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Periphyton as a UV-B filter on seagrass leaves: a result of different transmittance in the UV-B and PAR ranges

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Abstract

Periphyton is considered detrimental to seagrasses as it reduces the amount of light, i.e. photosynthetically available radiation (PAR), that reaches the plant surface. This study evaluated the possibility that periphyton can also be beneficial to seagrasses by reducing ultraviolet (UV)-B radiation that reaches seagrass leaves. Periphyton on UV-B transparent artificial leaves transmitted a significantly lower amount of radiation in the UV-B than in the PAR range. Therefore, periphyton is an effective UV-B filter on seagrass leaves.

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1. Introduction

The increase in nutrient concentrations in coastal waters (eutrophication) has led to the decline of seagrass abundance in many locations around the world (Orth and Moore, 1983; Cambridge and McComb, 1984; Silbertstein et al., 1986; Walker and McComb, 1992; Short and Wyllie-Echeverria, 1996). Eutrophication often leads to increased phytoplankton growth in the water column and periphyton (here defined as the complex matrix of living and dead organisms as well as mucus and sediment particles; Borowitzka and Lethbridge, 1989) on seagrass leaves (Phillips et al., 1978; Dennison et al., 1993; Wear et al., 1999), processes that reduce the light availability to benthic vegetation such as seagrasses (Sand-Jensen,

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1977; Bulthuis and Woelkerling, 1983; Kemp et al., 1983). As a result, seagrass beds may be completely lost (Silbertstein et al., 1986; Short and Burdick, 1996), their density may be reduced (Bulthuis, 1983; Short et al., 1995) and/or their depth of distribution may become shallower (Duarte, 1991; Arnold et al., 2000). When seagrasses are forced into shallower waters, they become exposed to additional environmental stresses such as increased periods of desiccation, higher salinities, increased wave energy and elevated ultraviolet (UV)-B levels (Dawson and Dennison, 1996; Koch, 2001).

Although seagrasses can acclimate to moderate UV-B levels via the synthesis of UV-B absorbing pigments (Abal et al., 1994; Dawson and Dennison, 1996; Detrés et al., 2001), elevated levels of UV-B radiation have been shown to be detrimental to seagrasses (Trocine et al., 1981; Wells and Nachtwey, 1982; Larkum and Wood, 1993; Dawson and Dennison, 1996). Damage was found to occur in chloroplasts (Dawson and Dennison, 1996) leading to inhibition of photosynthesis (Wells and Nachtwey, 1982; Larkum and Wood, 1993), a shift in depth distribution (Trocine et al., 1981; Dawson and Dennison, 1996), and a reduction in competitive potential (Dawson and Dennison, 1996). Based on the observation that photosynthesis of seagrasses is less inhibited by UV-B when these plants are covered by periphyton than when they are periphyton-free (Trocine et al., 1981), we hypothesize that relatively low periphyton densities may be beneficial to seagrasses. Low periphyton densities are here defined as those that do not negatively interfere with photosynthesis, i.e. periphyton densities that allow seagrasses to still photosynthesize near their maximum rate. This UV screening process of periphyton may be of particulate relevance in oligotrophic tropical marine environments where UV-B levels are high and periphyton loads relatively low when compared to temperate estuaries (personal observation). While UV-absorbing pigments in periphytic algae can reduce the magnitude of UV-B induced damage to the algae themselves (Post and Larkum, 1993), they could also pose a potential benefit to the seagrasses they cover. The goal of this study was to test the hypothesis that low densities of periphyton may be beneficial to seagrasses by filtering UV-B radiation.

2. Materials and methods

2.1. Study sites

The experiment was conducted at a relatively pristine and at a eutrophic site in the summer of 2001. The relatively pristine site (Boynton et al., 1996; Chaillou et al., 1996), Chincoteague Bay (38°12'N, 75°10'W), is a coastal lagoon located between Chesapeake Bay and the Atlantic Ocean (east coast of the USA). Chincoteague Bay is colonized by extensive but relatively short (20 cm) *Zostera marina* beds. The eutrophic site, Horn Point Beach (38°37'N, 76°07'W), is located in the Choptank River (tributary of Chesapeake Bay) and, during the study period, was colonized by a few small (<1 m diameter) patches of *Ruppia maritima*. Both sites are apparently suitable seagrass habitats (Table 1) as the light availability is within the limits established in Dennison et al. (1993) and the sediment characteristics and wave heights are within the limits established in Koch (2001).

