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Response of the seagrass *Halophila ovalis* to altered light quality in a simulated dredge plume

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ABSTRACT

Seagrass meadows are globally threatened, largely through activities that reduce light quantity (photosynthetic photon flux density) such as dredging. However, these activities can simultaneously alter the spectral quality of light. Previous studies showed that *Halophila ovalis* seagrass productivity is reduced under monochromatic yellow/green light, wavelengths associated with dredge plumes, but it is unclear how they respond to spectra produced by real dredging projects. We simultaneously subjected adult *H. ovalis* plants to altered light quality and quantity simulating a real commercial dredging operation (15 mg L^{-1} TSS, 50 and 200 μmol photons m^{-2} s^{-1}). There was a significant effect of reduced light quantity on physiological and morphological variables and a significant effect of light quality on the pigment antheraxanthin. The lack of effect of light quality on growth indicates that while seagrass are sensitive to changes in light quality, natural- and anthropogenic-driven changes may not always be sufficient to produce strong effects on *H. ovalis*.

1. Introduction

Seagrasses commonly occur in estuaries and shallow coastal zones, where they provide significant ecosystem functions and services that rival tropical rainforests and coral reefs (Orth et al., 2006; Barbier et al., 2011; Fourqurean et al., 2012). These include habitat for commercially important juvenile fish (Bertelli and Unsworth, 2014), cycling of nutrients (Marbà et al., 2007), stabilizing sediments (Koch et al., 2006), and storage of organic carbon (Orth et al., 2006; Lavery et al., 2013). Seagrasses require high levels of light for survival (Longstaff, 1999) and their global decline has been attributed primarily to human activities that alter light, such as eutrophication, sediment loading and dredging (Erftemeijer and Robin Lewis, 2006; Orth et al., 2006; Waycott et al., 2009). While the effects of reduced light quantity on seagrasses are well documented (Ralph et al., 2007; McMahon et al., 2013), effects of the associated changes in spectral quality are unclear and have been identified as a crucial knowledge gap within the seagrass literature (York et al., 2016).

Only one study of the few investigating seagrass responses to changes in light quality, used yellow and green light, the wavelengths associated with dredging (Strydom et al., 2017). Here, plants were grown under narrow wavebands of light at a constant above- saturating light intensity. *Halophila ovalis* adult plants grown in monochromatic yellow and green light had lower below-ground productivity than plants grown in full-spectrum light but seed germination was enhanced in yellow light compared to green, and seedling survival under yellow light was not significantly impacted (i.e. did not differ to full-spectrum treatments). This study confirms that seagrasses do respond to different wavelengths of light, but there is a limited understanding of what drives these responses, and how species respond to interactive effects of changes in light quality and quantity. Seagrass responses to reduced photosynthetic photon flux density (PPFD) include changes to chlorophyll (chl) content, carbohydrates, productivity, leaf area and shoot density (Ralph et al., 2007). Therefore, it is reasonable to expect an interactive effect of altered light quality and reduced light quantity on seagrasses as it has been reported for understory species in terrestrial forest which receive reduced quantity and a green-enriched quality of light (as the upper foliage absorbs blue and red light) (Folta and Maruhnich, 2007). Plants can respond to this under-canopy light by altering their physiology, morphology and reproductive responses, e.g. the shade-avoidance response (Neff et al., 2000).

Both the quality and quantity of light in aquatic ecosystems will vary simultaneously due to a number of factors. For suspended particles, such as sediments and phytoplankton, changes in benthic light quality are dependent on the optical properties of the suspended particles (Kirk, 1994), and the concentration of those suspended particles

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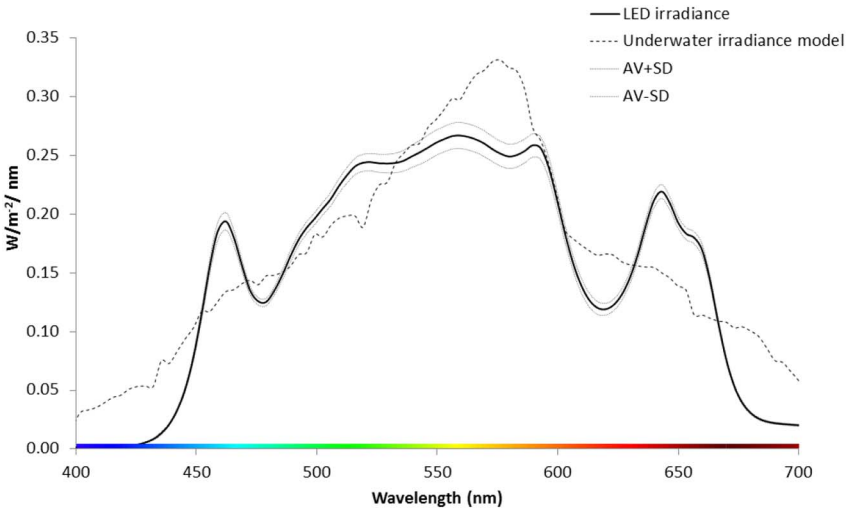

Fig. 1. The underwater downwelling irradiance model (dashed line) was used to create the "dredge spectrum" LED irradiance output (solid black line) based on a dredge plume near Onslow, Western Australia with a measured TSS of 15 mg L^{-1} at 3 m depth. Average (AV) ± SD irradiance spread across light module 30 cm below lights.

