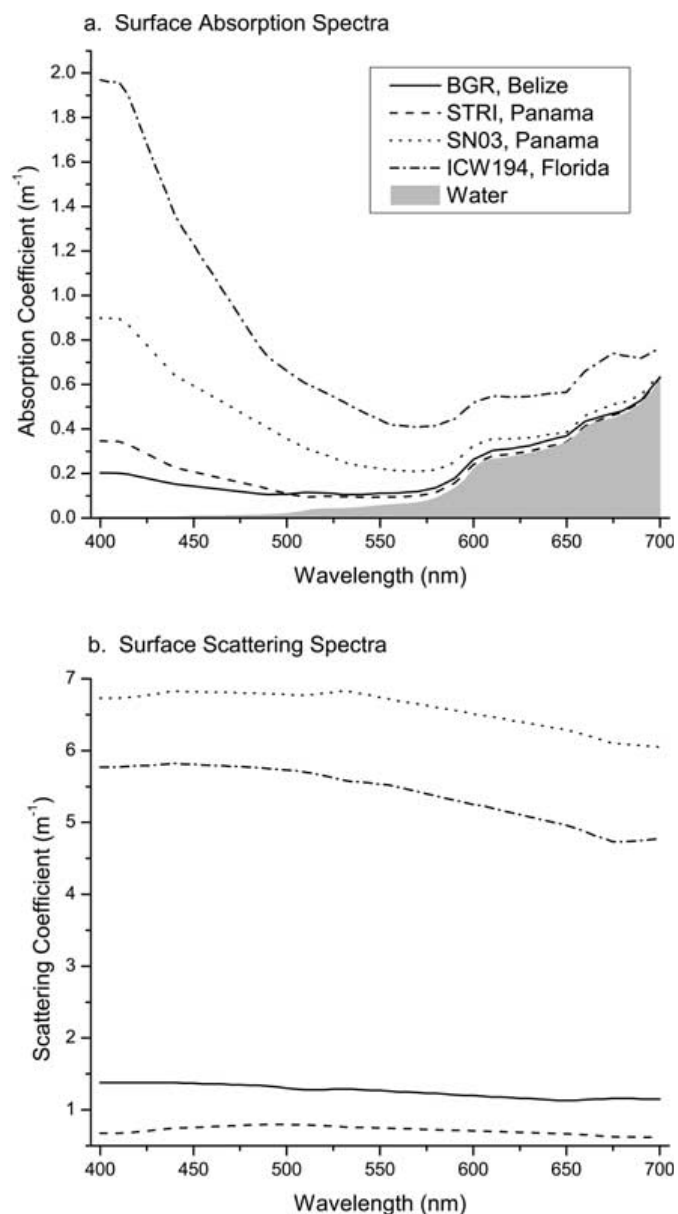


FIGURE 2. Surface water absorption spectra (a) and surface water scattering spectra (b) at sites sampled in Belize, Panama, and Florida.

PAR AND PUR PROFILES

Profiles of normalized downwelling PAR and PUR based on the measured absorption spectrum (PUR_m) and PUR based on the hypothetical action spectrum (PUR_h) are shown for the stations having the least and the most separation between PAR and PUR in Figure 4. The diffuse attenuation coefficients for each of the three quantities are reported for all stations in Table 1. At the Blue

Ground Range station in Belize, diffuse attenuation coefficients for PAR and PUR_m were indistinguishable, while that for PUR_h was only 7% higher than for PAR (Table 1). The largest differences among the three attenuation coefficients occurred at the IRL. The relative differences between attenuation coefficients for PAR and PUR_m (13%) and between PAR and PUR_h (31%) were similar for the IRL and SN03 site in Panama, although the absolute coefficients were smaller at SN03 (Table 1).

