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Posidonia sinuosa tolerates the cumulative effects of a short-term heatwave and low light event

Theme: Benthic Habitats and Communities
WAMSI Westport Marine Science Program

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ABOUT THE MARINE SCIENCE PROGRAM

The WAMSI Westport Marine Science Program (WWMSP) is a $13.5 million body of marine research funded by the WA Government. The aims of the WWMSP are to increase knowledge of Cockburn Sound in areas that will inform the environmental impact assessment of the proposed Westport development and help to manage this important and heavily used marine area into the future. Westport is the State Government's program to move container trade from Fremantle to Kwinana, and includes a new container port and associated freight, road and rail, and logistics. The WWMSP comprises more than 30 research projects in the biological, physical and social sciences that are focused on the Cockburn Sound area. They are being delivered by more than 100 scientists from the WAMSI partnership and other organisations.

DATA
Finalised datasets will be released as open data, and data and/or metadata will be discoverable through Data WA and the Shared Land Information Platform (SLIP).

FRONT COVER IMAGE
Theme: Benthic habitats and communities
Front cover image: Seagrass (Posidonia australis) in Cockburn Sound. Photo courtesy of: Rachel Austin (The University of Western Australia).

Contents

Posidonia sinuosa tolerates the cumulative effects of a short-term heatwave and low light event

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Theme 2, Project 2.2: Pressure-response relationships, building resilience and future proofing seagrass meadows

Executive Summary

Climate change disturbances are intensifying whilst the human global population continues to grow. Consequently, ecosystems and species are threatened by multiple stressors. Environmental impact assessment (EIA) predicts potential impacts to marine ecosystems through understanding response thresholds but these are generally derived from single stressor studies. For marine dredging proposals within seagrass habitat, this threshold is generally related to light requirements. As marine heatwaves are increasing in intensity and frequency in Western Australia, and therefore, the likelihood of seagrass being exposed to combined stress of a heatwave event whilst a dredging operation occurs could be increasing. Exposure to high temperatures can modify how seagrasses respond to light deprivation, which may require the current light thresholds to be changed. In this context, multi-stressor research is necessary for improving environmental impact assessment (EIA) in relation to dredging and for management and conservation of sensitive benthic species under a changing climate.

Under controlled experimental conditions, we simulated a dredging and heatwave scenario to investigate the interactive effects of low light and high temperature on the response of the dominant seagrass *Posidonia sinuosa* collected from Kwinana Shelf in WA. Shading experiments carried out on *P. sinuosa* have shown that exposure to 2 mol photons m^{-2} d^{-1} for more than 3.5 months led to shoot density declines of 69 % and meadows would need ~ 3 years to recover from losses of this magnitude (Collier et al., 2009). This light level and duration has therefore generally been used in accordance with the Zone of Moderate Impact (ZoMI) of light reduction from dredging on *P. sinuosa* and to establish the spatial extent of impacts (EPA, 2021). Therefore, we used the current light threshold of (2 mol photons m^{-2} d^{-1}) as the low light level and ambient light was 8 mol photons m^{-2} d^{-1}. We hypothesised that these two factors would interact synergistically such that the combined effects of reduced light and high temperature would be greater than the effects of either factor in isolation.

Key findings for informing the EIA of the Westport dredging proposal and other future marine infrastructural developments are:

- The individual factors, light or temperature, impacted the photophysiology of *P. sinuosa* and generally, these trends reflected that the effects of low light were negative, whilst the effects of high temperature were positive for the temperate seagrass *P. sinuosa* over a three-week exposure period.

- Over the three-week duration assessed, maximum electron transport rate, light saturating irradiance, and shoot density were significantly reduced by low light, but these losses were not of the magnitudes where recovery time would be expected to exceed 5 years.

- The effect of temperature was independent of the light treatment. Plants under heatwave temperatures were more productive and lost fewer shoots compared to those under ambient temperatures.

- Shoot density was significantly reduced under low light, and therefore suggests that a light level of 2 mol photons m^{-2} d^{-1} can impact *P. sinuosa* at the lethal level but the low magnitudes of loss (< 10 %) indicate that meadows can tolerate longer durations of exposure (> 2 weeks). These results suggest that there is no need to modify light threshold of 2 mol photons m^{-2} d^{-1} for the Zone of Moderate Impact under a heatwave of the intensity and duration tested (28°C, 21 days).