(total suspended solids or TSS). Dredging, and other processes that introduce turbidity, will have the dual effect of reducing the PPFD and simultaneously altering light quality (Jones et al., 2016). The amount of light reduction is dependent on the density of the plume, as is the spectral shift, with shifts towards green light at low plume densities and towards yellow (~490 nm) with increased suspended sediment loads (Chartrand et al., 2012). These changes will also be related to the distance from the dredging operation, with highest TSS concentrations occurring close to dredging activities (near-field) but decreasing with distance (i.e. in the far-field) (Jones et al., 2016). The effects of light quality may manifest with increasing distance from the plume, in areas where light quantity is not below minimum light requirements (i.e. PPFD) required to maintain plant survival.

In this study we assessed whether *H. ovalis* responds to shifts in light quality and quantity typical of those produced by real dredge plumes. We tested the interactive effect of reduced quantity (2 levels: 50 and 200 µmol photons $m^{-2} s^{-1}$) and altered spectral quality (2 levels: simulated dredge spectrum and full-spectrum) on the physiology, productivity and morphology of the widespread seagrass *H. ovalis*. Specifically, we hypothesised that a) physiological adjustments would occur under low light treatments (e.g. increased chl *a* concentration) to enhance light capture, and in addition, b) reduced below-ground productivity would be evident in plants grown under the dredge spectrum (yellow-green shifted spectral quality), and c) an interactive effect of both factors.

2. Methods

2.1. Experimental design and set-up

Adult *H. ovalis* plants were subjected to two fixed factors in a fully orthogonal design: 'Light quality' (provided at two levels: control and dredge spectrum) and 'Light quantity' (provided at high 200 µmol photons $m^{-2} s^{-1}$ and low 50 µmol photons $m^{-2} s^{-1}$ PPFD). The light quantity of 200 µmol photons $m^{-2} s^{-1}$ has been used to successfully grow *H. ovalis* (Strydom et al. 2017; Hillman et al., 1995) and was similar to that measured at canopy height at the site used to collect plants for the experiment (230 µmol photons $m^{-2} s^{-1}$ measured at 11:00 AM). The low light quantity treatment (50 µmol photons $m^{-2} s^{-1}$) has previously induced lower growth rates in *H. ovalis* (Hillman et al., 1995; Kilminster, 2006). The light quality treatments mimicked a full-spectrum sunlight (control) and far-field dredge sediment plume conditions, as identified from TSS data measured over seagrass meadows during a commercial dredging operation near Onslow, Western Australia (TSS data provided by Mark Broomhall, CSIRO). The sediment concentration of 15 mg L^{-1} was entered into an empirical spectral irradiance model developed for dredge conditions in the region around Onslow to generate an expected spectral light availability at a depth of 3 m (spectrum developed by Dr. Mathew Slivkoff, In-situ Marine optics). This spectrum was chosen because it reflected a far-field dredging plume of moderate TSS concentrations and at a depth that seagrasses typically occur at. Using light characteristics from plumes with much higher TSS concentrations would drastically reduce light intensity, and therefore inhibit our ability to detect an effect of light quality on seagrasses, as the light quantity would be below that required to sustain plant growth. The treatment therefore represents a plume spectrum suitable for studying sub-lethal effects of altered light quality and quantity on *H. ovalis*.

For each combination of factors and levels, four replicate aquarium tanks were established (total $n = 16$ independent glass tanks). Light quality treatments were provided through aquarium Light Emitting Diode (LED) Grow 8 modules (MarinTech Pty Ltd). For the control light quality treatments, the LED modules were customised to a spectrum similar to full sunlight. The dredge spectrum LED modules were customised at In-situ Marine Optics Pty Ltd. (Bibra Lake, Western Australia) by altering the LED configuration and the addition of green and yellow filters (Rosco super gel) using an underwater irradiance model (Fig. 12 in Jones et al., 2016, Slivkoff et al., in prep) to produce a spectrum as close to the field plume as possible (Fig. 1). An underwater hyperspectral radiometer (USSIMO, In-situ marine optics Pty Ltd.) was used to measure the LED output spectrum. The light quantity treatments were achieved by placing the LEDs at a height above tanks that provided 200 µmol photons $m^{-2} s^{-1}$ at the seagrass canopy for the controls. For the 50 µmol photons $m^{-2} s^{-1}$ treatment, a layer of neutral density shade cloth (ARMAShade, Jaylon Pty Ltd.) was placed between the LED units and the tank.

