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Thresholds for morphological response to light reduction for four tropical seagrass species



C.J. Collier ^{a,b,*}, M.P. Adams ^c, L. Langlois ^b, M. Waycott ^d, K.R. O'Brien ^c, P.S. Maxwell ^{c,e}, L. McKenzie ^b

- ^a College of Marine and Environmental Sciences, James Cook University, Townsville 4811, Australia
- ^b Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER), James Cook University, Cairns 4870, Australia
- ^c School of Chemical Engineering, The University of Queensland, Brisbane 4072, Australia
- d School of Earth and Environmental Science, Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, Adelaide 5005, Australia
- ^e Healthy Waterways Ltd., Brisbane 4004, Australia

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ABSTRACT

Seagrasses worldwide are highly vulnerable to, and at increasing risk from reduced light availability, and robust light thresholds are required for evaluating future impacts of changing light conditions. We tested the morphological response (shoot density and growth) of four Indo-West Pacific seagrass species (Cymodocea serrulata, Halodule uninervis, Halophila ovalis and Zostera muelleri) to six daily light levels ranging from 0 to 23 mol m⁻² d⁻¹ (0–70% surface irradiance) in cool (\sim 23 °C) and warm temperatures $(\sim\!28\,^\circ\text{C})$ over 14 weeks. The impact of light limitation on shoot densities and growth rates was higher at warm than at cool temperatures, and for Z. muelleri and H. ovalis than for C. serrulata and H. uninervis, in terms of both the time taken for the low light treatment to take effect and the predicted time to shoot loss (e.g. 17-143 days at $0 \text{ mol m}^{-2} \text{ d}^{-1}$). Using fitted curves we estimated temperature-dependent thresholds (with estimates of uncertainty) for 50% and 80% protection of growth and shoot density, defined here as "potential light thresholds" in recognition that they were derived under experimental conditions. Potential light thresholds that maintained 50% and 80% of seagrass shoot density fell within the ranges 1.1-5.7 mol m⁻² d⁻¹ and 3.8-10.4 mol m⁻² d⁻¹, respectively, depending on temperature and species. Light thresholds calculated in separate in situ studies for two of the same species produced comparable results. We propose that the upper (rounded) values of $6 \,\mathrm{mol}\,\mathrm{m}^{-2}\,\mathrm{d}^{-1}$ and $10 \,\mathrm{mol}\,\mathrm{m}^{-2}\,\mathrm{d}^{-1}$ can be used as potential light thresholds for protecting 50% and 80% of shoot density for these four species over 14 weeks. As management guidelines should always be more conservative than thresholds for biological declines, we used error estimates to provide a quantitative method for converting potential light thresholds into guidelines that satisfy this criterion. The present study demonstrates a new approach to deriving potential light thresholds for acute impacts, describes how they can be applied in management guidelines and quantifies the timescales of seagrass decline in response to light limitation. This method can be used to further quantify cumulative impacts on potential light thresholds.

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1. Introduction

Water quality affects benthic light and has been linked to globally accelerating decline in seagrass (Waycott et al., 2009). Terrestrial input and dredging, which re-suspends fine sediments, are two processes that drive declines in benthic light (Brodie et al., 2012; Erftemeijer and Robin Lewis, 2006). Seagrasses can acclimate to changing light levels but under extreme reductions in

light availability, photosynthetic carbon fixation is directly reduced (McMahon et al., 2013; Ralph et al., 2007). Therefore, reductions in light can cause light limitation which de-stabilises seagrass carbon budgets (Collier et al., 2011) and limits the amount of carbon that is available for growth and biomass production (Ralph et al., 2007). Given the ecological importance of seagrass as food, structural habitat and for carbon sequestration (Coles et al., 1993; Costanza et al., 1997; Cullen-Unsworth and Unsworth, 2013; Fourqurean et al., 2012; Unsworth et al., 2012), changes to seagrass biomass and growth caused by light limitation are of critical concern to environmental managers.

Setting light guidelines for seagrass survival in reduced benthic light is an essential prerequisite in preventing local-scale seagrass

^{*} Corresponding author at: Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER), James Cook University, Cairns 4870, Australia. E-mail address: Catherine.collier@jcu.edu.au (C.J. Collier).

declines. Guidelines can be used to set mandatory standards for activities that affect environmental condition (e.g. dredging), or they can be used as benchmarks to trigger further lines of enquiry (e.g. monitoring) (Moss et al., 2005). Environmental guidelines are developed for ecosystem protection and are ideally based on scientifically derived thresholds, which are known levels that trigger a specified impact (Qian and Cuffney, 2011). Environmental managers therefore require data sets that define biological thresholds in order to set environmental guidelines (Moss et al., 2005).

Minimum light requirements (MLR) are thresholds that define the light required for seagrass survival over ecologically-relevant time frames (typically annual) and are calculated from light at maximum colonisation depth (Abal and Dennison, 1996; Adams et al., 2015; Choice et al., 2014; Dennison et al., 1993; Steward et al., 2005). However, MLR cannot be applied for the management of acute impacts, which drive loss much more rapidly than annual timeframes, and do not account for species-specific differences in response time to acute disturbances. Furthermore, MLR do not provide a high level of protection, as they are a threshold that defines complete loss or absence of seagrass.

In the Great Barrier Reef region, light thresholds have been developed and applied for localised management of risk to seagrass habitat from dredging. In Port Curtis, field experiments and long-term light monitoring were used to develop site-specific acute light thresholds for *Zostera muelleri* dominated meadows (Chartrand et al., 2012). These locally-derived light thresholds have been effective in a local management context because they were developed specifically for the species and environmental conditions present at the site.