- Shoot declines of a much greater magnitude (>50 %) would be expected from longer durations of exposure (≥ 2 months) to this threshold (Collier et al., 2009). These results align with the outcome from a separate but complimentary field experiment that support keeping the current light threshold for the ZoMI for *P. sinuosa* of 2 mol photons m^{-2} d^{-1} for a maximum duration of 2 months (Said et al., 2024b).

- Light thresholds may need to change under more intense and/or more persistent heatwaves based on reduced performance of *P. sinuosa* plants cultured under low light and heatwaves conditions (lowest growth rates and carbohydrate stores). We highlight this as a key knowledge gap for future research.

- Above ground biomass was significantly higher for plants in ambient light and heatwave conditions indicating that meadows can handle thermal stress with access to more light. Additionally, plants under higher temperatures stored more starch; such diversion of energy sources away from growth suggests these conditions were somewhat stressful. These are important findings considering heatwaves are expected to become more intense. We recommend future experiments be designed and carried out with combinations of light and temperature levels that reflect a variety of dredging campaign and heatwave scenarios.

- *P. sinuosa* plants cultured under low light and heatwaves conditions had the lowest growth rates and carbohydrate stores. These indicators were not significantly affected by the interaction between light and temperature in this study but mass mortality of seagrass has been attributed to low light and high temperature conditions (e.g. Shark Bay) implying that this combination of conditions can be detrimental for meadow resilience.

Overall, these results imply that *P. sinuosa* can tolerate light reduction induced by dredging during a short-term (≤21 days) heatwave. On this basis, we propose that the current light thresholds for *P. sinuosa* do not need to be modified for short-term heatwave events, but if low light events with or without heatwaves continue beyond 21 days, a more conservative approach should be considered. Given high sediment sulphide levels have been documented at sites within Cockburn Sound (Fraser et al., 2015), and warming is known to exacerbate the effects of sulphide intrusion, avoiding or minimising light reduction for specific meadows may be warranted, especially considering the positive effects of warming when plants have adequate light. We recommend future threshold research consider incorporating additional temperature and light levels and longer durations into experimental designs.

1 Introduction

Marine ecosystems are increasingly impacted by multiple stressors (Glibert et al., 2022), particularly from coastal developments (Neumann et al., 2015; Syvitski et al., 2009), rising sea surface temperatures and extreme events (Xu et al., 2022). Coastal developments that require dredging can have substantial impacts on sensitive benthic communities via direct removal, burial, or elevated turbidity (Cunning et al., 2019; Hendrick et al., 2016). Dredging-related impacts can be minimised if operations are managed based on known biological or pressure thresholds for the organisms likely to be impacted (Wenger et al., 2018). To date, most pressure threshold information available is from investigations into single stressors, which may not be adequate when stressors co-occur and produce synergistic, additive or antagonistic effects (Ontoria et al., 2019). Between 1925 to 2016, the occurrence and intensity of marine heatwaves (MHWs) has risen by 34% and 17% respectively (Oliver et al., 2018). Critical life processes, like growth, survival and reproduction, are affected by temperature and these responses vary over the thermal tolerance range (Bennett et al., 2018), and exposure to ocean temperatures that exceed thermal tolerances can result in mass mortality (Eakin et al., 2010). However, thermal tolerances can shift when another stressor is introduced; an organism may become more tolerant of temperature when conditions in another stressor change (Ontoria et al., 2020). Thresholds provide critical information for environmental impact assessment (EIA) of dredging proposals, however, these may need to be adjusted to account for when operations coincide with climate change induced temperature disturbances (Guerrero et al., 2013). This knowledge is imperative for developing management and actions to prevent undesirable shifts in ecosystem state, and loss of ecosystem goods and services in the context of multiple stressors (Samhouri et al., 2011).