Aquarium tanks (600 × 300 × 300 mm, volume of 54 L) were lined with unsorted, washed, quartz river sand to 10 cm depth containing 1.3% by weight shredded seagrass wrack as a nutrient/organic matter supply (Statton et al., 2013) and filled with approximately 52 L of seawater with a salinity of 36 ppt. The water in each tank was circulated through its own sump tank containing a pump and filter (300 µm foam block), thus ensuring that each replicate tank was independent (full experimental set up described in Strydom et al., 2016).

Light treatments were randomly allocated to aquarium tanks, and each tank was isolated from the others using PVC boards to ensure no leakage of light from surrounding treatments. Light intensity in each tank was measured at the top of the *H. ovalis* canopy using an underwater quantum sensor (MicroPAR). Water temperature and salinity were monitored using a WTW™ conductivity meter. The water temperature was maintained at 20–21 °C, which was measured at the collection site (see below) and has previously been used as an optimal

range for growing *H. ovalis* in aquaria (Hillman et al., 1995). Salinity was adjusted using rainwater and kept within 1.0 of the target salinity, 36.

2.2. Seagrass collection and acclimation

H. ovalis ramets were collected in November 2015 from Woodman Point (32° 8′10.84″S, 115°44′46.35″E), Western Australia, where *H. ovalis* grows among *Posidonia* spp. meadows. Salinity and water temperature at the time of collection were 36 and 20 °C respectively. Ramets with five shoots (leaf pairs) preceding the apical meristem were haphazardly collected by gently excavating the sediment at the edge of the meadow, and placed into an aerated cooler box filled with seawater for transportation. In the laboratory, ramets were standardised to three shoots preceding the apical meristem in order to allow accurate comparisons of biomass measures, and then planted into experimental tanks within 4 hof collection.

Seven ramets were randomly assigned to each tank and acclimated for 11 days at 20–21 °C, 36 salinity and 200 µmol photons $m^{-2} s^{-1}$ of control light spectrum (the same sunlight spectrum used for the experiment). Ramets were separated using thin PVC boards wedged into the sediment to ensure that growing tips would not overlap so that growth rates of individual ramets could be determined. The growing tip of one ramet per tank ('acclimation ramet') was tagged by placing PVC-coated wire over the rhizome behind the youngest leaf, in order to compare new shoot production over the acclimation period. Additionally, photosynthetic characteristics (quantum yield of PSII) of the plants were made using a WALZ Pulse Amplitude Modulated (PAM) diving fluorometer and compared to yield measurements made on undisturbed plants in the field at the time of collection as an indicator of plant stress. The maximum quantum yield values were in the range identified as healthy, 0.73–0.75 (Ralph and Burchett, 1995) for aquarium and field plants, indicating successful acclimation to the aquarium conditions. Furthermore, newly formed shoots in front of the tag on the acclimation ramet demonstrated new growth under tank conditions, which were similar across all tanks.

After the acclimation period, the growing tips of each of the remaining ramets were tagged by placing PVC-coated wire over the rhizome behind the youngest leaf, in order to determine growth rates over the experimental period. At this point, the experiment was started by applying the light quality and quantity treatments. Due to fast growth rates of plants (e.g. 3.7 mg $apex^{-1} day^{-1}$ or new leaf formation every 1.6 days, (Kilminster et al., 2014), we considered an experimental period of 25 days adequate time to detect a range of ecophysiological responses.

At the end of the experiment, photosynthetic measurements were taken on one ramet per tank (see below) and six leaves were removed per tank, wrapped in foil and immediately stored in the dark at − 80 °C for pigment analysis. All ramets were then gently removed from the tanks and stored at − 20 °C (apart from pigment and carbohydrates samples which were stored at − 80 °C) prior to processing for carbohydrate, growth and production, morphology and biomass measures (Table 1). In some cases, multiple measures were taken per tank and these were averaged for the statistical analyses, although the number of measures per tank varied depending on the amount of plant material required for sampling (Table 1).

2.3. Photosynthetic characteristics

The effective quantum yield and maximum quantum yield of PSII and Rapid Light Curves (RLCs) were measured on one randomly selected ramet per tank on the last day of the experiment prior to harvesting. Measurements were made on one mature leaf in the shoot preceding the apical shoot. The absorption factor (AF) for each leaf was determined by measuring the incident PPFD and transmitted PPFD through the leaf using the PAM quantum sensor (Beer and Björk, 2000).

Table 1
Dependent variables measured on *Halophila ovalis* plants following 25 days exposure to different light quality and quantity treatments.

Variable type	Component on which measure was made per tank
Physiology	
Photosynthetic characteristics: ETR_{max}, E_k, α	One mature leaf
Pigments: chl (*a* + *b*), carotene, antheraxanthin, violaxanthin, neoxanthin	Six mature leaves (pooled into 1 replicate)
Carbohydrates: rhizome and leaf starch and sugars	Three ramets separated in rhizome and leaves (pooled into 1 replicate)
Biomass & density	
Total biomass, above-belowground biomass, leaf density	Entire tank
Growth	
Leaf, root and rhizome productivity	All tagged ramets
Shoot mortality, shoot production, rhizome	All tagged ramets
Extension rate	All tagged ramets
Morphology	
Leaf area	Three mature shoots
Internode and root length	Three mature shoots

Electron transport rates (ETR) were calculated as described in Strydom et al. (2017) and RLCs (at 53, 153, 454, 663, 885, 1267, 1662 µmol photons $m^{-2} s^{-1}$) were fitted to the equation described by Jassby and Platt (1976) to estimate ETR_{max}, photosynthetic efficiency (α) and half-saturating irradiance (E_k) using SigmaPlot (version 7).