There is a need, however, to further develop species-specific seagrass light thresholds that provide a margin of confidence (rarely defined and summarised in Erftemeijer and Robin Lewis III 2006 with some exceptions e.g. Choice et al., 2014), specify the degree of damage associated with light decline, indicate timescales and consider the cumulative impact of other environmental factors such as temperature. Measures of uncertainty also increase the confidence that there will be successful management outcomes because they provide a means to distinguish between light thresholds associated with changes in other environmental conditions or those required for different species or populations (Rolfe and Windle, 2010). Furthermore, uncertainty may provide a quantitative means to conservatively convert a biological response threshold into a more conservative management threshold. Elevated water temperature can drive faster rates of respiration and carbon loss, which counteracts the increased carbon fixation by simultaneously elevated photosynthetic rates at high temperatures; therefore, increasing temperature may exacerbate effects of light limitation on productivity, growth and biomass (Lee et al., 2007; Marsh et al., 1986).

We measured changes in shoot density and leaf growth rates across a range in daily light for 14 weeks and calculated time to seagrass loss at two temperatures. Then, using an approach similar to determination of toxicity of chemical pollutants (dose–response curves; Flores et al., 2013), we fitted curves between growth rate, seagrass loss and daily light. From this, we demonstrate a method for measuring thresholds for morphological response, with uncertainty, and use this method to identify potential light thresholds that can be applied across all four species.

2. Materials and methods

2.1. Plant collection

Changes in shoot density and growth rates in response to photosynthetic photon flux density (PPFD) were tested on four species of seagrass: *Cymodocea serrulata*, *Halodule uninervis*, *Halophila ovalis*, and Z. muelleri. The tropical species, H. uninervis and C. serrulata, occur throughout the Indo-West Pacific in coastal and reef habitats. *H. ovalis* is a broadly distributed species occurring in estuarine, coastal and reef habitats through the Indo-Pacific and in southern Australia. All three of these species were collected from Cockle Bay, Magnetic Island (19° 10.612 S, 146° 49.737 E; Fig. A1). Z. muelleri is a predominantly subtropical to temperate species with the northern limit of its distribution extending to the Torres Strait. Z. muelleri plants were collected from Pelican Banks, Gladstone Harbour (23° 46.005 S, 151° 18.052 E). H. uninervis, H. ovalis and Z. muelleri were collected via plugs (including roots, rhizome and sediment) and transferred to the experimental facility at James Cook University in Townsville. Due to the large internodes between shoots, C. serrulata were collected as sprigs with three to five shoots on each rhizome, and transported to the experimental facility in seawater before planting. Plugs and sprigs were planted into $10 \, \text{cm} \times 10 \, \text{cm}$ orchid pots (5 cm deep) lined with a swimming pool filter sock; which enabled direct exchange of water and gases to minimise sediment anoxia. All species were placed in aquaria within 5 and 30 h of collection from Cockle Bay and Gladstone Harbour, respectively. The plants were maintained in 1000 L closed circulation seawater aquaria, under 30% photosynthetic photon flux density (PPFD), and acclimated to the experimental conditions for more than 1 month prior to the initiation of experiments.

2.2. Experimental set-up

The experiments were conducted outdoors under natural diurnal solar radiation. Surface PPFD was recorded using an Odyssey 2π quantum sensor (Dataflow, Odyssey photosynthetic recording system), calibrated against a manufacturer-calibrated Li-Cor 2π sensor using a constant light source (Li-Cor) in laboratory conditions. The experiments consisted of six light treatments: 0, 5, 10, 20, 40 and 70% of surface PPFD, achieved by applying black neutral density shade cloth with various light reducing properties. Dual light loggers were deployed to ensure reliability and the mean daily PPFD calculated. The surface PPFD was 32.8 mol photons m^{-2} d^{-1} and treatments were 0, 1.6, 3.3, 6.6, 13.1 and 23.0 mol photons m^{-2} d^{-1} for the 0%, 5%, 10%, 20%, 40%, and 70% treatments, respectively.

There were two temperature treatments maintained by chillers feeding two sump tanks (1000 L): "warm" with a mean of 27.7 °C; and "cool" with a mean of 22.7 °C. Water temperature varied with outdoor air temperatures, approximating those occurring at the collection sites (Collier and Waycott, 2014). On average, temperature ranged between 24.1 and 30.8 °C for the warm and 19.3-25.5°C for the cool over the 14 weeks. Temperature was recorded every 30 min using iBTagTM 22 L autonomous loggers in six randomly selected tanks for the duration of the experiment. As the temperature loggers ceased recording after 7 weeks, we used a linear relationship between water and air temperature (collected at Townsville airport over the duration of the experiment by the Bureau of Meteorology) to calculate water temperature in the treatments over the remaining 7 weeks. For this reason we refer to temperature treatments as "cool" and "warm" in acknowledgement that water temperature is only estimated.

One pot of each seagrass species was placed in each of four replicate tanks (n = 4), for each light and temperature combination (six light levels × two temperature levels × four replicate tanks). Tanks were randomly distributed throughout the experimental set-up. Experimental tanks were constructed of clear plastic, with 25 L of water (depth of 20 cm) and three small water jets to create water movement around the seagrass leaves.

To ensure nutrient limitation did not compromise growth rates, a complete nutrient mix including macro- and micro-nutrients (f/2 algal culture mix – Varicon Aqua Solutions) was added every second day and water was sampled for nutrient concentrations six times

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