Table 1

Habitat characteristics (mean \pm S.D. (*n*)) of the two seagrass sites during the study period (Summer 2001)

	Chincoteague Bay	Horn Point Beach
Temperature ($^{\circ}$ C)	24.2 \pm 2.5 (3432)	26.7 \pm 1.6 (3396)****
Salinity	35 (6)	12 (5)
Maximum MTL seagrass depth (m)	0.8 (3)	1 (3)
Wave height (cm) (minimum/maximum)	6.1 \pm 1.7 (804000) (2.2/11.4)	6.0 \pm 1.8 ns (858000) (1.0/11.6)
Light on the bottom at noon (μ mol photons $m^{-2} s^{-1}$)	1204 \pm 566 (6)	766 \pm 434 ns (5)
Light attenuation coefficient (m^{-1})	0.56 \pm 0.36 (6)	0.99 \pm 0.38 ns (5)
Sediment silt + clay (<63 μ m; %)	2.4 \pm 0.2 (3)	7.7 \pm 0.5 (3)
Sediment organic content (%)	0.4 \pm 0.02 (3)	1.0 \pm 0.03 (3)
Water column nitrate + nitrite (μ M)	0.05 \pm 0.03 (18)	7.65 \pm 1.64**** (15)
Water column ammonium (μ M)	1.51 \pm 0.38 (18)	3.50 \pm 0.89**** (15)
Water column orthophosphate (μ M)	0.46 \pm 0.33 (18)	0.38 \pm 0.11 ns (15)

****: Significant differences (*t*-test, $P < 0.0001$) between sites; ns: non-significant differences. No other levels of significance ($P < 0.05$, 0.01 and 0.001) were found. MTL stands for mean tidal level.

2.2. Experimental design

Artificial seagrass leaves (0.9 cm \times 20 cm) were constructed of a flexible UV-B-transparent plastic (Aclar[®], Honeywell, Pottsville, PA) and were attached (4 cm apart) to negatively buoyant frames. A small foam float was attached to the top of each artificial leaf ($n = 10$ per frame) to simulate the natural buoyancy of seagrass leaves. Five frames were placed in a bare patch within a dense *Z. marina* bed in Chincoteague Bay and four other frames were placed at Horn Point Beach. At both sites, the frames were positioned at a depth of approximately 0.5 m (mean tidal level), a common depth for seagrass growth in these areas. Ten artificial leaves (strips hereafter) were collected at days 1, 3, 5, 7 and 12 after deployment in Chincoteague Bay and after 1, 3, 5 and 7 days at Horn Point Beach. The strips were cut from the frames and placed in plastic bags while still underwater to minimize any possible impact to the periphyton.

On the day of deployment as well as on the days of collection, triplicate water samples were taken in mid water column and were analyzed for nitrite + nitrate, ammonium and orthophosphate according to Whitley et al. (1981). Additionally, light (photosynthetically available radiation, PAR) measurements were made just below the surface and just above the sediment using an underwater spherical quantum sensor (LI193-SA, LiCor, Lincoln, NE). These data were then used to calculate the light attenuation coefficient (K_d) with the Lambert–Beer equation. Temperature was recorded every 5 min over the duration of the experiment by a TidBit temperature logger (Onset Computers, Pocasset, MA) positioned in mid water column.

After collection, 5 cm sections were cut from the middle of the strips and carefully placed in quartz cuvettes filled with autoclaved and filtered (GF/F) seawater from the study site. The periphyton remained intact as much as possible. The cuvettes were placed in a dual spectrophotometer (Hitachi U1113) equipped with an integrating sphere and scanned for transmittance between 250 and 760 nm at 1 nm intervals. The transmittance spectra for 10 strips collected on each day were averaged. Data for days 1 and 3 at Horn Point