The array of goods, cultural value and services provided by the marine environment, largely due to the roles and functions performed by habitat-forming species (Gaylard et al., 2020), are often degraded by human activities (Halpern et al., 2019). This study focuses on seagrasses as habitat-forming species that influence biogeochemical cycles (Marba et al., 2006), stabilise sediments (Terrados and Duarte, 2000) and provide food, shelter and habitat for various fauna (Renkawitz et al., 2011) in marine ecosystems across all continents except Antarctica (Dewsbury et al., 2016). Like other plants, the ability of seagrasses to grow and survive is inextricably linked with the ability to maintain a positive carbon balance, i.e. rates of photosynthesis are greater than rates of respiration (Touchette and Burkholder, 2000). Temperature and light are two key factors that influence photosynthesis and respiration (Lee et al., 2007). Consequently, reductions in light and increasing temperatures are often reported as primary drivers of seagrass decline (Lefcheck et al., 2017; Quiros et al., 2017), although how these factors interact is poorly understood. Going forward, mitigating seagrass decline will require an increased understanding of the cumulative effects of these stressors. To date, such assessments are limited to a few species e.g. *Halodule uninervis*, *Zostera muelleri*, *Amphibolis antarctica* and *Zostera marina* (Collier et al., 2011; Fraser et al., 2014; York et al., 2013). Understanding the cumulative impacts of multiple stressors will inform management decisions for coastal developments that aim to minimise impacts to the receiving environment. For example, dredging campaigns near seagrass can be managed by conducting operations at specific times or environmental windows that lessen the impacts of the disturbance(s) (Fraser et al., 2017; Wu et al., 2017).

In coastal habitats, light and temperature regularly change, therefore, seagrasses have various strategies to meet their respiratory and growth requirements, although their ability to do so is bounded by light and thermal thresholds (Lee et al., 2007). Under reduced light, photosynthesis declines, and seagrasses minimise their respiratory load to avoid a negative carbon balance; generally, this involves making physiological adjustments first. For example, plants can maintain their productivity as conditions change by adjusting their photosynthetic efficiency (α), which invariably impacts the amount of light required to maximise photosynthesis, referred to as saturating irradiance (E_k). Changes in the values of these photophysiological indicators can be easily interpreted in relation to light and temperature disturbances; for example, *Posidonia oceanica* had higher E_k values in summer because of increased respiration under higher temperatures (Alcoverro et al., 1998). If light is reduced

below Ek, plants are light limited, and under prolonged stress, plants will then make morphological adjustments which is usually related to trying to reduce their respiratory demands (e.g. decreased leaf length) (Abal et al., 1994) or loss of shoots (Collier et al., 2007). Under persistent or extreme stress, responses will become more severe including eventual mortality (Collier et al., 2011). Plant-scale responses, including changes in shoot morphology and density, affect meadow-structure and productivity, which are important features critical to the habitat and food value of seagrass meadows (Jones et al., 2021; Sheppard et al., 2010). Overall, if light levels are adequate, plants can 'override' any increases in respiration associated with higher temperatures. This is less likely under low light conditions which limit photosynthetic capacity. Accordingly, thermal tolerances tend to be lower in low light and higher in high light (Bulthuis, 1987). The relationship between light and temperature on seagrass response implies that there may be some situations where the current light threshold needs to be modified, such as if low light conditions induced by dredging co-occur with marine heat waves (MHWs). Currently, thresholds for the environmental impact assessment of dredging are generally based on turbidity (as a function of light) and ambient temperatures.

Cockburn Sound in Western Australia is an ideal location for exploring the cumulative effects of coastal development and climate change on seagrasses. Cockburn Sound is a multiple-use marine embayment renowned for its substantial socio-economic and ecological value of which seagrass communities are a significant contributor (Lemmens et al., 1996; Wakefield et al., 2013). Like other regions around the world, Cockburn Sound is heavily industrialised which historically resulted in substantial seagrass decline (Cambridge and McComb, 1984) and climate change is also emerging as a key stressor (Andrys et al., 2017). Cockburn Sound is projected to undergo further development including dredging to support an increase in waterborne trade (https://westport.wa.gov.au/). Simultaneously, more frequent and intense MHWs are also projected for WA (Kajtar et al., 2021). Thus, there is an increased likelihood of seagrasses being exposed to combined low light and high temperature stress. Historical seagrass loss has motivated research focused mostly on impacts associated with reduced light (e.g. intensity and duration) so the response mechanisms and the most appropriate indicators for one of the dominant species *P. sinuosa* are established (Collier et al., 2009, 2007; Gordon et al., 1994). The optimal temperature for *P. sinuosa* in Shoalwater, Perth is 26.4 (Said et al. 2024a). This temperature is below the water temperatures recorded following actual MHWs e.g. 27.6 °C in Cockburn Sound following the MHW in 2010/11 (Pearce and Gaughan, 2011). Moreover, the amount of light that seagrasses need is known to vary under different temperatures (Bulthuis, 1987) and has been demonstrated for *P. sinuosa* (Masini and Manning, 1995). Therefore, we consider that these current thresholds need to be reassessed to enable application for EIA to contemporary conditions, particularly in relation to cumulative stressors from MHWs and reduced light from dredging.

