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Recreating the shading effects of ship wake induced turbidity to test acclimation responses in the seagrass *Thalassia hemprichii*

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Elevated sediment delivery and resuspension in coastal waters from human activities such as shipping can have detrimental effects on seagrass health by limiting light penetration. Managing seagrasses requires knowledge of their light acclamatory abilities so guidelines for coastal activities (e.g. ship movements) that influence sediment dynamics can be created. Guidelines typically focus on ensuring that seagrasses are able to meet their minimal light requirements (MLR). MLRs can be achieved by different light regimes, but it remains unknown whether a chronically low yet stable light regime is less or more detrimental than a highly variable regime with periods of extreme low to no light. To test this, we compared the physiological and morphological responses of *Thalassia hemprichii* among three light regimes: an open control (30-40% ambient light), a shaded control with (11-15% ambient light), and a fluctuating shade (4-30% ambient light). The MLR for the *T. hemprichii* we studied was lower (4-10% ambient light) than previous reports (mean = 18%) illustrating enhanced light acclimation in Singapore's chronically turbid waters. Seagrass shoots in the shaded control, however, exhibited significantly more morphological stress symptoms, with reduced shoot growth and lower below ground biomass. These data suggest that for seagrass exposed to periods of acute light stress, energetic costs associated with photo-acclimation to more variable light regimes can be offset if the plant can meet its daily light requirements during periods of high light. Management of seagrass beds should incorporate regular light monitoring and move towards an adaptive feedback-based approach to ensure the long-term viability of these vulnerable ecosystems.

1. Introduction

The environmental conditions in ports and harbours are often stressful for coastal marine organisms and systems. In particular, activities such as shipping, dredging and coastal modification result in increased rates of turbidity, leading to light attenuation and sedimentation, which both have serious consequences for sensitive marine ecosystems such seagrass habitats (Erftemeijer and Lewis III, 2006). Light is one of the primary limiting factors for seagrass growth (Ralph et al., 2007) and recent work has demonstrated the importance of the duration and intensity of light reduction (Lavery et al., 2009) as well as the interactive effects of light reduction with environmental factors such as water quality (Leoni et al., 2008; Michael Kemp et al., 2004). It is generally agreed that reduced light availability is a major threat to seagrass beds worldwide (Herzka and Dunton, 1997; Uy, 2001; Waycott et al., 2009).

As photosynthetic organisms, seagrasses harness light energy to meet their daily carbon budget (Kaldy et al., 2002). To maintain a positive carbon budget, gross photosynthetic yield (CO_2 taken up during photosynthesis) has to be equal or greater than the carbon expended during respiration and growth. Seagrasses have a relatively high respiratory demand due to the extensive non-photosynthetic tissues (e.g. roots and rhizomes) that the plant has to support, hence, they have developed several adaptations that range from physiological (e.g. increased photosynthetic efficiency) to morphological changes (e.g. leaf length and shoot density; Collier et al., 2012; Ralph et al., 2007; Yaakub et al., 2014). These adaptations, which include the capacity to rapidly acclimate to low light levels (Tuya et al., 2016), have improved the ability of seagrasses to meet daily carbon requirements. The results of these

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previous studies indicate that, as long as seagrasses receive the minimum light requirement (MLR) throughout the day, they can survive substantial periods of low to no light due to storage of carbon reserves.

Sediment resuspension events contribute to the highly variable light conditions in shallow intertidal environments. The duration of a sediment resuspension event is largely dependent on sediment characteristics (which affects rate of settlement) and hydrodynamics (which affects the transport and movement of the resuspended particles; Madsen et al., 2001) and can last from minutes to hours. Prolonged resuspension events affect primary productivity of seagrass by reducing light availability and may impact the capacity of seagrass to acclimate to, and recover from, further disturbances in light availability (Yaakub et al., 2014). The physical effects of sediments, however, appear to be less detrimental and many common seagrass species are comparatively tolerant of scouring and settling sediments (Cabaço et al., 2008).

Anthropogenically driven sediment resuspension can reduce light levels in shallow seagrass beds from 10-20% ambient photosynthetically active radiation (PAR) (Duarte, 1991; Kenworthy and Fonseca, 1996) to <5% (Browne et al., 2015; Larsen et al., 2017). These light conditions are considered to be below the MLR for most species (Duarte, 1991; Longstaff and Dennison, 1999), thereby impacting their daily carbon budget. However, it is possible that the daily carbon budget of the plant can be met during periods of low turbidity and higher light, such as those found in between pulsed turbidity events, for example. This could provide sufficient energy for seagrasses to meet their daily carbon requirement, but the physiological adjustment to these large fluctuations in light availability—and the required energetic expense of photo-acclimation at the expense of other processes (Major and Dunton, 2002)—may be too stressful for seagrasses and exceed their acclimation potential. Improved understanding of how seagrasses respond to large fluctuations in light availability will help determine whether short acute stress events are more detrimental than longer chronic stress events. This knowledge will aid in the management of activities such as dredging and dumping of sediments in marine waters, with the ultimate aim of preventing impacts to seagrass meadows.