Beach were lost. After transmittance was recorded, periphyton on each section of each strip ($n = 10$) was quantified by gently scraping the periphyton from both sides of the strip onto a Petri dish filled with autoclaved and GF/F filtered seawater from the study site. This water/periphyton mixture was then filtered onto a pre-weighed and pre-ashed GF/F filter. The filters were dried, re-weighed, ashed, and weighed once again to determine total and inorganic periphyton, respectively. The length of each strip was measured to the nearest 0.1 cm. Average periphyton was then calculated as mg DW cm^{-2} . In order to compare periphyton on artificial and natural leaves, the same procedure was repeated for natural leaves. Thirty shoots of *Z. marina* and *R. maritima* were collected and the leaves cut at the top of the sheath. These were then separated by age (leaf 1 being the youngest/shortest and leaf 5 being the oldest/longest) and the periphyton quantified for each species' leaf age group. In order to estimate periphyton-substrate/leaf age (cf. Cebrian et al., 1999), growth rate (leaf elongation) was determined for natural plants in Chincoteague Bay (*Z. marina*) using the hole-punching technique (Dennison, 1990).

2.3. Data analysis

Statistical analysis of the data was performed via regressions, *t*-tests and analysis of variance. The data were tested for normality and homogeneity of variance and log transformed when necessary. Unless otherwise specified, the results are presented as means and standard deviations.

3. Results

Water parameters at Horn Point Beach showed features characteristic of eutrophic sites while those at Chincoteague Bay were characteristic of less eutrophic conditions (Table 1). Nitrogen concentrations in the form of nitrate + nitrite and ammonium were significantly higher at Horn Point Beach than in Chincoteague Bay and light availability immediately above the bottom tended to be lower at Horn Point Beach than in Chincoteague Bay (Table 1). Although light attenuation coefficients tended to be lower in Chincoteague Bay than at Horn Point Beach, this difference was not significant. The temperature during the experiment was significantly higher at Horn Point Beach than in Chincoteague Bay (Table 1).

Periphyton mass on the strips increased faster at Horn Point Beach than at Chincoteague Bay (Fig. 1) reaching levels of 7.3 ± 1.1 and $0.8 \pm 0.2 \text{ mg DW cm}^{-2}$ by day 7 after deployment, respectively. In Chincoteague Bay, periphyton on the artificial leaves increased significantly between days 5 and 7 ($P < 0.05$) and days 7 and 12 ($P < 0.001$). At Horn Point Beach, on days 1 and 3, periphyton mass was only slightly higher than at Chincoteague Bay but by day 5, there was almost a four-fold increase and by day 7 periphyton mass doubled again (Fig. 1). The inorganic fraction (determined by weight) of periphyton on the strips was significantly higher at Horn Point Beach ($83.0 \pm 7.1\%$) than at Chincoteague Bay ($73.5 \pm 3.5\%$; $P < 0.001$, $n = 19$).

Periphyton (total and inorganic) on natural seagrass leaves was also higher at Horn Point Beach ($4.0 \pm 0.3 \text{ mg DW cm}^{-2}$, $85.8 \pm 6.1\%$, total and inorganic matter, respectively) than in Chincoteague Bay ($0.81 \pm 0.33 \text{ mg DW cm}^{-2}$, $75.6 \pm 6.4\%$, respectively). Based on the

