



Light Thresholds to Prevent Dredging Impacts on the Great Barrier Reef Seagrass, *Zostera muelleri* ssp. *capricorni*

Kathryn M. Chartrand^{1,2*}, Catherine V. Bryant¹, Alex B. Carter¹, Peter J. Ralph² and Michael A. Rasheed¹

¹ Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Cairns, QLD, Australia, ² Plant Functional Biology and Climate Change Cluster, University of Technology Sydney, Sydney, NSW, Australia

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*Correspondence:

Kathryn M. Chartrand
Katie.Chartrand@jcu.edu.au

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Coastal seagrass habitats are at risk from a range of anthropogenic activities that modify the natural light environment, including dredging activities associated with coastal and port developments. On Australia's east coast, the tropical seagrass *Zostera muelleri* ssp. *capricorni* dominates intertidal mudbanks in sheltered embayments which are also preferred locations for harbors and port facilities. Dredging to establish and maintain shipping channels in these areas can degrade water quality and diminish light conditions that are required for seagrass growth. Based on this potential conflict, we simulated *in-situ* light attenuation events to measure effects on *Z. muelleri* ssp. *capricorni* condition. Semi-annual *in situ* shading studies conducted over 3 years were used to quantify the impact of prolonged light reduction on seagrass morphometrics (biomass, percent cover, and shoot density). Experimental manipulations were complimented with an assessment of 46 months of light history and concurrent natural seagrass change at the study site in Gladstone Harbour. There was a clear light-dependent effect on seagrass morphometrics during seagrass growing seasons, but no effect during senescent periods. Significant seagrass declines occurred between 4 and 8 weeks after shading during the growing seasons with light maintained in the range of 4–5 mol photons m⁻² d⁻¹. Sensitivity to shading declined when applied in 2-week intervals (fortnightly) rather than continuous over the same period. Field observations were correlated to manipulative experiments to derive an applied threshold of 6 mol photons m⁻² d⁻¹ which formed the basis of a reactive light-based management strategy which has been successfully implemented to ensure positive ecological outcomes for seagrass during a large-scale dredging program.

Keywords: seagrass, shading, light attenuation, thresholds, dredging management, *Zostera muelleri*, indicators

INTRODUCTION

Seagrasses cover 38,079 km² of habitat on Australia's east coast within the boundary of the Great Barrier Reef World Heritage Area (GBRWHA; Coles et al., 2015). Coastal seagrasses are an integral part of the health and ecosystem function of the GBRWHA and provide key habitat linkages, feeding grounds for globally threatened turtles and dugong,

habitat for commercially important fisheries, sediment trapping and stabilization, effective nutrient filtering from coastal inputs, and carbon sequestration (Hemminga and Duarte, 2000; Jackson et al., 2001; Orth et al., 2006; Romero et al., 2006; Heck et al., 2008; Duarte et al., 2010). Despite being highly valued globally for their contribution to ecosystem services, seagrass habitats are threatened by a range of anthropogenic activities including coastal development and declining water quality from poor catchment management activities (Waycott et al., 2009; Grech et al., 2012; Costanza et al., 2014). Anthropogenic pressures on seagrasses are often compounded by natural events such as severe storms and flooding that may cumulatively lead to widespread seagrass decline. This has occurred on the tropical and subtropical east coast of Australia where severe tropical storms have contributed to widespread seagrass declines in recent years (Devlin et al., 2012; Rasheed et al., 2014).

A major cause of seagrass losses globally relates to human induced changes to the inshore environment that reduce available light, the primary driver of seagrass growth and distribution (Dennison, 1987; Duarte, 1991; Ralph et al., 2007). The risk of these types of impacts along the Great Barrier Reef (GBR) coast tends to be highest in areas where urban development and port infrastructure have a strong foothold (Grech et al., 2011). In the GBRWHA, extensive seagrass meadows commonly occur in proximity to large port facilities (Grech and Coles, 2010). Recent, well-publicized port expansions (BREE, 2012; Grech et al., 2013) place adjacent seagrass meadows under increased pressure. The capital works required for port developments can include large-scale dredging programs, which can have negative impacts on seagrass through direct burial and/or physical removal, and indirectly from turbidity plumes and the associated reduction in available light (Erftemeijer and Robin Lewis, 2006). In the GBRWHA, recent studies have shown that these plumes can have a substantial impact on seagrass (York et al., 2015). While physical damage to seagrass is relatively easy to quantify or directly avoid, it is the potential for large and persistent sediment plumes which are much harder to effectively forecast the scale of impact or to mitigate against seagrass loss.

The impact of dredge plumes are typically managed using measures not directly related to the ecological requirements of marine plants, such as reference to a background level of turbidity (Sofonia and Unsworth, 2010). Using the plant's light requirements to ensure minimal impacts is seldom attempted, largely due to a lack of understanding on what the *in situ* light requirements are for most seagrass species (Ralph et al., 2007). Turbidity can provide a measure of added pressure from dredging activity to the ecosystem, but does not necessarily have any direct biological relevance or account for the in-built resilience of an organism or whole system over short timescales (Sofonia and Unsworth, 2010). Adopting a direct measure of available light as a threshold for seagrass management is directly related to the plant's growth requirements making it far more preferable to turbidity.

Determining an appropriate light threshold for seagrasses involves several challenges: the light environment can be naturally highly variable over multiple timescales; plants can have dramatically different light requirements depending

on time of year (Staehr and Borum, 2011); seagrasses can tolerate periods of time below their minimum light requirement without long-term impacts; and a range of other environmental parameters including water temperature and sediment chemistry can further influence *in situ* light requirements (Koch, 2001; Lee et al., 2007). The plant response to fluctuating light begins with explicit gene regulation driving changes in photosystems and pigment composition before growth rates and eventual plant morphology or meadow scale reductions become apparent (Abal et al., 1994; Collier C. J. et al., 2012). While laboratory experiments have helped to resolve the fundamental timeline of many of these responses (Abal et al., 1994; Collier C. J. et al., 2012; McMahon et al., 2013), the actual timeline of *in situ* seagrass growth dynamics is likely to be quite different due to additional extrinsic factors that cannot easily be replicated in laboratory or mesocosm trials such as nutrient availability, water temperature, hydrodynamics, epiphyte loads, water column oxygen fluxes and sediment chemistry (Carruthers et al., 2002; Waycott et al., 2005; Raun and Borum, 2013). *In situ* shading studies provide an empirical approach to measuring impacts of prolonged incident light attenuation and identify potential warning signs of decline in meadow-scale seagrass health as related to dredging or other anthropogenic-induced light reduction under realistic field conditions (Longstaff and Dennison, 1999; Collier C. et al., 2012).

Identifying the relevant timeframe to elicit a negative response by local seagrasses is a key component of developing a regionally-specific light threshold. Most seagrasses can tolerate periods of time below their minimum light requirement without long-term impacts (Alcoverro et al., 1999; Collier C. J. et al., 2012). Short-term re-allocation of carbon from storage tissues and adjustments to photosynthetic machinery can help bide time until conditions improve (Alcoverro et al., 2001; Cayabyab and Enríquez, 2007). A light threshold must establish the juncture at which compensatory physiological mechanisms are superseded by plant-scale declines (Collier C. J. et al., 2012). An applied light management strategy must consider the light quantity, quality and duration of light that is required to sustain local seagrass populations.

Many coastal seagrass species are well-adapted to the variable conditions that occur in a near-shore environment, including naturally turbid waters related to runoff, large tidal fluxes, complex hydrodynamics and oscillating temperatures creating constantly shifting optical and metabolic challenges (de los Santos et al., 2010; Collier et al., 2011; Petrou et al., 2013). Strategies to tolerate temporary light reduction are broadly the same for all species: adjusting light harvesting capacity and the efficiency of light use (Abal et al., 1994; Enríquez, 2005); adjustments to rates of growth and plant turnover (Collier et al., 2009; Collier C. J. et al., 2012; and drawing upon carbohydrate reserves to maintain a positive carbon balance (Burke et al., 1996; Touchette and Burkholder, 2000). While seagrasses adapted to marginal environments may be tolerant of wide fluctuations in light, they can also be acutely sensitive to reductions in light beyond the natural range of conditions (Ralph et al., 2007). When light drops below a critical level, seagrass productivity is compromised and significant physiological, biochemical and

structural changes begin to take place eventually manifesting into broader meadow-scale losses with consequences for ecosystem function (Lee and Dunton, 1997; Ralph et al., 2007; Hughes et al., 2008).