The percentages of surface light remaining at the deep edges of the seagrass beds varied widely among the locations, from about 5% at the Blue Ground Range site in Belize to about 30% at the IRL (see Table 1). The percentages based on PUR were, as expected, lower than those based on PAR, but the differences among sites was still large (Table 1). Because of the extremely large differences among sites in the percentage of light at the seagrass bed deep edge, the calculation of PUR did not yield a consistent value across sites. The overall range was, however, somewhat smaller for PUR than for PAR (Table 1). Spectra of downwelling irradiance at the deep edges calculated by Hydrolight are shown in Figure 5. The overall fraction of surface irradiance remaining at the deep edges at the different locations follows the percentages in Table 1. Qualitative differences in the spectra of light remaining at

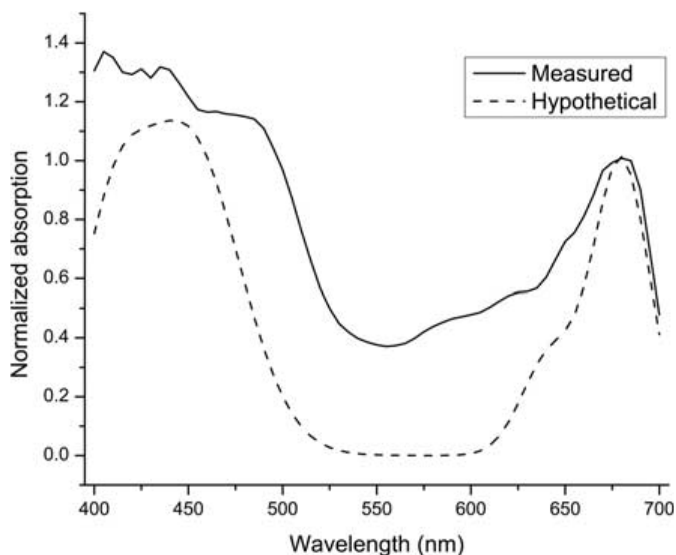


FIGURE 3. Normalized absorption spectra used for calculating photosynthetically usable radiation, based on absorption spectrum measured on *Thalassia testudinum* leaves (solid line), and a hypothetical action spectrum derived by assuming only light absorbed by chlorophylls *a* and *b* drive photosynthesis in *Thalassia* (dashed line).

the deep edges also occur. Because of absorption by water, virtually no light is present at wavelengths greater than 600 nm at the BGR location in Belize and very little at STRI in Panama. Increasing amounts of red wavelengths are present at the SN03 and IRL sites as a result of the shallower depths of the deep edges. The peaks of the in situ spectra shift progressively toward green wavelengths along the progression from BGR to IRL, and the greatest similarities are at 400 to 410 nm, where the percentage of surface irradiance remaining ranges from 2% to 6%.