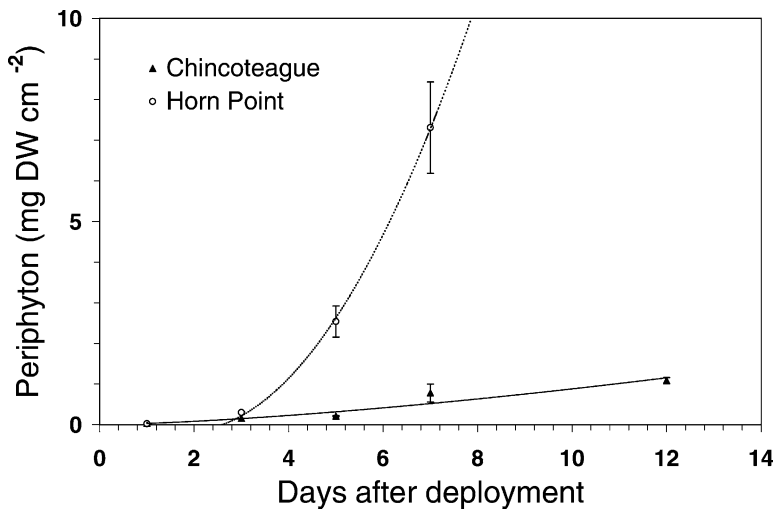


Fig. 1. Periphyton biomass (organic and inorganic) on artificial seagrass leaves deployed at a relatively pristine, Chincoteague Bay and an eutrophic, Horn Point Beach site for 1, 3, 5, 7 and 12 days. Vertical bars represent one standard deviation. Bars for days 1 and 3 at Chincoteague Bay, have no standard deviation bars as the periphyton from all samples was lumped onto one filter to reach a detectable amount. The best fit for the Horn Point Beach data was a polynomial distribution ($y = 0.28x^2 - 1.04x + 0.81$, $r^2 = 0.99$) and the best fit for the Chincoteague Bay data was a power distribution ($y = 0.029x^{1.48}$, $r^2 = 0.96$). Although these lines fit the data quite well, S-shaped curves may have shown the tendency of periphyton biomass to level off over time. Unfortunately the data for day 12 at Horn Point were missing; they could have shown a leveling off tendency. Periphyton at Chincoteague had not yet reached that point by day 12.

leaf elongation rates measured for *Z. marina* in this study (0.41 ± 0.16 cm per day) and the growth rates of *R. maritima* (0.2 cm per day) observed by Dunton (1990), we estimated that the youngest measured leaves (leaf 1) of *Z. marina* and *R. maritima* were 14 ± 4 and 16 ± 8 days old, respectively. The periphyton biomass we measured on these youngest natural leaves (1.15 ± 0.85 and 3.64 ± 1.27 mg DW cm⁻², respectively) compare well (i.e. are not significantly different, $P > 0.05$, t -test) with the periphyton biomass on the 12-day old artificial leaves in Chincoteague Bay (1.08 ± 0.07 mg DW cm⁻²) and the 5-day old artificial leaves at Horn Point Beach (2.54 ± 0.38 mg DW cm⁻²). These growth rate-based comparisons were possible as *Ruppia* and *Zostera* at the study sites reach approximately similar leaf lengths (≈ 20 cm).

While transmittance of UV-B and PAR decreased as periphyton biomass on the strips increased (Fig. 2), this decrease was stronger in the UV-B than in the PAR range (Figs. 2 and 3). For example, in Chincoteague Bay, by day 7, $98 \pm 1\%$ PAR at 663 nm was still transmitted on each side of the strip but only $88 \pm 2\%$ UV-B at 300 nm was transmitted. Although a significantly lower amount of total light was transmitted, transmittance through the periphyton layer on strips placed at Horn Point Beach showed a similar progression as observed for Chincoteague Bay (Fig. 2). A small amount of UV-B at 300 nm ($13 \pm 5\%$) was still transmitted on each side of the strip on day 5 but by day 7, UV-B transmittance was only $3 \pm 1\%$.