This study focuses on the sporadic loss of light associated with ship-wake induced sediment resuspension. This is an ongoing problem in Singapore, one of the world's busiest ports, due to layers of sediment on and near sensitive ecosystems such as coral reefs and seagrass beds being frequently disturbed by the hydrodynamic forces associated with ship-wakes and/or dredging activities (van Maren et al., 2014). We conducted a four week aquarium experiment to test the hypothesis that consistently low levels of light are more detrimental to seagrass than large fluctuations in light. Seagrass condition was compared between seagrasses that received constant low light levels and those that were exposed to large and variable fluctuations in light. Similar mean light levels between the two treatments were maintained to ensure that any difference in condition was due to the pattern of light availability and not total light levels. The experiment required the fabrication of novel apparatus whereby light conditions were pre-programmed to follow light levels measured within sediment resuspension zones in Singapore. These variable light levels were delivered by electronically-controlled shading apparatus.

2. Methods

2.1. Site description

Approximately 250 ramets of *Thalassia hemprichii* were collected from the reef flat at Cyrene Reef (N 01°15′31, E 103°45′20), Singapore's largest patch reef system situated approximately 3 km south of the mainland (Yaakub et al., 2013). Cyrene Reef is surrounded by busy shipping channels with several hundred ships passing the reef daily (Chou, 2006, Fig. 1) but, despite these pressures, the reef (1.4 × 0.4 km) hosts 37 coral genera and supports an abundant seagrass meadow comprising *Enhalus acoroides, Cymodocea rotundata, Cymodocea serrulata, Halodule uninervis, Halophila ovalis, Thalassia hemprichii* and *Syringodium isoetifolium* (Yaakub et al., 2013). *Thalassia hemprichii* was chosen for the present study as it is a climax species that is relatively widespread in Singapore and often dominates seagrass beds in the Indian Ocean and the western Pacific Ocean (Prathep, 2003; Tanaka and Kayanne, 2007).

2.2. Experimental design

Seagrass ramets were transported within 2 h of collection to the aquarium facilities at the Tropical Marine Science Institute (TMSI) on St. Johns Island. Seagrass ramets were then placed immediately into open-topped transparent acrylic chambers (20 cm diameter × 30 cm high) that had been filled with a 7 cm thick layer of sediment collected from Cyrene Reef. A total of 21 of these chambers were placed in a flow through seawater bath (1.5 × 1.6 m) in an outdoor aquarium (Fig. 2). The outdoor aquarium was covered in shading cloth that allowed ~30-40% of natural ambient sunlight through to represent light attenuation within 1–3 m water depth. Seawater was fed into each individual acrylic chamber from a central reservoir tank. Each chamber was also supplied with an air feed which pumped air directly into the sediments to reduce the build-up of anoxic conditions.

The 21 chambers were distributed randomly among three treatments ($n = 7$): Open Control (OC), Shaded Control (SC) and Fluctuating Shade (FS). Seagrass shoots in the open control received ~30-40% natural ambient sunlight while the shaded control treatment received ~11-15%. In contrast, seagrass shoots in the fluctuating shade were exposed to 8 to 12 rapid declines in light followed by a gradual increase in light availability (Rapaglia et al., 2011). These conditions closely followed field observations where sites close to heavy boat traffic receive 8 to 15 sizable ship-wakes (>0.4 m) during daylight hours (pers. Obs.). The severity of a sediment resuspension event following the ship wake is variable, hence the length of each suspension event (10–30 min) as well as the frequency of events, were varied daily in the experiment. In the fluctuating shade, light reduction events were executed by automated apparatus that created three light levels via a system of shading nets on motor-controlled rollers. At the start of an event, all three layers of shading net covered the fluctuating shade chambers, reducing light to 4% of natural light levels. Over the course of the next 10-30 min, light levels increased back to 30% as the other two shading layers were removed, thus mimicking the natural slow inclines in light levels following the rapid reduction during a sediment resuspension event.

The amount of photosynthetically active radiation (PAR) received for the duration of the experiment was measured using Odyssey Photosynthetic Active Radiation Logger (Dataflow Systems Ltd, New Zealand). Odyssey loggers were calibrated with a high quality PAR sensor (LI-COR 192 S) over a 24 h period in a range of light conditions. On a typical day, light levels ranged from 400 to 700 μmol photons m^{-2} s^{-1} in the open control, from 100 to 300 μmol photons m^{-2} s^{-1} in the shaded control and from 50 to 450 μmol photons m^{-2} s^{-1} in the fluctuating shade (Fig. 3). These values are comparable to light levels measured at clear and turbid water seagrass sites in Singapore (Yaakub et al., 2014). Over the course of the 4 week experiment, mean light levels in the fluctuating shade were ~13% of natural ambient light, comparable to