Zostera muelleri ssp. *capricorni* is a key coastal seagrass species found along the tropical east coast of Australia (Waycott et al., 2004) and occurs in the muddy, inshore estuarine environments few other seagrass species inhabit (Lee Long et al., 1993; Carruthers et al., 2002). In port areas of the GBRWHA it is often the dominant species present, including in the Gladstone region, where it is found in monospecific intertidal meadows covering up to 40 km² within the port limits (Thomas et al., 2010; Supplementary Figure 1). With no known functional replacement, a large-scale dieback due to a stress event such as dredging could have wider implications for the ecological success of the inshore marine community.

The goal of this study was to develop a species-specific, light threshold for the effective management of *Zostera muelleri* ssp. *capricorni* in Gladstone, Australia. Recent expansion of port infrastructure and shipping channels around Gladstone has involved large-scale dredging and the removal of ~26 million m³ of sediment over 3 years. *In situ* shading studies were used to elicit a response in a local seagrass population to determine a light threshold at which seagrasses will decline and over what time scale a decline is detectable in plant abundance. The approach used does not attempt to simulate a given dredging scenario but rather to apply information on how locally-adapted seagrasses withstand constant light attenuation or how regular short-term reprieves from light attenuation events affect the overall seagrass condition and its' recovery in order to better manage threats from dredging related turbidity plumes. This information was used to apply a management-based light threshold to protect seagrasses from light stress during dredging. Long-term monitoring of the seagrass meadow at an adjacent site also provided information on the status and trend of local seagrass in relation to seasonality, light history, and water temperature. The adjacent site also provides a testing ground to assess the suitability of our light threshold against seagrass condition over the long term.

Our study focused on the development of locally-relevant light thresholds that can be applied for effective management of coastal and port development activities in a way that maintains seagrass health. The term threshold, as used here, is defined as the point at which a change in external conditions causes a significant negative change in seagrass physical condition, i.e., above-ground biomass, cover, or shoot density. It is important to note that this is different to defining a minimum light requirement (MLR) for effective seagrass photosynthesis. Rather, the goal is focused around developing a biologically relevant management tool, which incorporates other local environmental drivers such as tidal cycles, seasonality and sediment chemistry dynamics that influence seagrass condition together with light *in vivo*.

MATERIALS AND METHODS

Shading Study Experimental Design

This study was conducted at Pelican Banks, Gladstone Harbour (151° 18' 30"E, 23° 45' 58"S), Australia (see Supplementary

Figure 1) from 2010 to 2013. At Pelican Banks the tropical subspecies *Z. muelleri* ssp. *capricorni* forms a predominantly monospecific intertidal seagrass meadow on intertidal mud banks. Studies were carried out during two growing seasons for local seagrasses (ca. July to December) and two senescent seasons (ca. January to June) when seagrasses naturally decline with the onset of the tropical monsoon and subsequent cooler months in the austral winter (Mellors et al., 1993; McKenzie, 1994). Studies are described accordingly: growing seasons 1 and 2 (G1 and G2) and senescent seasons 1 and 2 (S1 and S2). The study location was chosen for its accessibility, semi-firm sediment composition for repeated measurements during emergence at low tide without compromising site integrity, and year-round seagrass cover to assess seasonal effects. A semi-diurnal tide cycle with a maximum range of 5 m meant seagrasses were exposed at least fortnightly, depending on the time of year.

The study site was ~30 × 20 m with experimental plots randomly assigned to each of three shade treatments or as controls ($n = 4$). Vertical isolation borders (sever root connection between shaded and non-shaded areas) were inserted for the shade experiments by hammering 0.25 m² quadrats with a 0.25 m depth into the sediment until flush with the sediment surface to isolate plots where seagrass would be measured. This ensured seagrass outside of the experimental plot could not translocate nutrients/carbohydrates to seagrass within treatment plots. Plots were also "gardened" around the isolation border perimeter prior to each sampling event to prevent seagrass growing over the border and into experimental plots. Aluminium frames were secured into the sediment and covered with 1 m² neutral density polyethylene shade cloth of varying intensities fixed 0.15 m above the sediment surface. Shade treatments were used to assess three levels of reduced light on seagrass health; high, medium and low shade, equivalent to ~15, 30, and 45% of incident benthic light, respectively. Control plots were established using quadrats with steel frames and isolation borders but without shade screens. No control was used for the effect of rhizome severing based on the work of Rasheed (1999) which found no border effect using an identical experimental design and field materials to measure shading effects on the same species. Controlling for the additional effect of shade screens on water movement was not possible without creating additional shading or fouling over control plots (see Fitzpatrick and Kirkman, 1995). Shade screens were changed and cleaned fortnightly to reduce the effects of fouling on shade treatments. Light intensities under shade treatments fluctuated with natural insolation but maintained consistent patterns among treatments and relative differences to naturally occurring benthic light, indicating that fouling of the shade screens was minimal. Shade screens were removed at the end of each experiment to track potential recovery from treatment conditions.

Experimental plots were randomly assigned to varying durations of continuous shading (between 1 and 3 months) during each seasonal study (Table 1). This variation in shading study duration and tracking of recovery was necessary to align the program with expected timeframes for managing impacts to seagrass health during dredging operations as required by managers and regulators. Therefore, comparison among seasonal

TABLE 1 | Shading study design during senescent seasons 1 and 2 (S1, S2) and growing seasons 1 and 2 (G1, G2).

Study	Date Commenced	Shading Duration	Shade Treatments	N
S1	May 2010	1 month	H, M, L, C	4
G2	Sept 2010	3 months and fortnightly	H, M, L, C	4
S2	May 2012	3 months	H, M, L, C	4
G3	Sept 2013	3 months	H, M, L, C	4

Shade treatments included high shade (H), medium shade (M), low shade (L), and control (C). N is the number of replicates per shade treatment for each study.

studies was limited to shading durations comparable between studies. In addition, fortnightly cyclic shading was carried out during G1 to assess the impact of periodic turbidity plumes (i.e., shorter periods of reduced light and subsequent respites) on seagrass condition.

Light Climate

Light (photosynthetically active radiation, PAR) was measured within the seagrass canopy and under shade treatments using 2π cosine-corrected irradiance loggers (Submersible Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems Pty. Ltd., New Zealand) calibrated using a cosine corrected Li-Cor underwater quantum sensor (LI-190SA; Li-Cor Inc., Lincoln, Nebraska USA) and corrected for immersion using a factor of 1.33 (Kirk, 1994). Loggers were deployed on site for the duration of shading and maintained using automated wiper units. Readings were made at 15 min intervals and used to measure total daily light ($\text{mol photons m}^{-2} \text{ day}^{-1}$) reaching seagrasses under each shading treatment.

Substantial tidal flux in Gladstone Harbour leads to dramatic shifts in daily light intensities on the intertidal banks due to fortnightly intertidal exposure cycles and this has the potential to control light availability to the plant (Koch and Beer, 1996). To evaluate light over a practical timeframe for measuring impacts, light data was integrated as a rolling 14 day mean of the total daily benthic light under each shading treatment, controls, as well as the long-term monitoring site (detailed below). Current understanding of seagrass response indicates under low light stress conditions, physiological adjustments first occur over a matter of days, whereas plant-scale changes take place after a number of weeks and are a reflection of the integrated light history over that period rather than short term daily fluxes (McMahon et al., 2013). This 2 week rolling average incorporated spring and neap tide conditions, variation in tide height, and the associated degree of exposure that affects the light conditions reaching the seagrass. An assessment of integrated light over a 2-week period is therefore in line with both tidally-driven fluxes in light, as well as a period of time preceding apparent morphological changes to seagrass.

Seagrass Morphometrics

Seagrass above-ground biomass, percent cover and shoot density were measured at fortnightly or monthly intervals in each treatment plot during S1 and G1 studies, while only biomass

and percent cover were recorded during S2 and G2 studies. Above-ground biomass was measured using a “visual estimates of biomass” technique (Kirkman, 1978; Mellors, 1991; Rasheed, 1999). Biomass was estimated for each plot by an experienced observer recording a rank of seagrass biomass from photographs of each plot taken during sampling. Biomass ranks were assigned in reference to a series of photographs of similar seagrass habitats for which above-ground biomass has previously been measured. The same observer was used for the duration of each study to remove any inter-observer variability. At the completion of recording ranks, the observer ranked a series of additional photographs that had been previously harvested, dried, and weighed and which represented the range of seagrass biomass in the survey. A regression of ranks and biomass from these calibration quadrats was generated for each observer ($r^2 = 0.97$; see Supplementary Figure 2) and applied to the measuring plot ranks to determine above-ground biomass estimates. Biomass ranks were then converted into above-ground biomass estimates in grams dry weight per square meter (g DW m^{-2}). Shoot density was estimated by counting all shoots within a mini-quadrat (0.01 m^2) randomly placed three times in each measuring plot except where total-plot shoot density was less than 30 shoots and all shoots were counted within the 0.25 m^2 plot. Seagrass percent cover estimates were made for each plot by an observer using a standardized photo guide sheet.