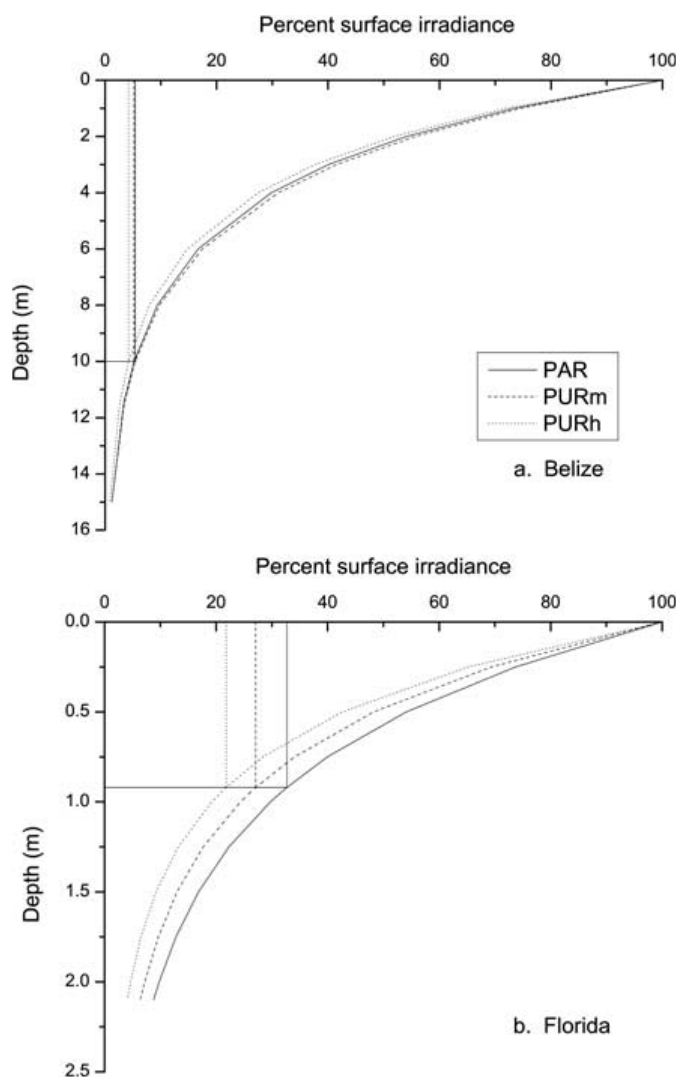


FIGURE 4. Vertical profiles of photosynthetically active radiation (PAR, solid line), and photosynthetically usable radiation (PUR) based on measured absorption spectrum (PUR_m; dashed line) and hypothetical action spectrum (PUR_h; dotted line) in (a) Belize and (b) the Indian River Lagoon (IRL), Florida. Profiles were normalized to the irradiance incident at the surface (100%).

TABLE 1. Depths of seagrass deep edge (Z_{\max}) and attenuation coefficients for photosynthetically active radiation (K_{PAR}) and photosynthetically usable radiation (PUR) weighted by measured absorption spectrum of *Thalassia testudinum* leaves (K_{PURm}) or weighted by a hypothetical action spectrum (K_{PURh} ; see Figure 2). Percentage of surface light penetrating to the seagrass deep edge is given in parentheses.

Site ^a	Z_{\max} (m)	K_{PAR} (m^{-1})	K_{PURm} (m^{-1})	K_{PURh} (m^{-1})
BGR, Belize	10	0.293 (5.2%)	0.293 (5.4%)	0.314 (4.2%)
STRI, Panama	8.5	0.232 (13.6%)	0.247 (12.0%)	0.304 (7.4%)
SN03, Panama	2.4	0.836 (14.1%)	0.945 (11.0%)	1.098 (7.7%)
IRL, Florida	0.92	1.157 (32.7%)	1.301 (27.1%)	1.52 (21.8%)

^a BGR, Blue Ground Range; STRI, Smithsonian Tropical Research Institute; SN03, Panama creek station; IRL, Indian River Lagoon.

DISCUSSION

At all three study sites we were able to locate a distinct deep edge of the *Thalassia testudinum* meadows, characterized by a transition from moderate and sparsely vegetated seagrass to either unvegetated substrate or patches of the smaller, low light adapted seagrass *Halophila decipiens*. Where we were able to sample shallower sites in Belize and Panama, there were substantially higher densities of *T. testudinum*. The presence of *H. decipiens* at the Blue Ground Range (BGR) station in Belize and the STRI site in Panama further confirmed that we were sampling at light-limiting edges of the *T. testudinum* distribution. *Halophila decipiens* is a small, ruderal species of seagrass commonly found growing in deep or turbid water and has lower light requirements than *T. testudinum* (Kenworthy, 2000; Gallegos and Kenworthy, 1996; Kenworthy et al., 1989). The presence of *H. decipiens* at these two stations was a good indication of light-limiting conditions for *Thalassia*. Although we did not record *H. decipiens* at SN03 in Panama, a thorough visual examination by divers at deeper depths than the observed *T. testudinum* distribution confirmed there were no seagrasses growing beyond 2.4 m depth.