This study aims to investigate the individual and cumulative effects of dredging and climate change on the resilience of *P. sinuosa* meadows within Cockburn Sound. To achieve this, we experimentally compared the response across photophysiological, physiological, plant- and meadow-scales under ambient light and temperature, low light (dredging) and high temperature (heatwave). We hypothesised that the cumulative effects of low light and high temperature would be worse than the effects of each factor in isolation. This information will help progress EIA for multiple stressors on seagrass.

2   Materials and Methods

2.1   Plant material

Ramets of *P. sinuosa* were collected from the edge of meadows in February 2023 from Kwinana shelf in Cockburn Sound, a semi-enclosed embayment in southwestern Australia (-32.190419, 115.74389). Each plant collected included the growing shoot and ≥ 3 shoots. During collection, the water temperature was 21 °C and salinity was 36 ppt. Plants were placed in aerated cooler boxes with seawater from the site and were transported back to the mesocosm facility. Plants were placed in holding tanks with seawater at ambient site conditions.

2.2   Experimental design

The response of *P. sinuosa* to the cumulative effects of temperature and light stress was assessed under controlled experimental conditions in an outdoor mesocosm facility. Two levels were chosen to assess the effect of temperature: ambient temperature (AT) and heatwave temperature (HT). AT was 23 °C to simulate the summer average water temperature in Cockburn Sound and HT was 28 °C which is slightly above water temperatures reached in Cockburn Sound (range: 26.6 to 27.6 °C) following the 2010/2011 MHW (Pearce and Gaughan, 2011) but also qualifying as a MHW by exceeding the 90th percentile of the 30-year historical baseline period and the period of five days specified in the heatwave definition of Hobday et. al (2016). This is also higher than the photosynthetic thermal optima assessed by Said et al (2024a). Across all the tanks, temperature was increased by 1 °C per day to reach 23 °C to simulate the summer average water temperature (Mohring and Rule, 2013). The AT treatment tanks were held at 23 °C. Temperature ramping of 1 °C per day to reach 28 °C was continued for the HT tanks and this temperature was maintained for two weeks simulating the duration of high water temperatures recorded *insitu* in Cockburn Sound (Pearce and Gaughan, 2011). The two experimental light treatments were ambient light (AL) and low light (LL). AL was 8 mol m^{-2} day^{-1} (ambient) which simulated the range of light conditions recorded in the field at Cockburn Sound (Collier et al., 2009). LL was 2 mols m^{-2} day^{-1} simulating the light levels that occurred closest to the dredger (0.2 km) based on a case study in Barrow Island where light was measured during the dredging operation (McMahon et al., 2017) and based on previous research by Collier et al. (2009) which has been used for setting EIA light thresholds criteria for *P. sinuosa* and therefore allows for comparative assessments. Note that McMahon et al. (2017) took benthic light measures between June and August (austral winter) whereas in summer, when light levels are generally higher, it may be that the area exposed to these levels of light reduction is even closer to the dredge (i.e. a smaller area of high impact).

To test the interactive effects of light (AL, LL) and temperature (AT, HT), four replicate tanks for each experimental treatment combination were established in a fully factorial design (n=20 tanks). Within each tank, there were two pots containing four ramets. Each tank set up was independent and comprised a main tank (volume: 850 L) and sump tank (volume: 100 L). Heater-chiller units (TK-1000) were used to maintain the water temperature ± 1 °C of the target temperature. Seawater was circulated through both tanks and the heater-chiller units by aquarium pumps (2 per tank, 1 per sump). Pilot trials indicated the need to acclimate plants to the light conditions in the facility. Therefore, the amount of light the plants were receiving was increased slowly starting with 24 hours under shade reduction cloths of decreasing intensities: 90%, 70%, 50% and 30% under which the ambient light treatment conditions were achieved. Salinity was maintained at 36 (± 0.2) ppt over the entire experimental period. At the start of the treatment, a 70% reduction shade cloth was used to cover the LL tanks. For the HT tanks, the temperature started at 23 °C and then increased by 1 °C per day over 5 days to reach 28 °C which was then maintained for two weeks. To verify plant health after the acclimation period, maximum quantum yield was measured on 8 random plants per tank (at least one within each pot). Plants were considered to have acclimated as yield values were in the same range as plants checked in the field (0.68-0.75) and in line with reported ranges in the literature (Ralph and Burchett, 1995).