Light History, Environmental Conditions and Seagrass Trend in the Meadow

A monitoring site was established in the *Z. muelleri* ssp. *capricorni* meadow adjacent to the shading study site to assess incident light and temperature at the seagrass canopy and its potential influence on seagrass meadow condition over longer time scales under natural harbor conditions. Light was recorded continuously between November 2009 and September 2013. Light loggers were deployed and operated in the same manner as in the shading studies through June 2012. From July 2012, irradiance loggers were replaced with LiCor underwater sensors with inbuilt wiper units and customized telemetered systems (Vision Environment QLD., 2013) to ensure continuous data collection and immediate availability of data during dredging operations. Water temperature was measured in the seagrass canopy (Thermodata Pty Ltd, Melbourne, Australia), daily rainfall (Bureau of Meteorology Australia¹) and total hours of daytime tidal air exposure of the meadow (Maritime Safety Queensland, Department of Transport and Main Roads) were also collected.

Seagrass condition was assessed at three 50 m transects nested in two 50 x 50 m sites. Sites were selected within a relatively homogenous section of the *Z. muelleri* ssp. *capricorni* meadow. Seagrass above-ground biomass was estimated within a 0.25 m^2 sampling quadrat placed at 0 m and then every 5 m along each transect (eleven sampling points per transect) using the same technique described above (observer regression of ranks, $r^2 = 0.95$). Mean biomass was calculated for each sampling event ($n =$

¹www.bom.gov.au

66 quadrats) with change in biomass calculated from consecutive sampling events.

Data Analysis

All values displayed are means \pm standard error (SE). Differences in morphological responses of seagrass among shading treatments and over time were assessed using repeated measures analysis of variance (rmANOVA). Data were checked for homogeneity of variance by assessing residual plots. Significant deviations from normal variance were found in G1 biomass data which were log-transformed prior to analysis. If data still did not meet the criteria, the p -value was set to 0.01 to minimize the risk of a Type I error (Underwood, 1997). For repeated measures ANOVAs, matrices were tested for sphericity using Mauchly's test. If the assumption of sphericity was not met ($p < 0.05$) the Greenhouse-Geisser (G-G) epsilon adjustment was applied to the numerator and denominator degrees of freedom. Differences among treatment effects at a given sampling time were compared using Tukey's *post-hoc* analysis. For data collected during the "recovery phase," a one-way ANOVA was

performed when a single recovery time point was measured with shading intensity as a fixed effect and tests for homogeneity of variance and transformation applied as previously described. Statistical analyses were performed using Statistica 7.0. When multiple recovery period measurements were taken, rmANOVA methods as described for the shading period were applied.

RESULTS

Seagrass Morphometrics

Shading treatments did not have a significant effect on *Z. muelleri* ssp. *capricorni* morphology during either senescent season study (S1 and S2). However, after 1 month of shading there was a significant increase in shoot density during S1 ($p < 0.05$), but no significant changes in biomass or percent cover ($p > 0.05$, **Table 2**; **Figures 1–3**). Above-ground biomass and percent cover declined significantly over the 12 weeks of shading among all treatments during S2 (both $p < 0.001$); significantly lower above-ground biomass and percent cover in treatments compared to

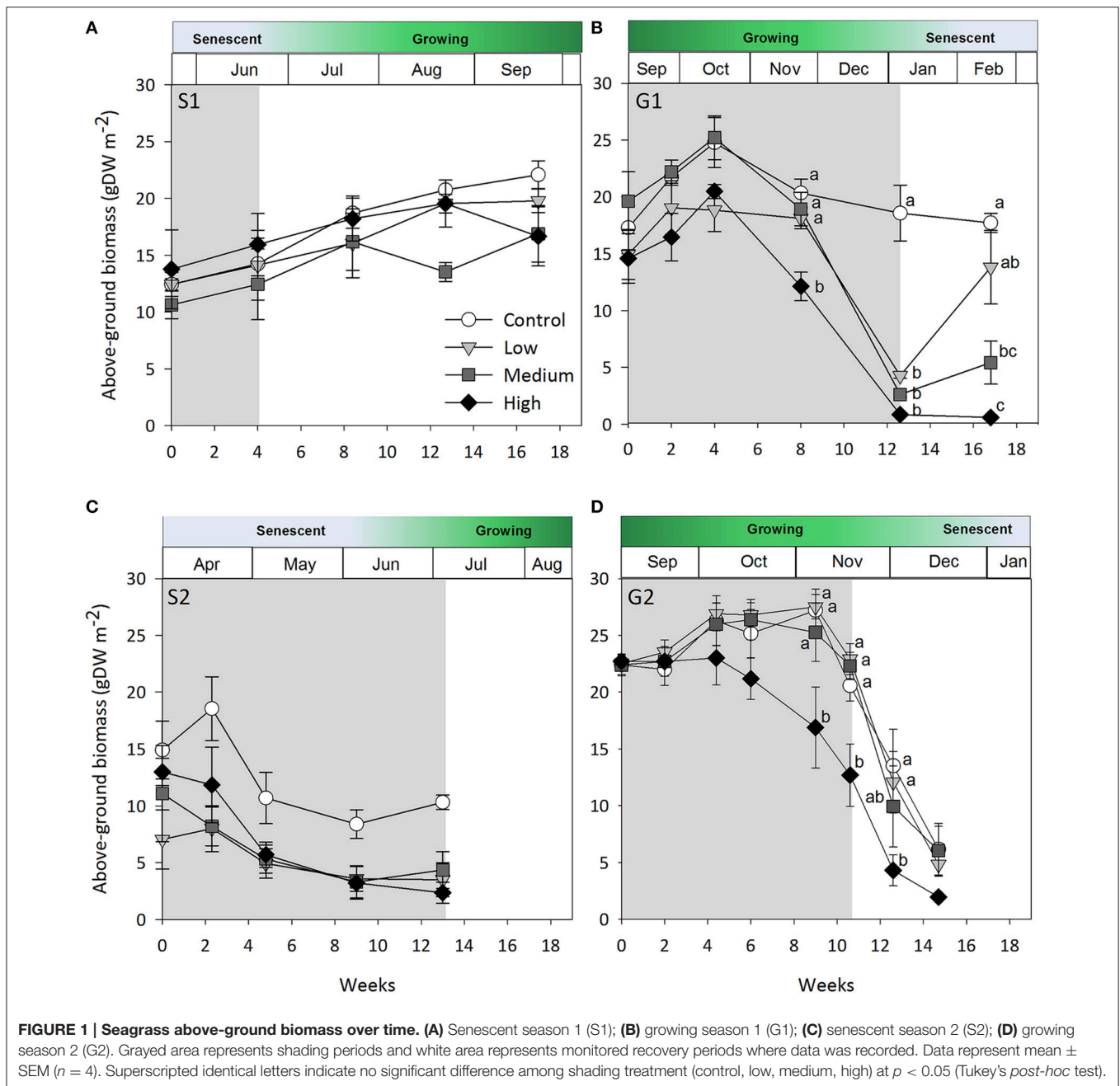
TABLE 2 | Repeated measures ANOVA of the effects of shading treatment (among groups effect) and time (within groups effect) for biomass, percent cover and shoot density during senescent seasons 1 and 2 (S1, S2) and growing seasons 1 and 2 (G1, G2).