2.4. Pigment analysis

The concentrations of chl *a* and *b* and the accessory pigments lutein, β, β carotene, neoxanthin, violaxanthin, zeaxanthin, and antheraxanthin content were determined for duplicate sets of three pooled mature leaves per tank using HPLC, by the method described previously in Strydom et al. (2017).

2.5. Carbohydrates

Carbohydrate analysis was performed separately on leaf and rhizome material from three pooled ramets per tank to ensure a minimum weight of 75 mg DW. Dried material (60 °C for 48 h) was homogenized and ground into a fine powder in a mill grinder (Mixermill Germany). The samples were analysed for soluble sugars and starch content as adapted from Karkalas (1985) and McCleary and Codd (1991).

2.6. Productivity, biomass and leaf density

To determine productivity of ramets growing under treatments, all ramets were sorted into newly produced tissue (the tissue in front of the rhizome tag), and initial material (all the material behind the rhizome tag), and the number of nodes, shoots and leaves counted. The newly produced material was sorted into leaves plus petioles, rhizomes and roots, dried at 60 °C for 48 h and weighed. Leaf, root and rhizome productivity (mg DW $ramet^{-1} d^{-1}$) was calculated by summing the weight of all newly produced plant material in each tank, divided by the number of ramets per tank and the number of days of the experiment. Shoot production (shoots $ramet^{-1} d^{-1}$) was calculated as the sum of newly produced nodes in a tank, divided by the number of ramets and the number of days. Similarly, shoot mortality was calculated by dividing the number of new nodes without leaves by the number of ramets and the number of days (shoot mortality $ramet^{-1} d^{-1}$). Rhizome extension rate (cm $ramet^{-1} d^{-1}$) was estimated by measuring the length of the newly produced rhizome material, summing for all rhizomes and then dividing by the number of ramets and the number of

days (cm ramet^{-1} d^{-1}). The total biomass for each tank was calculated by summing the DW of all plant material harvested.

2.7. Morphology

All ramets from each tank were photographed and the images used to measure leaf area (cm^2), petiole length (cm), internode length (cm) and root length (cm) in the program Image J©. All variables were measured on the three mature shoots preceding the apical and a mean per tank was calculated. Branching was calculated by summing the total number of secondary branches (that is a branch coming off the main rhizome with an apical at the growing tip) per tank.

2.8. Statistical analyses

Multivariate routines were used to test for effects of light quantity and quality (2 fixed factors, 2 levels each) on the full suite of response variables of *H. ovalis* using the PRIMER v7 and PERMANOVA + 2015 software (PRIMER-E, Plymouth, UK). A metric multidimensional scaling or *m*MDS plot (Kruskal, 1964) was run using the Bootstrap Averages routine which constructed smooth envelopes for the bootstrap average points (using 100 bootstraps per group at 95% confidence interval) for the same 28 response variables (created using the same normalised data and Euclidean distance) in order to visualise the separation among groups (Clarke and Gorley, 2015). A permutational analysis of variance (PERMANOVA) was used to test for statistically significant differences among treatment sub-groups. Prior to the analysis data were tested for homogeneity of variance (PERMDISP), the data normalised using the standard normalise function in PRIMER-E, and then PERMANOVA run on the resemblance matrix (created using Euclidean distance) containing the 28 response variables (Table 1). Where PERMANOVA indicated a significant effect, Similarity Percentage analysis (SIMPER, cumulative cut-off at 55%) was used to determine which response variables were contributing most to the differences, and those that did not were listed in the Supplementary material (Table S1). A pair-wise comparisons test was not required as there were only 2 levels within each factor; therefore, the SIMPER was performed without the pair-wise test. While SIMPER was first used to identify species driving patterns in multidimensional space, it is also appropriate for other forms of data (Clarke et al., 2014). Individual PERMANOVAs were carried out on all of the variables identified as important by the SIMPER analysis (Table 3), to further confirm if they were significantly affected by light quality and/or light quantity (Table 2). For brevity, only variables showing statistically significant differences were shown (Table 2), with the remaining statistical outputs displayed in Supplementary material (Table S2).