2.3 Experimental measures

After confirming the plants had acclimated to the aquarium conditions (day 0), temperature in the heatwave treatment tanks was ramped up from 23 °C on the following day (day 1) by 1 °C per day over seven days to reach 28 °C (Table 1). Then on Day 7, the heatwave temperature of 28 °C had been present for 48 hours, and on Day 14 the heatwave had persisted for one week, and by day 21 for two weeks. Shading was imposed on the Low Light (LL) tanks on Day 1. To assess the effects of light and temperature on seagrass, multiple response indicators were measured over time but at different frequencies depending on the variable (Table 1). For instance, photophysiology measures were taken during temperature ramping and the heatwave phase of the experiment as these variables were expected to respond quickest (hours to days) to the imposed experimental conditions (Table 1). Responses at the physiology-plant- and meadow-scale, which usually take longer (weeks to months), were measured after two weeks of heatwave conditions at the end of the experiment (Table 1).

Table 1 List of response indicators and frequency of measurement used to understand the effects of low light (2 mols m^{-2} d^{-1}) and high temperature (28°C) on the seagrass *Posidonia sinuosa.*

Days	1	2	3	4	5	6	7	14	21
Low light				2 mols m^{-2} d^{-1}					
Temperature ramping & heatwave (°C)	23	24	25	26	27	28	28	28	28
Photophysiology									
Maximum quantum yield (F_v/F_m)		✓	✓	✓	✓	✓	✓	✓	✓
Electron transport (ETR) under experimental conditions	✓	✓		✓		✓	✓	✓	✓
RLC: ETR_{MAX}	✓	✓		✓		✓	✓	✓	✓
RLC: saturating irradiance (E_k)	✓	✓		✓		✓	✓	✓	✓
RLC: photosynthetic efficiency (α)	✓	✓		✓		✓	✓	✓	✓
Physiology									
Sugars, rhizome starch, total carbohydrates (% DW)									✓
Plant-scale									
Shoot extension rate (mm day^{-1})									✓
Meadow-scale									
Relative change in leaf density (%)									✓
Relative change in shoot density (%)									✓
Biomass (above, below, total)									✓

Photophysiological indicators were measured using a diving Pulse Amplitude Modulated fluorometer (PAM, WALZ). To derive maximum quantum yield (F_v/F_m), measurements were taken before dawn on dark-acclimated leaves enabling all reaction centres to be open and oxidisation of all primary electron acceptors (Beer et al., 2001). Measures of F_v/F_m were taken by placing the leaf between the fibre optic cable and index finger approximately 3 cm above the sheath. After approximately 4 hours of illumination, rapid light curves (RLC) were performed using the step-wise program with nine pre-

determined light levels that were selected to encompass saturating and non-saturating irradiance of increasing intensity (0, 12, 36, 78, 120, 177, 320, 440, 780 µmol photons $m^{-2}s^{-1}$ for 10 s at each light step). A leaf was selected from a mature shoot and the leaf clip was placed approximately 3 cm above the sheath and then the rapid light curve (RLC) commenced immediately. Electron transport rate derived from the RLC were fitted to the equation described by Jassby and Platt (1976) and plotted against irradiance using Sigmaplot (Version 11) to estimate photosynthetic efficiency (α) and maximum absolute electron transport rate which is defined as the maximum productivity under saturating light (ETR_{max}). Electron transport rate (ETR) which represents a measure of productivity relative to the absorbed irradiance was calculated as per the following formula: Y x Ei x AF x 0.5, where Y is the initial yield at the start of the light curve after approximately 4 hours of illumination, Ei is the light intensity generated by each point in the RLC (µmol photons m^{-2} s^{-1}), AF is the absorption factor, 0.5 is the fraction of photons absorbed by PSII in plant and data was expressed as µmol electrons m^{-2} s^{-1} (Beer et al., 2014). For the AF, light was measured near a leaf (measure 1) and again after placing the same leaf over the light sensor (measure 2) and calculated as a proportion: (measure 1 - measure 2)/ measure 1. AF ranged from 0.62 to 0.98 over the course of the experiment. For consistency, RLCs were measured within the same two-hour window (10:00 – 12:00) on every sampling occasion and due to these time constraints, only three replicates for each treatment combination were measured on each sampling occasion (n=3). In addition to the RLC's, the effective quantum yield was measured and with the AF calculation described above and the light recorded by a spectral logger at the leaf canopy the ETR under experimental light conditions was also measured between the same two-hour window described above.