	<i>df</i>	<i>F</i>	<i>p</i>		<i>df</i>	<i>F</i>	<i>p</i>
S1				G1			
Above-ground biomass				Above-ground biomass[^]			
Shade	3	0.49	ns	Shade	3	13.31	***
Time	1	1.70	ns	Time	4	137.62	***
Shade \times Time	3	0.001	ns	Shade \times Time	12	12.87	***
Percent cover				Percent cover			
Shade	3	1.03	ns	Shade	3	3.21	ns
Time	1	2.32	ns	Time	4	72.56	***
Shade \times Time	3	1.54	ns	Shade \times Time	12	6.13	***
Shoot density				Shoot density			
Shade	3	0.30	ns	Shade	3	0.49	ns
Time	1	7.58	*	Time	4	21.55	***
Shade \times Time	3	0.17	ns	Shade \times Time	12	2.58	*
S2				G2			
Above-ground biomass				Above-ground biomass			
Shade	3	4.33	*	Shade	3	2.73	ns
Time	4	22.14	***	Time	5	15.05	***
Shade \times Time	12	1.29	ns	Shade \times Time	15	4.16	***
Percent cover				Percent cover			
Shade	3	4.97	*	Shade	3	4.06	*
Time	4	19.41	***	Time	5	46.79	***
Shade \times Time	12	1.28	ns	Shade \times Time	15	3.27	***
Shoot density[†]				Shoot density[†]			
Shade	–	–	–	Shade	–	–	–
Time	–	–	–	Time	–	–	–
Shade \times Time	–	–	–	Shade \times Time	–	–	–

The ANOVAs were not significant (ns), or significant at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Probability values are Greenhouse-Geisser adjusted p values.

[^]Log transformed;

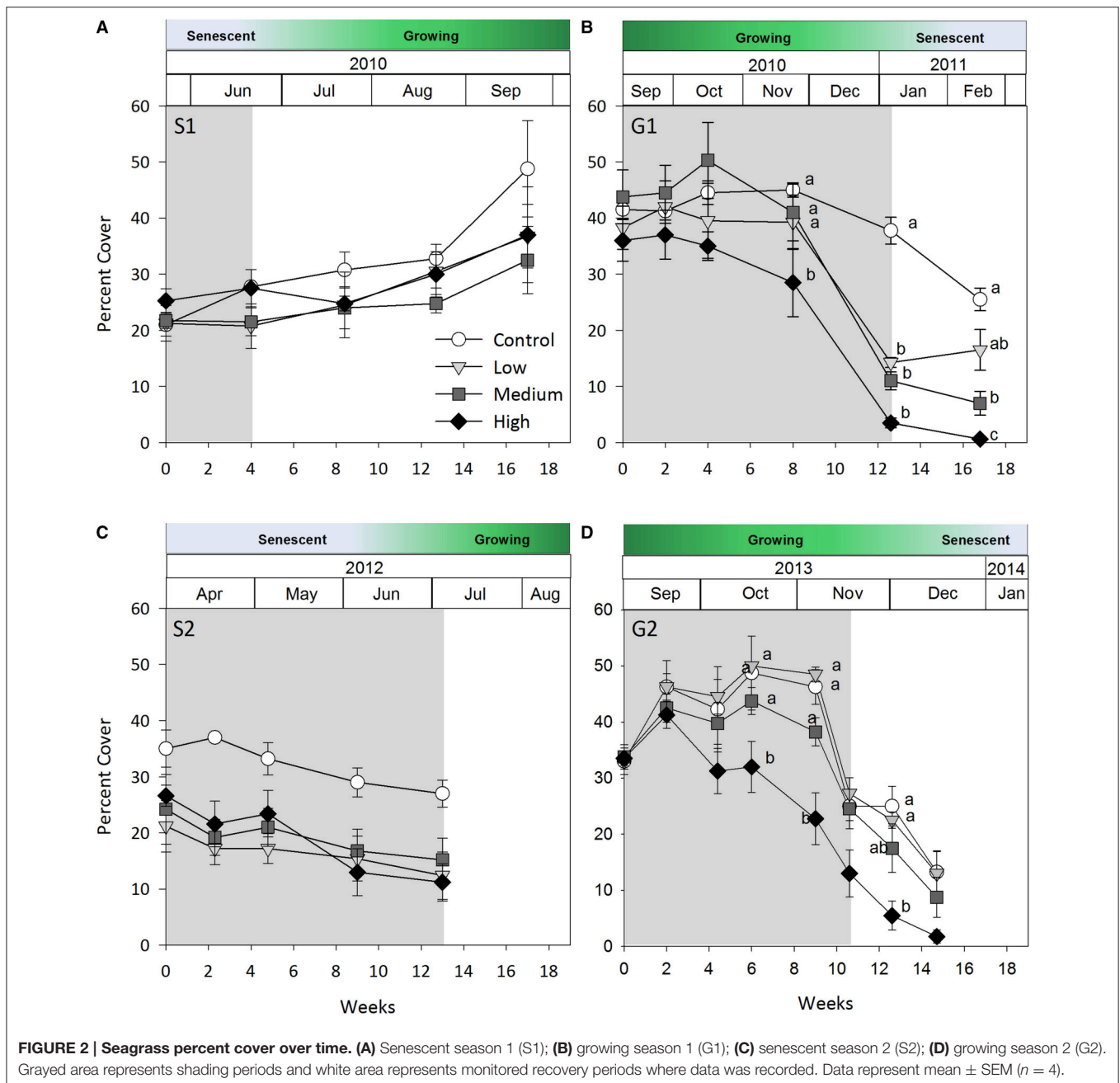
[†]Not recorded.



control plots; this was apparent from the start of the study (both $p < 0.05$, **Table 2**; **Figures 1–2**).

Shading had a detrimental effect on *Z. muelleri* ssp. *capricorni* above-ground biomass during the growing seasons (G1 and G2, shade \times time interaction $p < 0.001$, **Table 2**; **Figure 1**). During both growing season studies, biomass was significantly lower by the 8 week sampling under high shade treatments compared to controls and other treatments (**Figure 1**). This occurred between 4 and 8 weeks in G1 and 6 and 8 weeks in G2. There was significant loss of above-ground biomass under all treatments compared to control plots by 12 weeks during G1, including near total loss of above-ground biomass under

high shade plots (**Figure 1B**). Within 4 weeks of shade removal, above-ground biomass under low shade treatments recovered to control levels, whereas biomass under medium and high shade treatments remained significantly lower than control plots ($p < 0.001$; **Figure 1B**). Control plots did decline somewhat from a peak at 4–16 week measurements, likely due to the onset of characteristic seasonal senescence which occurred toward the end of the study (Jan–Feb 2011). Similarly, above-ground biomass under high shade was significantly lower than under control, low and medium shade treatments by 8 weeks of shading during G2. Declines in above-ground biomass and percent cover from mid-November in G1 and G2 across controls and all treatment

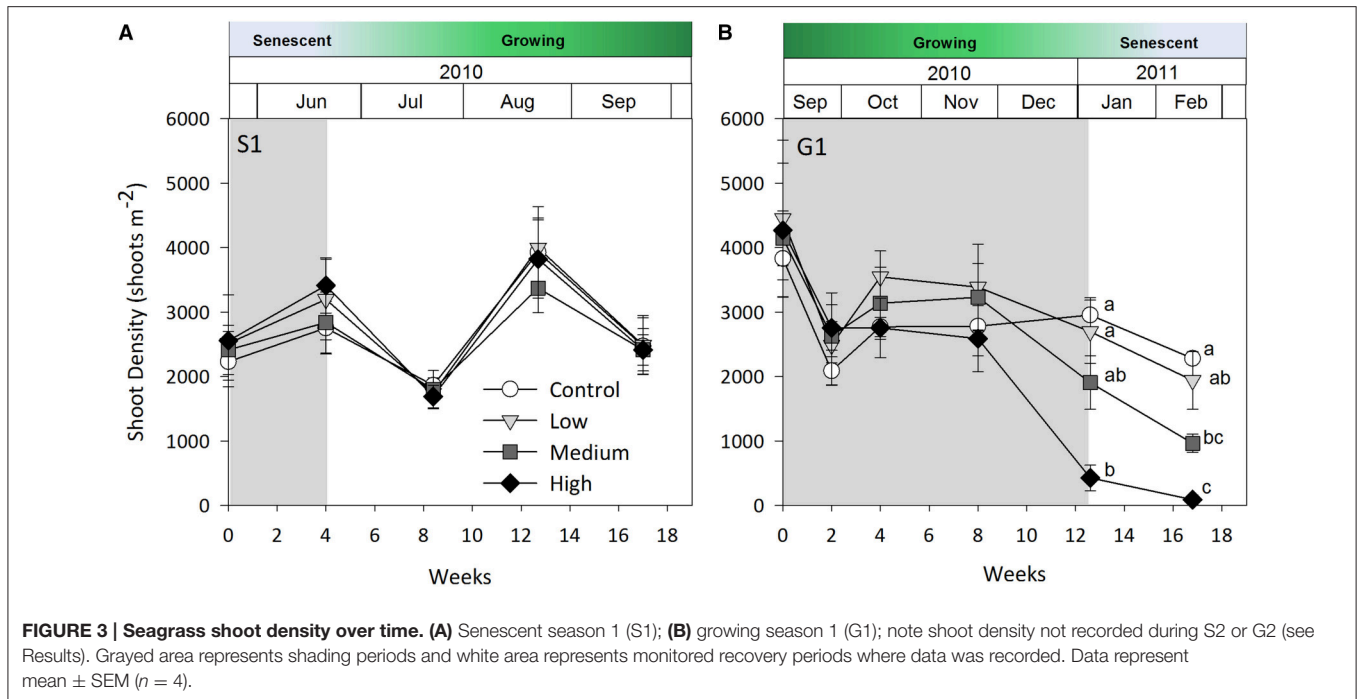


plots are consistent with seasonal declines with the onset of the senescent season (Figures 1B,D, 2B,D).