3. Results

There was a clear separation of the high and low light treatment groups along MDS Axis 1 and some separation along the MDS axis 2 between the High and Low treatments within the full-spectrum (Fig. 2). The main PERMANOVA test confirmed a significant ($p < 0.05$) effect of light quantity on adult *H. ovalis* plants but no significant effect of light quality, or the interaction of quantity and quality, when all variables were incorporate into the test (Table 2). The SIMPER analysis indicated that the differences between High and Low light treatments were driven by a range of physiological, growth and morphological variables (Table 3). Important physiological variables in explaining the differences between High and Low light treatments were pigments (chl *a*, chl *b*, carotenes, violaxanthin and neoaxanthin) and photosynthetic efficiency (α), which were all higher under low light treatments. E_k was another photosynthetic variable that contributed to the difference between High and Low light treatments, with greater values in High light compared to Low light treatments.

The PERMANOVAs carried out on the individual variables indicated a significant ($p < 0.05$) interactive effect of light quantity and quality on antheraxanthin concentrations, which were significantly lower in the dredge spectrum compared to the full-spectrum at high light intensities (Table 2, Fig. 3D). Photosynthetic efficiency (α) and violaxanthin concentration were both significantly ($p < 0.05$) higher in Low light treatments (Table 2, Fig. 3A, C). Conversely, leaf starch concentrations were significantly lower in the Low light treatments (Table 2, Fig. 3B).

Table 2
Results of PERMANOVA testing for significant effect of light quality and light quantity (both fixed factors) on *H. ovalis* response variables. * indicates significant difference at $p < 0.05$.

Source	d.f	MS	F	Unique perms	P
Main test					
Quantity	15	49.16	2.16	999	*
Quality	15	21.25	0.95	999	0.49
Quantity × quality	15	31.88	1.40	996	0.18
Individual Tests					
1) Antheraxanthin					
Quantity	15	1.90	24.6	997	*
Quality	15	6.02	7.79	997	*
Quantity × quality	15	4.12	16.8	998	*
2) Violaxantin					
Quantity	15	4.58	5.77	996	*
Quality	15	0.66	0.83	996	0.37
Quantity × quality	15	0.21	0.26	998	0.61
3) Alpha					
Quantity	15	0.40	4.80	998	*
Quality	15	0.62	0.73	996	0.39
Quantity × quality	15	5.43	6.37	998	0.80
4) Leaf starch					
Quantity	15	3.42	4.58	900	*
Quality	15	1.52	2.03	897	0.18
Quantity × quality	15	0.74	1.47	896	0.21
5) Root length					
Quantity	15	2.87	4.29	999	0.06
Quality	15	0.50	0.74	999	0.09
Quantity × quality	15	0.74	1.47	996	*

4. Discussion

The results from this study clearly show that reduced light quantity affects *H. ovalis* physiology, growth and morphology, and in a manner consistent with studies on this and other seagrasses and with well-documented response pathways (Longstaff, 1999; McMahon et al., 2013). In contrast, the hypothesised effect of altered light quality was not strongly supported.

4.1. Light quantity

The strong physiological response of *H. ovalis* to reduced light quantity was expected based on the findings of numerous studies into the effect of reduced light availability on seagrasses. For example, the increased photosynthetic efficiency and decreased E_k values in both Low light treatments are a typical dark-adaption response of seagrass to reduced light availability and have been recorded for other *Halophila* species (Durako et al., 2003). It is also well known that seagrasses alter chlorophyll content as a photo-adaptive response to reduced light in order to increase light capture (Abal et al., 1994; Collier et al., 2008; Lee and Dunton, 1997; Longstaff and Dennison, 1999), a response that was observed for plants growing in the Low light treatments of this experiment. Furthermore, antheraxanthin concentrations were significantly higher in the High light treatment with a full spectrum compared to Low light, perhaps indicating that the plants were receiving sufficient light to saturate photosynthesis and were converting violaxanthin to antheraxanthin through the process of non-photochemical quenching (NPQ) (Demmig-Adams and Adams, 1992), which

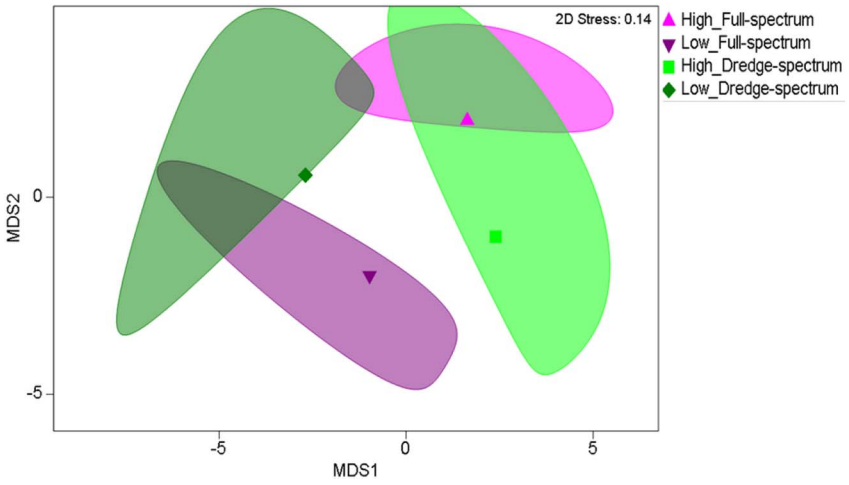

Fig. 2. 2-D *m*MDS displays the group means surrounded by a corresponding bootstrap region (with 95% confidence interval at 100 bootstraps per group) of the replicate *H. ovalis* adult plant samples grown under different light quantity (high and low), and light quality (full-spectrum and dredge-spectrum) treatments.