Shoot growth was estimated using the hole punch method (Short and Duarte, 2001). At the end of acclimation (day 0), sheaths from two ramets in each pot were hole punched and the number of leaves and number of shoots were counted to derive a total number per bath (total at start). At the end of the experiment, leaves and shoots were recounted and then the relative change for both variables calculated (the difference in the totals at end of the experiment expressed as a percentage relative to the total at the start). The length of new tissue (leaf and sheath) produced was measured (mm) and then expressed as a vertical extension rate per day (mm day^{-1}). Plants from each pot were sorted into separate categories: living leaf, dead leaf, living sheath, dead sheath, rhizome, root and if applicable, new tissue (leaf and sheath) produced. This material was dried in a 60 °C oven for 48 hours and weighed (g) to obtain a dry weight estimate of biomass. Samples of a portion of the dried rhizome material (~5 g) were sent to the University of Queensland and analysed for rhizome sugar and starch concentrations (%) based on enzyme colorimetric methods (Karkalas, 1985; McCleary and Codd, 1991). Total carbohydrates were calculated as the sum of soluble sugar and starch and expressed as a %.

2.4   Statistical analyses

To identify whether photophysiology differed between treatments due to Light (Levels: Ambient, Low), Temperature (Levels: ambient, high), over time (Days), or the interaction (light x temperature x day), data were subjected to a three-way Permutational Analysis of Variance (PERMANOVA) as there were multiple time points assessed. To identify whether physiology, plant-scale and meadow-scale responses differed between treatments due to Light, Temperature or the interaction (light x temperature), data were subjected to a two-way PERMANOVA as data was only collected at one time point. Analyses were conducted using PERMANOVA+ in Primer v7 (Anderson et al., 2008).

3 Results

3.1 Photophysiology responses

Photophysiology of *P. sinuosa* was affected by the experimental factors, either light only or temperature only, or interactions of these factors with time (Table 2). Average maximum quantum yield (F_v/F_m) ranged between 0.69 (±0.02) to 0.76 (±0.002) with a significant interaction between Light and Day (L x D, $p<0.05$, Table 2). On day 5 and 21, F_v/F_m values were significantly higher under low light (Figure 1A). The ETR under experimental light conditions was affected by a significant interaction between Light and Day (L x D, $p<0.05$, Table 2), except for Day 1, ETR was significantly reduced under LL compared to under AL (Figure 1B).