Negative effects of shading on percent cover during both growing seasons were similar to those recorded for above-ground biomass (both p -values for shade \times time interaction < 0.001 , Table 2; Figure 2). Percent cover was significantly lower under high shade treatments compared with control, low and medium shade treatments for G1 and G2 within 8 and 6 weeks, respectively, (Figures 2B,D). Within 12 weeks percent cover under all shade treatments was significantly lower than control plots during G1 (Figure 2B). Recovery of seagrass during G1 to a percent cover similar to control plots occurred within 4 weeks of

shades being removed for the low shade treatment, but there were no similar signs of recovery for treatments that had been under medium or high shade treatment (Figure 2B; Table 3). Percent cover of seagrass under high shade similarly demonstrated no sign of recovery 2 weeks following shade removal during G2 (Figure 2D; Table 3). High shade plots were nearly devoid of seagrass cover 4 weeks after shade removal for G1 and G2 (Figures 2B,D).

Shoot density was less sensitive to shading than percent cover and above-ground biomass. Seagrass shoot density decreased significantly by 12 weeks under the high shade treatment compared with control and low shade treatment plots during the



growing season (G1 study, shading \times time interaction $p < 0.05$, **Table 2; Figure 3B**). There were no signs of recovery to control levels 4 weeks after shades were removed (**Figure 3B**). Shading had no significant effect on temporal fluctuations in shoot density during the senescent season (S1 study, $p > 0.05$, **Table 2; Figure 3A**).

Seagrass was less sensitive to fortnightly cyclic shading than to continuous shading when tested during G1. Above-ground biomass data is only presented, but shoot density and percent cover results were analogous. Above-ground biomass under all shade treatments was similar to control plots for the first 8 weeks of the study; however, by week 12 biomass under all shade treatments was equally and significantly lower than under control plots (two-way rmANOVA, shade \times time interaction, $p < 0.01$, **Figure 4**). After 4 additional weeks without shading (weeks 12–16), no biomass recovery occurred under high shade treatments relative to controls ($p < 0.05$). While seagrass loss was delayed under cyclic shading, the magnitude of impact of these treatments was similar to those found under continuous shading after 12 weeks.

Above-ground biomass and percent cover in control plots throughout all studies was similar to that measured at the nearby long-term monitoring site (see **Figure 6**) indicating no effect of the physical presence of frames holding shade screens otherwise on the experiment.

Light Climate in Relation to Morphometric Results

During both senescent season studies (S1 and S2), light levels were strongly attenuated under all shade treatments compared to controls, while no measured loss of seagrass biomass, percent

cover or shoot density was recorded after 4 and 13 weeks, respectively, when shades were in place (**Figures 5A,C**). Light intensities measured under S1 and S2 shades were generally between 2 and 6 mol photons $m^{-2} d^{-1}$, a similar range recorded during the G1 study under the same shading treatments.

During the first growing season (G1), light intensities under the high shade treatment measured consistently below 2 mol photons $m^{-2} d^{-1}$ leading to significant declines in above-ground biomass and percent cover recorded by 8 weeks (**Figure 5B**). Light remained at or below 2 mol photons $m^{-2} d^{-1}$ for the remaining 4 weeks of shading over which time seagrass was completely lost from high shaded plots. Light under medium shade treatments was higher and more variable over the course of G1, but generally stayed above 4 mol photons $m^{-2} d^{-1}$ for the initial 10 weeks of the study, while light under low shades remained above 6 mol photons $m^{-2} d^{-1}$ during the same period. Light declined between weeks 10 and 12 of the experiment across controls and all treatments during a period of high rainfall in November and December 2010 (Australian Bureau of Meteorology²). Light levels were consistently below 4 mol photons $m^{-2} d^{-1}$ under all shade treatments in the fortnight leading up to the 12 week sampling event, when biomass and percent cover were significantly lower for all treatments compared with control plots (**Figure 5B**). Four subsequent weeks with shades removed (recovery; weeks 12–16) were insufficient relieve for biomass, percent cover or shoot density to recover under medium and high shade treatments while low shade treatments recovered when returned to ambient light conditions (**Figures 1B, 2B, 3B**).

²www.bom.gov.au/climate/data/

TABLE 3 | Repeated measures and one-way ANOVA of recovery from shading treatments (among groups effect) and time (within groups effect) for biomass, percent cover and shoot density during senescent seasons 1 and 2 (S1, S2) and growing seasons 2 (G2).

	<i>df</i>	<i>F</i>	<i>p</i>		<i>df</i>	<i>F</i>	<i>p</i>
	S1				G1		
Above-ground biomass				Above-ground biomass[^]			
Shade	3	1.54	ns	Shade	3	19.58	***
Time	3	4.89	**	Time [#]	–	–	–
Shade × Time	9	0.83	ns	Shade × Time [#]	–	–	–
Percent cover				Percent cover			
Shade	3	2.16	ns	Shade	3	21.86	***
Time	3	8.38	**	Time [#]	–	–	–
Shade × Time	9	0.38	ns	Shade × Time [#]	–	–	–
Shoot density				Shoot density			
Shade	3	0.13	ns	Shade	3	17.06	***
Time	3	26.74	***	Time [#]	–	–	–
Shade × Time	9	0.39	ns	Shade × Time [#]	–	–	–
	S2				G2		
Above-ground biomass[†]				Above-ground biomass			
Shade	–	–	–	Shade	3	1.85	ns
Time	–	–	–	Time	2	24.65	***
Shade × Time	–	–	–	Shade × Time	6	0.89	***
Percent cover[†]				Percent cover			
Shade	–	–	–	Shade	3	5.30	*
Time	–	–	–	Time	2	55.96	***
Shade × Time	–	–	–	Shade × Time	6	1.43	ns
Shoot density[†]				Shoot density[†]			
Shade	–	–	–	Shade	–	–	–
Time	–	–	–	Time	–	–	–
Shade × Time	–	–	–	Shade × Time	–	–	–

The ANOVAs were not significant (ns), or significant at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Probability values are Greenhouse-Geiser adjusted p values.

[^]Log transformed;

[†] Not recorded;

[#] Not tested, one-way ANOVA applied.

During the second growing season (G2), light under high shaded plots was less than 5 mol photons $m^{-2} d^{-1}$ in the fortnight leading up to detection of a significant decline in seagrass percent cover at 6 weeks (**Figure 5D**). Light declined further to <4 mol photons $m^{-2} d^{-1}$ for the fortnight leading up to sampling at 9 weeks, when significant declines in percent cover and above-ground biomass were detected. Light under low and medium shade treatments mostly stayed above 5 mol photons $m^{-2} d^{-1}$ for the duration of the G2 shading study; one exception was when light dropped below 5 mol photons $m^{-2} d^{-1}$ under medium shade for ~ 1 week at week 9; although with no detectable change in seagrass biomass or percent cover recorded. In contrast, significant declines in seagrass biomass and/or percent cover were recorded following more prolonged periods of light <5 mol photons $m^{-2} d^{-1}$ under high shade treatments at weeks 6, 9, and 10.

Climate History and Seagrass Trend

From September 2009 to September 2013, seagrass above-ground biomass at the monitoring site followed a typical oscillating

seasonal pattern. *Z. muelleri* ssp. *capricorni* reached maximum biomass between October and December each year which coincided with higher water temperatures and ambient light (**Figure 6**). Light levels in the meadow were relatively high during the growing season which paralleled net positive growth. Light intensities remained above 8 mol photons $m^{-2} d^{-1}$; well above the levels at which significant impacts were measured under shade treatments. Annual seagrass senescence began at approximately the start of the year when temperatures consistently reached $>30^{\circ}C$ in the meadow and the onset of rain and flooding events led to reductions in light (**Figure 6**). The relationship between seagrass above-ground biomass and mean maximum daily water temperature for the month prior to sampling in the growing period likewise indicated water temperature correlated with seagrass biomass ($p < 0.01$, $r^2 = 0.55$) until water temperature exceeded $30^{\circ}C$ and seagrass declined, despite high light intensities over the same period. Seagrass abundance typically reached a minimum by April/May after which a return to growth and increased seagrass biomass was observed around July each year.