Table 3
SIMPER summary table indicating variables that contributed to the observed average distances between the High and Low light treatments (cumulative cut-off at 55%).

Variable	Av.Value High	Av.Value Low	Av.Sq. Dist	Sq.Dist/ SD	Contrib %	Cum. %
Antheraxanthin	0.614	− 0.614	2.63	0.96	4.98	4.98
Violaxanthin	− 0.535	0.535	2.45	0.75	4.64	9.62
Alpha	− 0.506	0.506	2.39	0.87	4.53	14.15
Rhiz extention rate	0.468	− 0.468	2.31	0.76	4.38	18.53
Leaf starch	0.463	− 0.463	2.30	1.03	4.37	22.90
Chlorophyll *a*	− 0.425	0.425	2.24	0.82	4.24	27.14
Root length	0.424	− 0.424	2.23	0.85	4.24	31.38
Chlorophyll *b*	− 0.420	0.420	2.23	0.79	4.22	35.60
Carotenes	− 0.419	0.419	2.23	0.79	4.22	39.82
Neoaxanthin	− 0.405	0.405	2.21	0.66	4.18	44.00
Leaf Area	0.387	− 0.387	2.17	0.58	4.12	48.12
E_k	0.384	− 0.384	2.17	0.75	4.11	52.23

has been reported for other seagrasses (Ralph et al., 2002). The observed decreased leaf starch response under low light conditions could be due to lower photosynthetic carbon fixation. Overall, the responses demonstrate a physiological acclimation pathway to reduced light, as shown in other studies, and illustrates the capacity for *H. ovalis* to acclimate to low light conditions in order to increase the chance of survival until conditions improve (Lee and Dunton, 1997; Longstaff, 1999).

There were more physiological responses (9 variables) across the low-light acclimation pathway than plant scale responses (3variables: rhizome extension, leaf area and root length), suggesting that the timescale for severe response (i.e. loss in biomass) had not been reached. The plant scale variables which showed a decline in low light were consistent with other studies, whereby plants attempt to maintain a positive carbon balance by reducing the respiratory demand of leaves and below-ground tissues (Lee and Dunton, 1997; Ralph et al., 2007; Collier et al., 2009). The potential disadvantage of these morphological acclamatory leaf adjustments is the subsequent loss of photosynthetic tissue available for light capture, and some species show an alternative response of increasing leaf area in response to light reduction (Abal et al., 1994; Longstaff and Dennison, 1999). Therefore, while responses to light quantity differ slightly among species the common theme emerging is that physiological and/or morphological leaf responses are prevalent, though mainly physiological adjustments were recorded in this study.

4.2. Light quality

In a previous study (Strydom et al., 2017), *H. ovalis* responded negatively to monochromatic yellow light quality, and because the dredge plume in this experiment was shifted towards the yellow wavelengths we hypothesised a similar response. While there were trends for some variables, generally there was no significant response to the dredge spectrum. The dredge plume spectrum used in this study is a more a realistic representation of an in situ spectral shift that seagrasses are likely to experience, with a wider range of wavelengths present compared to the monochromatic light quality experiment (Strydom et al., 2017). This indicates that while extreme light quality shifts produce clear responses (positive or negative, depending on the life history stage) in *H. ovalis*, more subtle spectral shifts that still retain a mixed spectrum, such as those produced in dredging or river discharge plumes, do not necessarily induce a strong response. This is not entirely surprising. Coastal waters typically have a range of spectral shifts related to river discharge (CDOM), storm induced re-suspension (TSS) and phytoplankton blooms (chl *a*) (Kirk, 1994; Kostoglidis et al., 2005), and as seagrasses have evolved in these environments, it is likely that they are able to cope with a range of spectral shifts. This has been demonstrated in adult *H. johnsonii* plants that acclimated to the addition of UVB light within 4 days (Durako et al., 2003). In another study, *H. johnsonii* riverine populations (strongly influenced by CDOM) exhibited higher gross photosynthetic rates and quantum efficiencies than marine inlet plants (low-CDOM environment) at shorter wavelengths (350, 400 and 450 nm) (Kahn and Durako, 2009), providing further evidence to suggest that seagrasses have the ability to acclimate to a range of spectral shifts.