Attenuation coefficients for PAR and PUR were nearly indistinguishable in Belize and Panama and differed only slightly in the IRL. Based on these one-time profiles, we calculated that seagrass grew to depths of penetration of

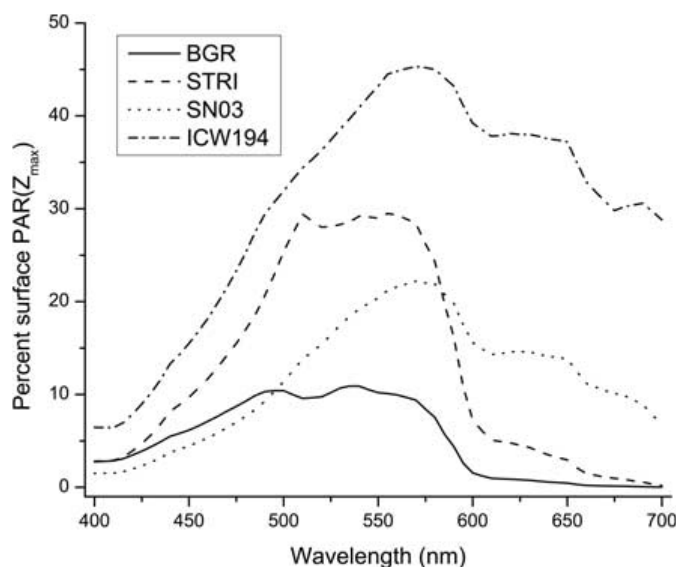


FIGURE 5. Spectra of photosynthetically active radiation (PAR) at the depth of the seagrass deep edge (Z_{max}) in Belize (BGR, solid line), Panama (STRI, dashed line, and SN03, dotted line), and Florida (IRL [ICW194], dot-dashed line).

33% of PAR in the IRL, 14% in Panama, and approximately 5% in Belize. Corresponding percentages for PUR were 27%, 12%, and 5% for IRL, Panama, and Belize, respectively. The accuracy of these estimates depends on the degree to which the profiles were measured under conditions that are typical for their respective growing seasons. We are fairly certain this was *not* the case in Belize, where strong northerly winds, atypical for the season, blew for several days before and on the day of sampling. Horizontally sighted Secchi disk visibility at a seagrass bed near Twin Cays was 5.5 m during the time of our measurements, compared with annual means of 10.1 m (± 0.38 m SE) for 2004 and 8.9 m (± 0.25 m SE) for 2005 (see Koltes and Opishinski, 2009: fig. 6, this volume). If the water column were more strongly stirred with higher than typical concentrations of particulate matter, then our estimates for Belize would be biased low, as we suspect they are. The estimated PAR light requirements for the IRL are, however, based on more frequent visits and are in agreement with other published estimates (Kenworthy and Fonseca, 1996; Steward et al., 2005). The limitation of our approach was the inability to determine the integral of light requirements for the whole growing season from only a few days of measurements. Because of this limitation, it is unlikely that the observed depth distribution of the seagrasses is fully captured by PAR and PUR

percentages calculated, and repeating this study during another season could yield different percentages.

Nonetheless, assuming that the light requirements for seagrasses at Belize are similar to those in Panama, the regional differences in light requirements between the IRL and the two tropical sites remain striking. Qualitatively, the differences are consistent with the observations of Duarte et al. (2007) that seagrasses growing in shallow, turbid waters (e.g., IRL) have higher light requirements than those growing in clear, deep water (Panama, Belize). Calculation of PUR closed the gap only slightly, leading us to conclude that factors other than spectral energy distribution contribute substantially to site-specific light requirements of seagrasses, especially at the deep edges. An extended growing season in the more tropical locations of Belize and Panama could possibly account for some of the difference. The tropical sites receive about 7% more incident radiation annually than the IRL site, most of which occurs during winter months (November through February) when temperatures are also more favorable in the tropics. Other possible differences between sites include leaf-shading epiphytes, sediment quality (e.g., grain size or organic matter content), and possible periods of low oxygen in thermally stratified deeper waters. These latter factors have management implications because they are all affected by coastal eutrophication. Improved understanding of the factors accounting for site-specific differences in seagrass light requirements is, therefore, urgently needed.

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