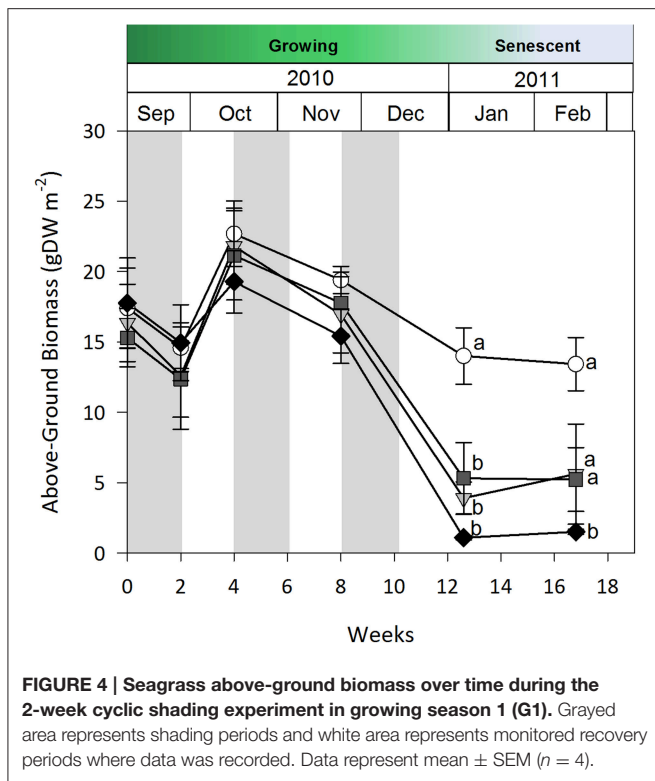


FIGURE 4 | Seagrass above-ground biomass over time during the 2-week cyclic shading experiment in growing season 1 (G1). Grayed area represents shading periods and white area represents monitored recovery periods where data was recorded. Data represent mean \pm SEM ($n = 4$).

DISCUSSION

Z. muelleri ssp. *capricorni* condition (biomass, shoot density and percent cover) was measurably driven by light reductions tested during the growing seasons but was unaffected by a reduction in light applied during either senescent season. Similar field shading experiments have demonstrated time-of-year is a critical factor in defining the magnitude of the plant's response to reduced light conditions, linked to seasonal light and water temperatures (Lavery et al., 2009). We found that *Z. muelleri* ssp. *capricorni* declined in the growing season when light was ≤ 5 mol quanta $m^{-2} d^{-1}$ for periods of time exceeding 4 weeks. This was successfully used to develop a conservative management threshold to protect seagrasses during dredging operations by maintaining light levels above 6 mol quanta $m^{-2} d^{-1}$.

The significant and consistent decline in *Z. muelleri* ssp. *capricorni* during the growing season shading studies highlights the sensitivity of this species during its period of peak productivity and expansion. *Z. muelleri* ssp. *capricorni* carbon fixation and above-ground biomass have been shown to significantly decline when grown under saturating or limiting light levels in conjunction with extreme temperatures ($>33^{\circ}C$; Collier et al., 2011) and for temperate *Z. muelleri* when grown under $30^{\circ}C$ conditions (York et al., 2013). Similar results have been found for the congeneric northern hemisphere species, *Zostera marina*, with summertime declines coinciding with low light and high temperatures (Zimmerman et al., 1989; Olesen and Sand-Jensen, 1993).

The high metabolic demand that comes with warmer conditions was typically supported by higher light (approximately July to December) at our study site (Figure 6). This likely allowed an increase in photosynthetic processes to keep up with rising seasonal temperatures up until a point, after which respiration would continue to increase without a concomitant increase in photosynthesis (Bulthuis, 1987; Lee et al., 2007). When such an imbalance occurs this can lead to die-off, whether seasonal or driven by episodic reductions in light. It was likely that *Z. muelleri* ssp. *capricorni* was not meeting its metabolic requirements during these warmer months when subjected to reduced light levels, leading to a dieback under our shading treatments. Similar trends were seen at our permanent monitoring location adjacent to the study site where seasonal cycles of seagrass growth and decline paralleled temperature and light regimes (Figure 6).

Seasonal seagrass growth rates are closely linked to light and temperature patterns (Lee et al., 2007). Intertidal *Z. muelleri* ssp. *capricorni* meadows along the Queensland coast follow typical seasonal fluctuations in condition linked to light, temperature and tidal exposure (Mellors et al., 1993; McKenzie, 1994; Carruthers et al., 2002; Petrou et al., 2013). From August to December, clearer waters and warmer temperatures spur rapid growth and expansion of seagrass meadows in the Gladstone region before typical dieback in late austral summer with the onset of high temperatures and wet season conditions.

The lack of a low light response in the senescent season could be due to a decrease in extrinsic energy requirements due to the lower seagrass standing crop and preferential use of carbohydrate reserves to support seagrass metabolic requirements (Burke et al., 1996; Touchette and Burkholder, 2000). Lavery et al. (2009) also found shading imposed over winter did not produce morphological changes; in contrast to their late summer results. They associated the effect of temperature on gross photosynthetic requirements of the plant to explain the disparity in seasonal effects. The saturating irradiance for photosynthesis (I_k) and respiration typically increase with temperature (Masini and Manning, 1997; Lee et al., 2007) equating to higher overall light requirements during summer growing periods compared to cooler months.

When light levels are sufficient, carbohydrate reserves are enhanced which help offset periods of high light attenuation by supporting short-term energy demands of the plant. In the first growing season study, medium shaded plots were not measurably affected until the 12 week sampling event and did not recover from losses within 4 weeks. While light under medium shaded plots during the first 10 weeks ($4-5$ mol photons $m^{-2} d^{-1}$) sustained *Z. muelleri* ssp. *capricorni* *in vivo*, it was likely near its' light requirement limit and may have exhausted energy reserves, making recovery unachievable in the short-term once shades were removed. Alternatively, light during G1 under low shaded plots, which received by and large > 6 mol photons $m^{-2} d^{-1}$ during the study, likely enabled excess energy to be stored in the plant and used to support recovery when shades were removed. These differences in treatment response illustrate that conditions leading up to an acute stress event are important in determining recovery success. Ensuring light is maintained at a level that not