Even though there was no overall significant effect of light quality on the whole plant, some individual physiological variables exhibited a response to changes in light quality. Antheraxanthin concentrations were significantly lower in the dredge spectrum (High and Low light) and full-spectrum (Low light) compared to the full-spectrum at high light intensity. This light harvesting carotenoid has an absorption peak at ~485 nm (Alberte and Andersen, 1986) and the difference in concentrations could be explained by the greater proportion of blue light within the full-spectrum treatment at high intensities, whereas the plants growing under the remaining three treatments received less blue light. Alternatively, the high antheraxanthin concentrations in the full spectrum High light treatments may indicate NPQ (i.e. the conversion of violaxanthin to antheraxanthin to release excess energy) (Demmig-Adams and Adams, 1992). The lack of NPQ in the High light dredge spectrum treatment is likely due to the nature of green and yellow wavelengths containing less energy per photon compared to blue light (which the High full spectrum treatments contained more of), therefore, plants in the dredge spectrum may not have had excess energy to release through NPQ and thus contained less antheraxanthin pigment content.

The half-saturating irradiance (E_k) values demonstrated a similar trend to antheraxanthin concentrations with lower values evident in

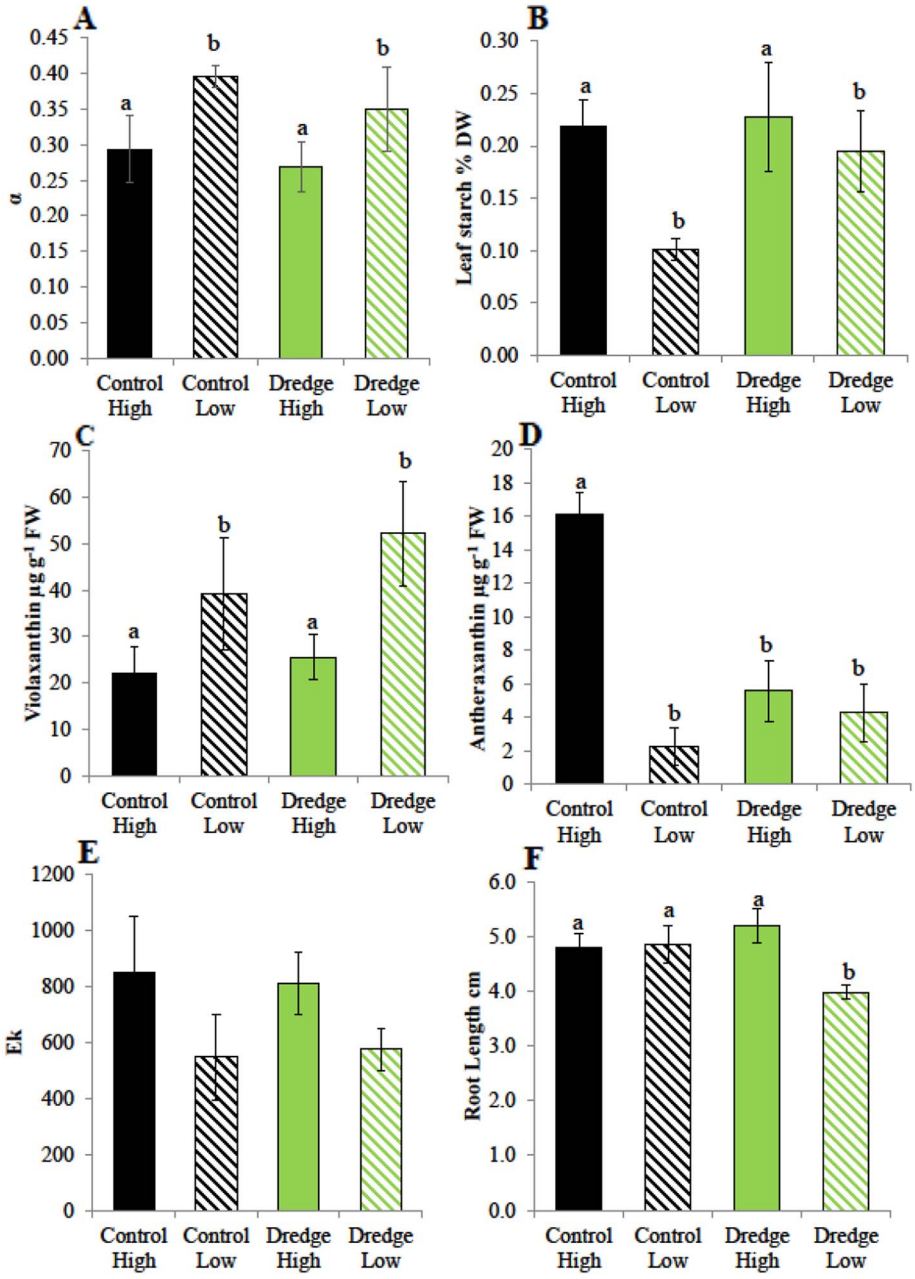

Fig. 3. Effect of altered light quantity (High 200 and Low 50 µmol photons $m^{-2} s^{-1}$) and quality (dredge and full-spectrum) on *H. ovalis* (A) alpha, (B) leaf starch, (C) violaxanthin, (D) antheraxanthin, (E) E_k and (F) root length. All data are means ($n = 4$) ± SE and different lower case letters denote significant differences ($p < 0.05$) among values.

both dredge spectrum treatments and in full spectrum at low light intensities. Previous research using monochromatic light treatments showed that the lowest half-saturating irradiance values occurred in *H. ovalis* leaves growing in green treatments (Strydom et al., 2017), which is consistent with our finding here since the dredge spectrum is closest to green and yellow light. As these wavelengths also dominate shade light, and shade adapted plants generally have low E_k values (Gómez et al., 2009), this suggests that the mechanism behind the response of *H. ovalis* plants growing in these treatments is indicative of a photophysiological acclimation to shade light. Furthermore, this result was expected as seagrasses often saturate at lower irradiance levels in response to reduced light availability (Ralph and Gademann, 2005).