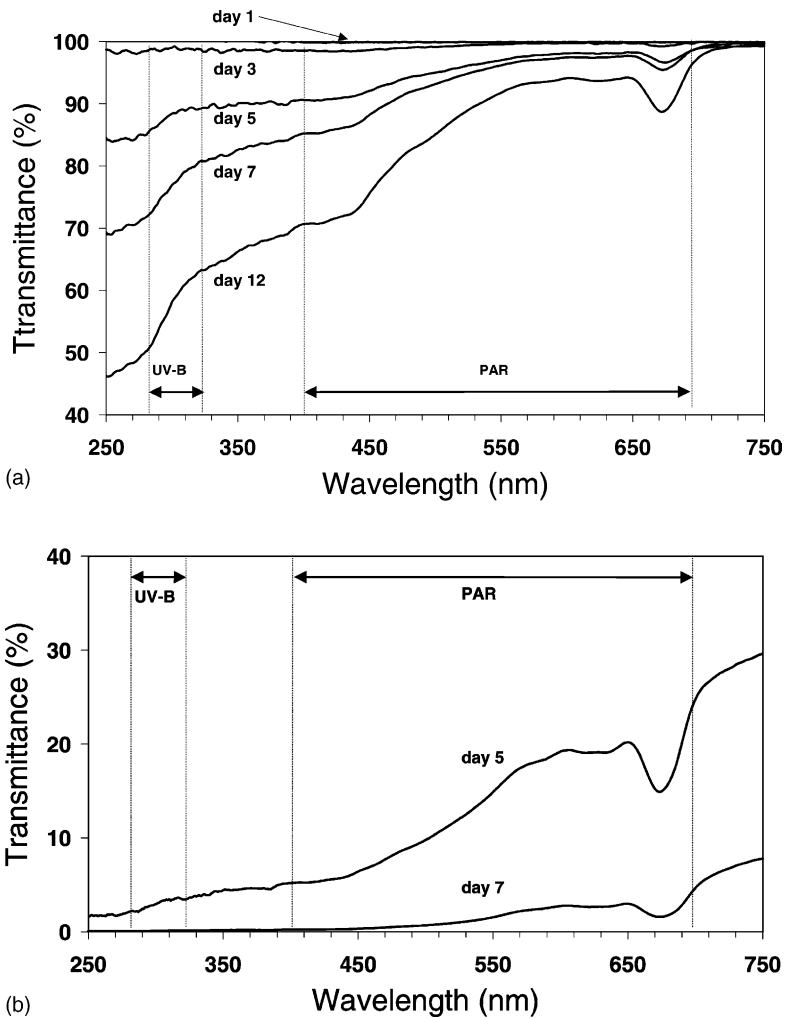


Fig. 2. Transmittance of ultraviolet-B (UV-B) and photosynthetically available radiation (PAR) through the periphyton layer (organic and inorganic) that developed/accumulated on artificial seagrass leaves deployed at a relatively pristine, Chincoteague Bay (A) and an eutrophic, Horn Point Beach (B) site for 1, 3, 5, 7 and 12 days. Note that: (1) data for days 1, 3 and 12 are missing in B; (2) scales on the Y-axes are different and (3) transmittance decreases (attenuance increases) in the chlorophyll a (430 and 663 nm) and carotenoid (400–518 nm) regions.

4. Discussion

The ecological importances of periphyton on seagrass leaves have been listed as: primary producer in seagrass systems, source of food and sediment particles (calcareous algae) and environmental indicator of water quality (Borowitzka and Lethbridge, 1989). We suggest that 'UV-B filter' be added to this list.

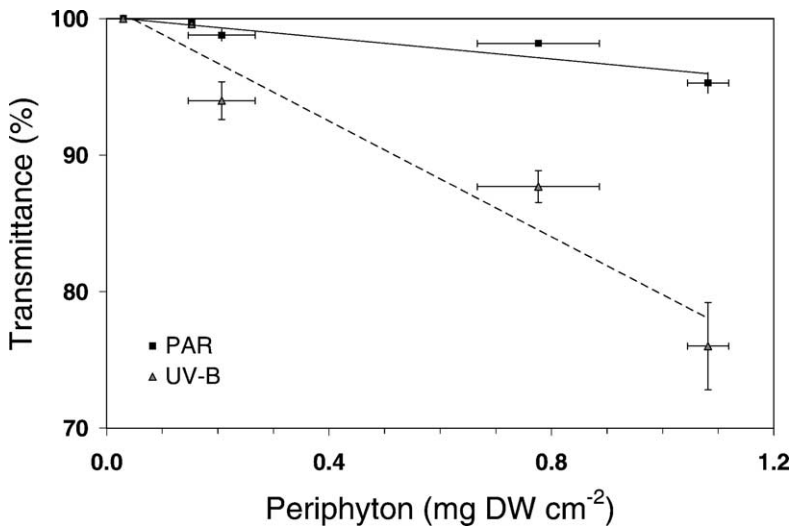


Fig. 3. Linear regression of the transmittance of ultraviolet-B (UV-B) at 300 nm and photosynthetically available radiation (PAR) at 663 nm as a function of the development/accumulation of periphyton (organic and inorganic) on both sides of artificial seagrass leaves deployed at a relatively pristine site, Chincoteague Bay. Horizontal and vertical bars represent one standard deviation. Regression lines: PAR ($y = 100.2 - 3.8x$, $r^2 = 0.87$); UV-B ($y = 101.0 - 21.2x$; $r^2 = 0.94$).