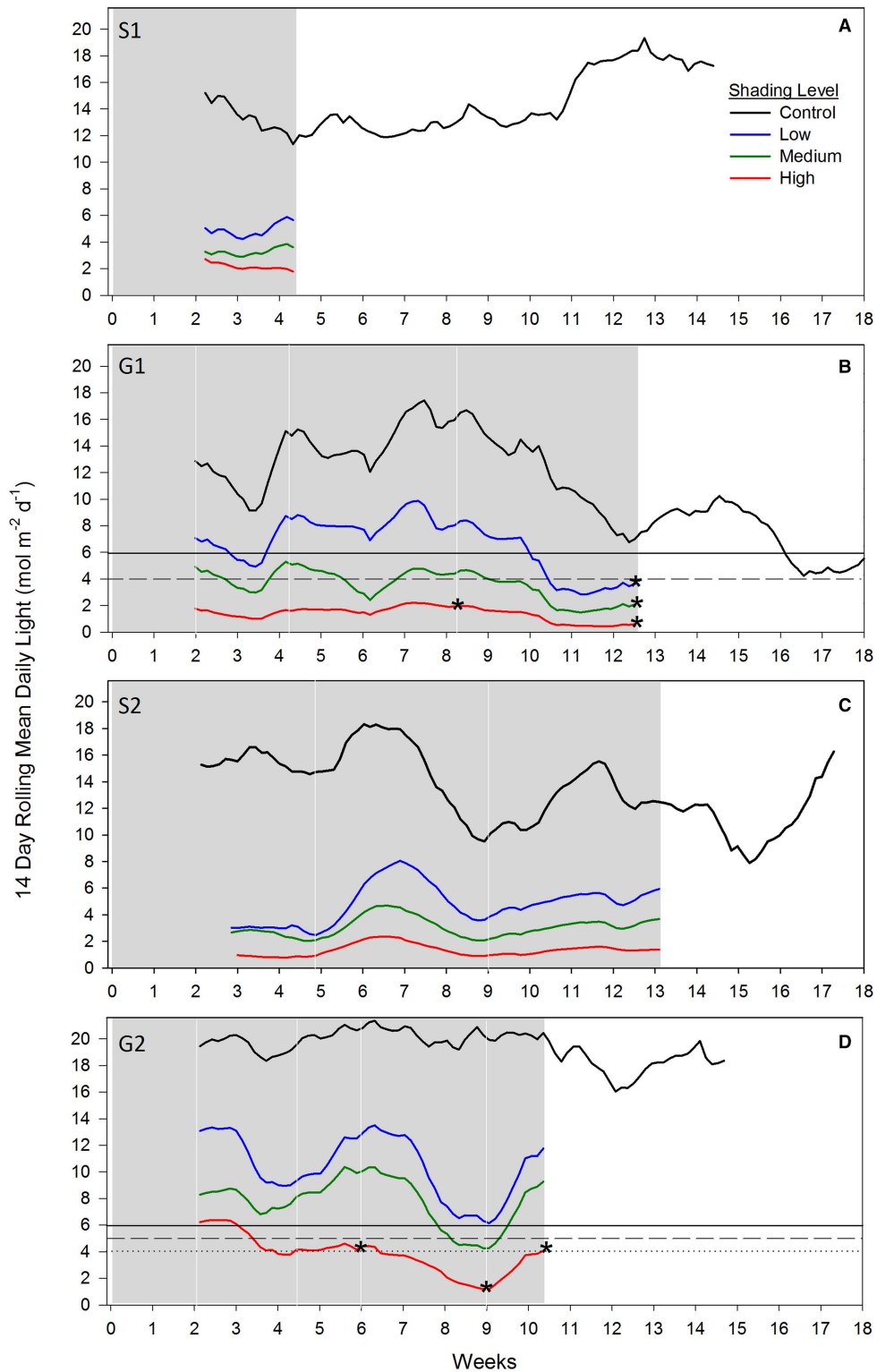
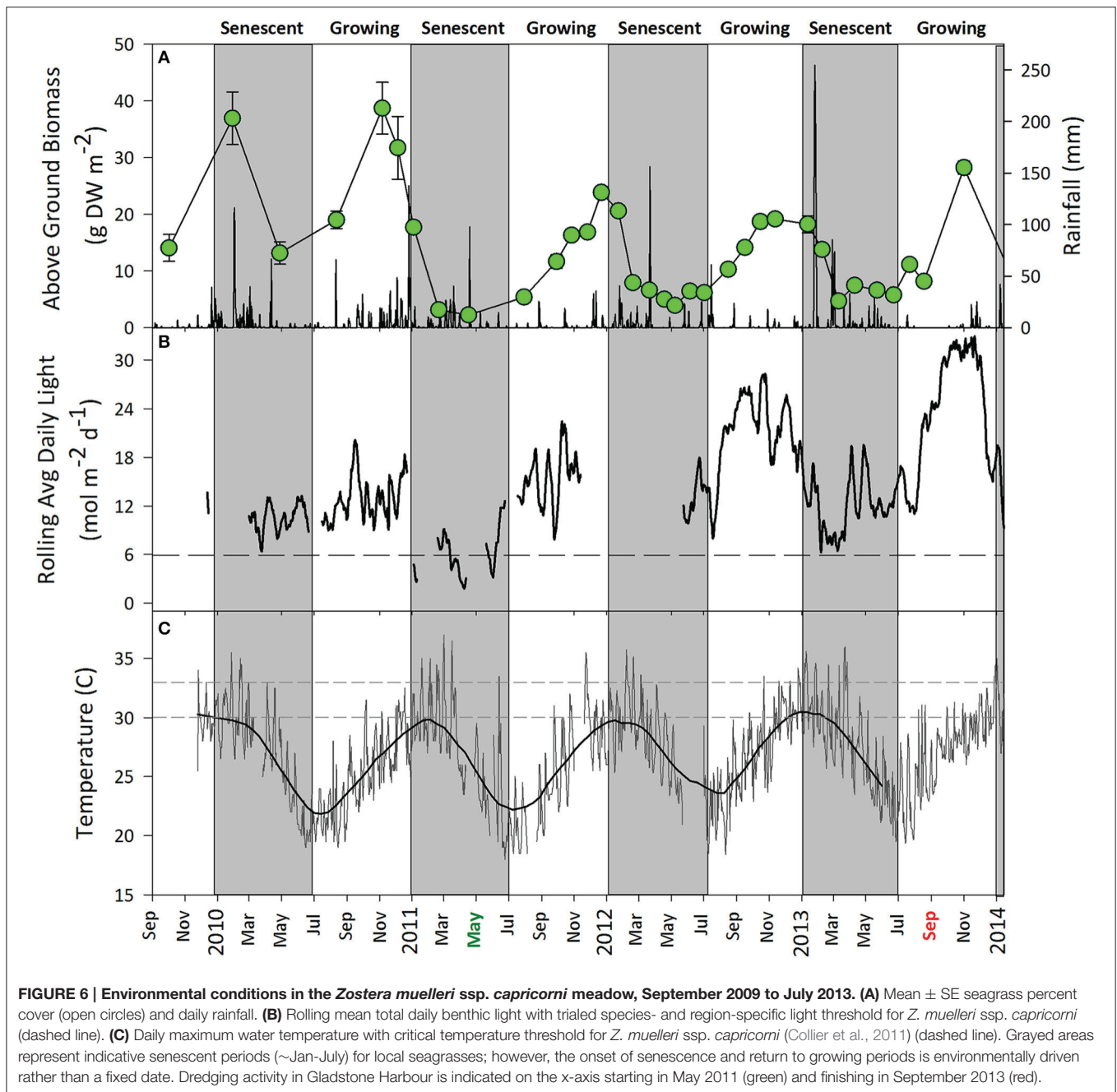


FIGURE 5 | Fourteen day rolling mean benthic light recorded under shade treatments across four shading studies. **(A)** Senescent season 1 (S1); **(B)** growing season 1 (G1); **(C)** senescent season 2 (S2); **(D)** growing season 2 (G2). Grayed area represents when shades were over experimental plots and white area when shades were removed. White vertical lines indicate sampling days; asterisks overlaying shade treatment light data indicates a significant reduction in seagrass above-ground biomass and percent cover relative to control for that sampling event (percent cover only for week 6 in G2); dashed lines indicate a biologically significant light threshold based on shading study results; solid black lines denote the derived management light threshold.



only sustains seagrass cover, but also provides energy reserves to be maintained or increased when conditions are good is likely important to ensure short-term stress events do not push the plant past a point of no return.

The quality of the light environment reaching seagrasses may be as important as the quantity of light received. Dredging, for example, typically increases particulate matter in the water column which affects spectral quality (Kirk, 1994). The size and type of particles re-suspended by dredging activity alter PAR transmission in a non-linear manner, with some wavelengths being more attenuated than others, resulting in a reduced light

environment with a shift toward yellow wavelengths (Kirk, 1994; Gallegos et al., 2009). Therefore, a light threshold value used for monitoring seagrass health during a dredging campaign, as determined according to the full PAR spectrum available, may overestimate the actual light available for photosynthesis as PAR measurements do not distinguish spectral shifts (Van Duin et al., 2001; Zimmerman, 2003). Light quality in Gladstone waters has explicit spatial variability, with broader spectral transmission in the outer harbor compared to the inner harbor, yet dredging had no effect on these spectral signatures when measured during the dredging campaign that occurred during

this study (Chartrand et al., 2012). The region is naturally highly turbid and therefore already exhibits a yellow-enhanced light signature due to the particle load in the water column and was not further skewed with additional sediment re-suspension from the dredge operation. While a more accurate threshold applying photosynthetic usable radiation (PUR) in place of PAR could resolve any effects of wavelength-specific water column absorption we did not need to alter light threshold values to incorporate spectral shifts from dredging in this instance.

Short term repeated shading and respite (fortnightly) in the present study was carried out to mimic repeated acute attenuation events from turbidity plumes followed by subsequent “relief” intervals. In providing a 14 day period of respite after shading was applied, *Z. muelleri* ssp. *capricorni* appeared to cope for 12 weeks with even the highest shade treatment, which had significantly impacted treatment plots shaded continuously after only 6–8 weeks. A study by Biber et al. (2009) also explored extreme attenuation events interspersed with recovery periods of varying length. They found that recovery intervals at least equal to the period of light deprivation were essential for long term survival.