4.3. Implications for dredging

This study found no severe impact of the dredge spectrum light quality conditions used in this study on *H. ovalis*, as no significant reductions in biomass were recorded. However, this experiment was limited to simulating the light quality of a single dredge plume and, therefore, the results cannot be presumed to apply to all possible types of dredge plumes. The TSS concentrations in dredge plumes vary greatly. For example, a dredging operation occurring over several months in Papua New Guinea had peak TSS concentrations of > 500 mg L^{-1} within the high impact zone, and > 25 mg L^{-1} for 90% of the time (Thomas et al., 2003). The specific spectrum used here was based on a plume that contained 15 mg L^{-1} TSS and the plants were subjected to this for 25 days. We cannot assume that our findings reflect those that might occur under light quality shifts associated with a denser plume or over a longer time frame. However, even though plumes with different TSS concentrations will produce different spectral shifts, light quantity will reduce concurrently and our results indicate that the effect of light quantity reduction would likely be greater than those of the associated shift in light quality, at least for adult plants, which were the focus of this study. This may be different for other causes of change in light quality such as river discharges, which may contain high concentrations of CDOM and cause different spectral shifts

without the associated effects of turbidity (see Kirk, 1994).

Responses to changes in light quality may differ across life-history stages and it should not be assumed that the adult responses in this study are representative of *H. ovalis* seeds and seedlings. Other evidence suggests that seeds and seedlings respond differently to the same spectral shift (i.e. monochromatic yellow light) compared to adults (Strydom et al., 2017). This has potential implications for tropical *H. ovalis* populations, where annual re-establishment of meadows is supported through germination of seed banks (Hammerstrom et al., 2006; Rasheed, 2004). This life cycle strategy has also allowed meadows to re-establish after periods of intense dredging (York et al., 2015). Therefore, further research should focus on defining the responses of seagrass seeds and seedlings to light quality under dredge plumes as the outcomes could be directly applicable to improving the management of seagrass meadow fecundity during dredging operations.

There are factors in addition to altered light quantity and light quality that have the potential to impact seagrasses under dredging conditions. For example, interactive effects such as increased water temperature are known to exacerbate negative impacts to low light conditions (Lavery et al., 2009; Collier et al., 2011) and, therefore, the impacts of altered light quantity and light quality in tropical waters might have greater impacts on local meadows. Additionally, other pressures associated with dredging include burial of seagrasses (Vermaat et al., 1997), which may further impact seagrass resilience and their ability to acclimate to changing light conditions.

5. Conclusions

This research has shown that *H. ovalis* grown in conditions simulating a dredging-derived sediment plume ($> 15\ mg\ L^{-1}$ TSS) in shallow water (3 m) are negatively impacted by reduced light quantity but that a more dramatic light quality shift (i.e. approaching monochromatic) would be required to produce a growth response. However, it is likely that any effect of light quality will be minor relative to that of reduced quantity of light. It remains unclear whether this finding can be generalised to other seagrasses, to different life-history stage or all types of dredge plumes or shifts in light quality induced by other causes. Further research using a range of light qualities associated with different plumes or environmental conditions is warranted in order to determine the threshold point between monochromatic and broader spectrum light quality shifts that produce effects in seagrasses.

Acknowledgments and author contributions

S.·S designed and built the experimental aquarium set up, ran the experiments, processed samples, conducted data analysis and drafted the manuscript. K.M and P.L substantially contributed to the conception and design of the study, interpretation of data as well as providing intellectual content to the manuscript through multiple edits. All authors provided final approval of the manuscript to be published. We are indebted to Jeramie Putman and Nicole Said for their assistance in the field and aquariums. This research was partially funded by the Western Australian Marine Science Institution (WAMSI, project Theme 5; agreement number G1001056) as part of the WAMSI Dredging Science Node, Woodside Energy, Chevron Australia, BHP Billiton as environmental offsets and by co-investment from the WAMSI Joint Venture partners. The commercial investors had no role in the data analysis, data interpretation, and the decision to publish or in the preparation of the manuscript. This work was also funded through the Australian Commonwealth Government's Collaborative Research networks scheme (Grant CRN2011:05), the School of Sciences, Edith Cowan University and by the Holsworth Wildlife Research Endowment (G1002158) and the Graduate Women of Western Australia Mary Walters Scholarship (G1002228).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marpolbul.2017.05.060.

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