Periphyton biomass on natural and artificial seagrass leaves is usually highest at sites where nutrient concentrations are elevated (Borum, 1985; Wear et al., 1999). This was confirmed in this study. The elevated temperatures at our high nutrient site (Horn Point Beach) may also have contributed to the growth of organisms in the periphyton layer.

It is well accepted that periphyton attenuates PAR and thereby negatively affects the productivity of marine and freshwater flowering plants (Sand-Jensen, 1977; Bulthuis and Woelkerling, 1983; Sand-Jensen and Borum, 1984). We have shown that the periphyton layer also reduces the levels of UV-B that reach the seagrass leaves and could, therefore, offset the negative impact of UV-B on seagrasses. The disproportionally low UV-B transmission when compared to PAR transmission (Fig. 3), may be especially important in intertidal seagrass beds as well as in the oligotrophic waters of tropical marine regions (Fig. 4) where UV-B levels are high (Madronich, 1993), UV penetrates relatively deep into the water column (Häder, 1997) and epiphytic growth is usually low (a small amount of periphyton may have a relatively large effect on UV-B). But it may also be important in areas with borderline periphyton densities where transmittance in the PAR range is above the minimum light requirement. However, in areas with high periphyton densities, phytoplankton growth is also expected to be higher and UV penetration into the water column is probably not as deep. At the same time, seagrass in such areas do not grow as deep as in waters with lower nutrients. Therefore, there is a complex interaction between depth of seagrass distribution (Kemp et al., 1983; Dennison et al., 1993), UV-B attenuation in the water column and on the leaf surface. As a result, in eutrophic areas, the amount of UV-B that reaches seagrasses (if these are present) may be minimal (Fig. 4).