Other investigations into *in situ* light requirements on *Zostera* spp. agree with the measured light effects and management threshold derived in this study (Dennison and Alberte, 1985; Moore et al., 1997; Thom et al., 2008; Collier C. J. et al., 2012). Collier C. J. et al. (2012) tested reduced light conditions during laboratory shading experiments on *Z. muelleri* ssp. *capricorni* also collected from Gladstone Harbour and found shoot density declined after 8.7 weeks under 4.4 mol photons $m^{-2} d^{-1}$ and 10.6 weeks under 9.5 mol photons $m^{-2} d^{-1}$. For the congeneric *Z. marina*, Dennison and Alberte (1985) found a significant reduction in *Z. marina* production rates with average daily scalar light levels of ~ 3.7 mol photons $m^{-2} d^{-1}$ under shades compared to unshaded controls (8 mol photons $m^{-2} d^{-1}$) during critical summer growing conditions. Moore et al. (1997) found similar results where sites with high light attenuation (2.7 mol photons $m^{-2} d^{-1}$) over 30 days was lethal to *Z. marina* transplants compared to those with higher water clarity (13.4 mol photons $m^{-2} d^{-1}$). More recent work on *Z. marina* found light requirements for long-term survival is 3 mol photons $m^{-2} d^{-1}$ and at least 7 mol photons $m^{-2} d^{-1}$ for non-light-limiting growth conditions during critical growing months (Thom et al., 2008).

Deriving a Light Threshold for Management

Developing effective management tools and appropriate mitigation strategies to protect seagrasses from a large-scale dredging campaign requires information on the distribution, light requirements and tolerances of local seagrass communities. Shading studies and the 4-year seagrass and light monitoring program provided the means to develop an effective and ecologically-derived management threshold. A 14 day integrated daily light value was used to establish a light threshold, which if maintained, would allow sufficient light to maintain local *Z. muelleri* ssp. *capricorni* seagrass condition in Gladstone Harbour during dredging.

With no significant effects of shading on seagrass growth during either of the senescent seasons, a seagrass light

management threshold was only defined for the growing season when *Z. muelleri* ssp. *capricorni* was sensitive to shading treatments. Both growing season studies clearly indicated light below 4 mol photons $m^{-2} d^{-1}$ is insufficient to maintain seagrass growth and or survival. In the second growing season study, light levels 2 weeks prior to a decline in seagrass measured between 4 and 5 mol photons $m^{-2} d^{-1}$, indicating morphological changes in *Z. muelleri* ssp. *capricorni* can take place in Gladstone at light intensities of ≤ 5 mol photons $m^{-2} d^{-1}$.

While the time to measurable loss in the first growing season was between 4 and 8 weeks, more frequent sampling during the second growing season documented appreciable declines in seagrass cover as early as 6 weeks under light limiting conditions. A study by Adams et al. (2015) found the timeframe over which light history and *Z. muelleri* above-ground biomass best correlated was from 8 to 35 weeks, however, they recognized management actions also should be triggered well before these measured reductions in biomass occur.

A range of bioindicators have been reviewed for use in seagrass monitoring programs to measure environmental pressures such as dredging (McMahon et al., 2013). While some metrics may be more sensitive on shorter time scales (e.g., rhizome sugars or ETR_{max}) to changes in the light climate (reviewed in McMahon et al., 2013), the ability to measure changes rapidly in relation to anthropogenic pressures (i.e., dredge operations) is important to apply an appropriate and timely management response. In the current study, above-ground abundance (either biomass or percent cover) reacted to light conditions within a timeframe that would allow a management response to be applied that could abate seagrass loss (i.e., move dredge to a new location), whereas shoot density was less sensitive to attenuated light. Other studies have also found shoot density to be a less sensitive metric; *Z. muelleri* ssp. *capricorni* alters leaf morphology before shoot loss under reduced light treatments, making above-ground biomass or cover a more sensitive indicator of change than shoot density as a consequence of environmental conditions (Rasheed, 1999; Collier C. J. et al., 2012).

As a conservative approach to protecting seagrass, a management light threshold needed to provide >5 mol photons $m^{-2} d^{-1}$ with some degree of buffer from potential impact to the plants and to ensure the plants not only maintained physical presence, but could generate energy stores. The threshold needed to ensure protection of seagrasses from deteriorating light conditions, while also having a credible fit with natural background light variability within the local meadow. If the threshold value was set too high and therefore routinely breached without measureable impacts to seagrass condition, it would be ineffective as a management tool. Conversely, a value too low that was never measured *in situ* in spite of concurrent declines in seagrass cover would likewise be inappropriate. A light threshold of 6 mol photons $m^{-2} d^{-1}$ was therefore used in a compliance framework by government regulators and management authorities to prevent measurable loss of seagrass from dredge related light attenuation in required management zones during dredging activity in Gladstone Harbour. This light threshold was considered in parallel with turbidity monitoring to ensure effects of turbidity related to the dredge vs. background

conditions could be resolved (GPCL, 2012b). During the dredging campaign light was maintained above the management threshold for the growing season at all of the prescribed seagrass management zones (GPCL, 2012a). This coincided with the presence of the largest seagrass meadows in the greater region during and post-dredging (Carter et al., 2015) and provides confidence that the approach used could be applied elsewhere for managing seagrasses.

While much research is focused on quantifying seagrass light requirements (Dennison, 1987; Staehr and Borum, 2011; Collier et al., 2016), this work has focused on the application of seagrass light requirements for use in a management setting of a large-scale dredging program. The absolute threshold value detailed here is not as critical as the approach used to derive a light-based model for seagrasses. The successful approach developed could readily be applied in other settings with sufficient knowledge of local seagrass dynamics and light conditions.

A range of additional measures would further improve the use of light thresholds to effectively manage seagrasses during dredging and other anthropogenic activities impacting on the light environment:

1. *Combine threshold assessments with effective sub-lethal bio-indicators of light stress*-A bioindicator that responds over days rather than weeks, and prior to actual physical declines in the plant, would dramatically improve the reaction time for management decisions to adjust dredging activities before declines occur. McMahan et al. (2013) identified a range of indicators that may be useful to measure sub-lethal changes, however, most still require substantial processing time. An indicator would ideally be measured and processed within 24–48 h for effective reactive management of dredging operations. Progress toward developing molecular indicators of sub-lethal seagrass light stress provides the most promising approach (Macreadie et al., 2014).
2. *Further investigations of the effect of water temperature*-Temperature is a known driver of temperate seagrass meadow dynamics and plant metabolism (Zimmerman et al., 1989; Olesen and Sand-Jensen, 1994; Staehr and Borum, 2011). However, the role of seasonally-driven temperature fluctuations on tropical seagrasses is inadequately described (McKenzie, 1994; Rasheed and Unsworth, 2011) despite work showing temperature governs the light intensity needed for a net carbon balance (Lee et al., 2007; Collier et al., 2011). Such effects need to be studied in other species and in greater detail to understand how temperature may act as a secondary driver of seagrass light thresholds for management.
3. *Research on the impacts of whole plant dynamics on light requirements*-Recent work has implicated cascade effects of reduced light on degradation of below-ground structures and the surrounding micro-environment (Terrados et al., 1999; Borum et al., 2006; Koren et al., 2015). Compromising below-ground root/rhizome integrity has negative implications for meadow resilience and the ability to resist short-term stresses (Vonk et al., 2015). Understanding whole plant dynamics

and how light reduction affects oxygen transport and below ground viability is vital to understand whether thresholds are in line with whole plant coping strategies.

4. *Modification of light requirements under cumulative long-term impacts*-Poor water quality prior to a major development may exacerbate efforts to manage additional impacts on already chronically stressed seagrass. Prolonged physiological strain from cumulative pressure over time may alter the plant's capacity to cope with further reduced light and may influence the light levels required for recovery.

CONCLUSION

This study characterized the tolerance of *Z. muelleri* ssp. *capricorni* to light attenuation on an intra- and inter-annual cycle using *in situ* shading studies and light history monitored over a 4-year period. This information was used to develop a locally-relevant management plan to protect seagrasses from dredging-related impacts to the light environment. A light threshold of 6 mol photons m⁻² d⁻¹ was successfully trialed as part of a compliance program for mitigating dredging impacts. This minimized the risk that *Z. muelleri* ssp. *capricorni*, the dominant local species, was affected by dredge turbidity plumes within prescribed management zones. When implementing a light management strategy it is critical that local conditions, species and context are considered.

AUTHOR CONTRIBUTIONS

KC, MR, CB, and PR together designed the research project. KC led the study and drafted the manuscript with the assistance of MR and AC. CB and AC provided major assistance in field execution and data analysis. All co-authors commented on and approved the final manuscript draft.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fmars.2016.00106>

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