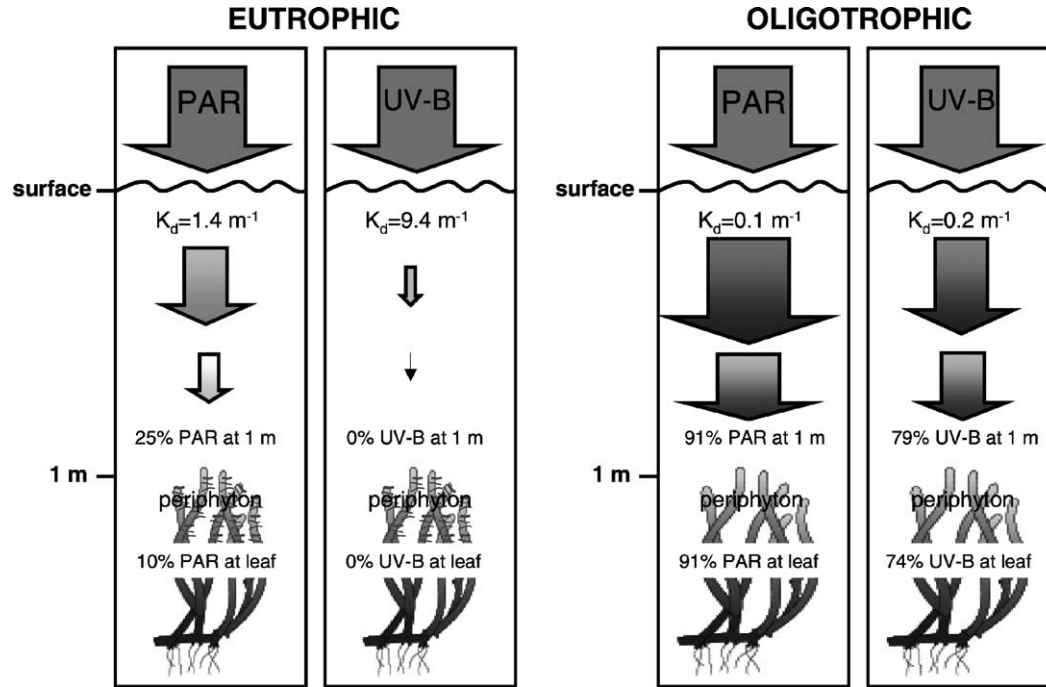


Fig. 4. A theoretical example of the influence of periphyton on the amount of PAR and UV-B that reaches leaves of seagrasses colonizing a eutrophic vs. an oligotrophic system. The percent PAR and UV-B reaching a seagrass leaf ($P_{\text{PAR}L}$ and $P_{\text{UVB}L}$, respectively) can be estimated based on an expansion of the equations suggested by Kemp et al. (2000): $P_{\text{PAR}L} = 100 \times (e^{(-K_{d\text{PAR}} Z)})(1 - Y_{\text{PAR}} B_p)$; $P_{\text{UVB}L} = 100 \times (e^{(-K_{d\text{UVB}} Z)})(1 - Y_{\text{UVB}} B_p)$. The light attenuation coefficient (K_d) for PAR and UV-B in the water column and the depth at which the plants are found (Z) will affect how much light reaches the periphyton layer (first portion of the equation) while the transmittance/attenuance of PAR and UV-B through the periphyton layer will affect how much of the beneficial (PAR) and detrimental (UV-B) radiation further makes it to the seagrass leaf (second portion of the equation). B_p = periphyton biomass and Y_{PAR} and $Y_{\text{UVB}} = (0.01 \times \text{slope of the line of transmittance of PAR and UV-B vs. periphyton biomass, respectively; } 3.83 \text{ and } 21.24, \text{ respectively in Fig. 3})$. The eutrophic example in this figure uses water column K_d values representative of the Wadden Sea (De Lange, 2000) and the percent light (PAR and UV-B) further attenuated by the periphyton layer on one side of the leaf on day 5 at Horn Point Beach. The oligotrophic example uses water column K_d values representative of the Caribbean–Curaçao (Visser et al., 2002) and the percent light (PAR and UV-B) further attenuated by the periphyton layer on one side of the leaf on day 5 at Chincoteague Bay.

Each component of periphyton (algae, bacteria, mucus, sediment particles, etc.) has a different PAR (Losee and Wetzel, 1983) and UV-B absorption spectrum. The transmittance spectra presented here integrate all these elements. The shape of the transmission spectra for Chincoteague Bay and Horn Point Beach suggests that algae as well as detritus are contributing to the reduction of light transmittance through the periphyton layer. The strong absorption (reduced transmittance) in wavelengths characteristic of chlorophyll *a* (430 and 663 nm) and carotenoids (401–518 nm) suggest that photosynthetic organisms are contributing to light attenuation. Additionally, the more concave spectra for Horn Point Beach than Chincoteague Bay suggests more attenuation of light due to detrital/inorganic material at the eutrophic, than at the pristine site (Kirk, 1986). This is confirmed by the higher inorganic fraction found on strips placed at Horn Point Beach than on strips placed at Chincoteague Bay.

When evaluating the magnitude of UV-B filtering a periphyton layer may provide, the transmission spectra in this study (Fig. 2) overestimate the attenuation of UV-B and PAR as the periphyton layer on both sides of the artificial leaves was taken into consideration, the equivalent of a doubled periphyton thickness on one side of a seagrass leaf. Therefore, the attenuation in UV-B and PAR is actually only the square root of the amount shown (Vermaat and Hootsmans, 1994). This suggests that day 5 leaves at Horn Point Beach still receive sufficient PAR to survive but by day 7, they are severely light limited.

Although not a part of this study, one can speculate that, as the synthesis of UV-B filtering pigments/compounds in periphytic algae increases with increasing UV-B levels (Beach and Smith, 1996; Karsten, 1998), seagrasses may benefit from this acclimation to UV-B in the periphyton layer. At the same time, periphytic algal growth may be inhibited by elevated UV-B levels (Friedlander and Ben-Amotz, 1991) exposing the seagrasses to more UV-B leading to complex, possibly non-linearly counteracting mechanisms. Therefore, studies on the effect of UV-B on seagrasses should take into consideration the impact that periphyton dynamics may have on the UV-B dosage received by the seagrass leaves.

In summary, we suggest that periphyton accumulation on seagrass leaves may provide an effective UV-B filter, a factor that may be especially important in tropical marine oligotrophic waters (Fig. 4). The higher transmission in the PAR than in the UV-B range allows the seagrasses to receive a higher proportion of beneficial light while reducing the detrimental radiation. This beneficial effect of periphyton as a UV-B filter is lost when PAR transmission reaches levels that strongly limit photosynthesis.

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