Photosynthetic parameters derived from the RLC were significantly affected by the experimental factors, either light only, temperature only, day only or interactions of light or temperature with day (Table 2). Maximum productivity (expressed as ETR_{max}) was significantly higher under the heatwave (HT) (38.8±2.1) compared to under ambient temperature (AT) (32.1±1.5) (T, $p<0.05$, Table 2, Figure 1C). Saturating irradiance (E_k) differed significantly due to Light, Temperature and Day as individual factors ($p<0.05$, Table 2). In relation to light, E_k was significantly higher under AL (135.4±5.1) compared to LL (117.3±6.3) (Figure 1D). Whereas for temperature, E_k was significantly lower under AT (116.8±4.3) compared to HT (136.5±6.9) (Figure 1E). At Day 2 and 4 E_k was higher at the start of the experiment but returned to initial conditions by Day 7 (D, $p<0.05$, Table 2, Figure 1F). Temperature and Day interacted to affect photosynthetic efficiency (α) (T x D, $p<0.05$, Table 2). After one week under heatwave conditions (day 14), α was significantly higher in HT (0.325±0.01) compared to under AT (0.256±0.02) whereas after two weeks of heatwave conditions (day 21), the reverse was observed; α was significantly higher in AT (0.313±0.02) compared to in HT (0.265±0.02) (Figure 1G).
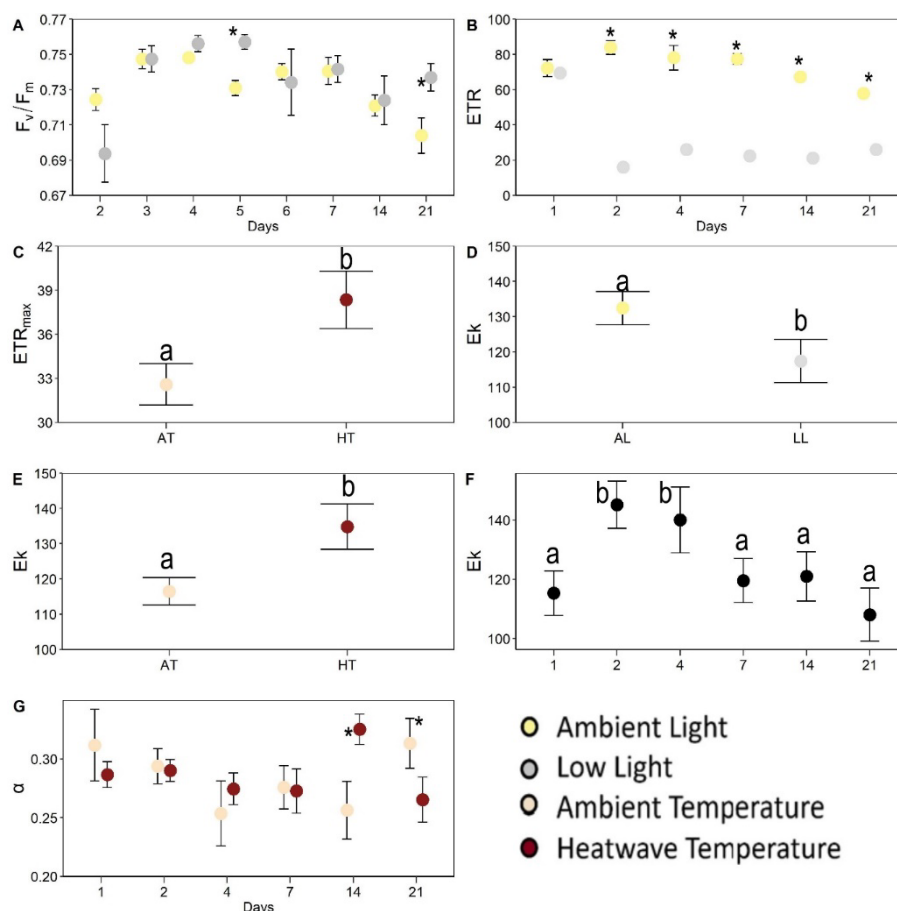

Figure 1 Effects of light, temperature and day tested on the photophysiology of *Posidonia sinuosa*.

Letters on graphs represent the significant pairwise comparisons determined by three-way PERMANOVA analyses for the factors of light (AL- Ambient Light; LL- Low Light) and temperature (AT- ambient temperature; HT- heatwave temperature) and day on variables including: maximum quantum yield (F_v/F_m) (A), electron transport rate (B), maximum electron transport rate (C), saturating irradiance (D, E, F) and photochemical efficiency (G).

3.2 Physiology and plant-scale responses

Rhizome starch was higher in the HT treatment (1.44±0.25) compared to AT (0.96±0.07, Figure 2A) but the effect of temperature was only marginally significant (p=0.0513, Table 2). For the rhizome sugars, which had the greatest pool of carbohydrates (20-30% DW) and total carbohydrates on average, lower values tended to occur in the 'LL x HT' treatment but this was not statistically significant (Figure 2B, C, D). Similarly, shoot extension rates were lowest in the 'LL x HT' treatment and highest in the 'AL x HT' treatment; however, this was not statistically significant (Table 2).

3.3 Meadow-scale responses

Shoots and aboveground biomass were the only meadow-scale indicators affected by the experimental factors (Table 2). Light had a negative and significant impact on shoots, LL resulted in a greater loss of shoots (-7±3) compared to under AL (-2±1, Figure 2F). In contrast, temperature had a significant positive effect on shoots, with fewer shoots lost under HT (-4±2) compared to AT (-7±3, Figure 2G). Light and temperature interacted to affect aboveground biomass (p<0.05, Table 2) whereby values were significantly higher in pots where plants were exposed to 'AL x HT' (13.3±1.7) compared to 'AL x AT' (7.8±0.9) pots (Figure 2H). Changes in leaves, belowground biomass and total biomass were not significantly affected by light and temperature over the two-week timeframe (Table 2).
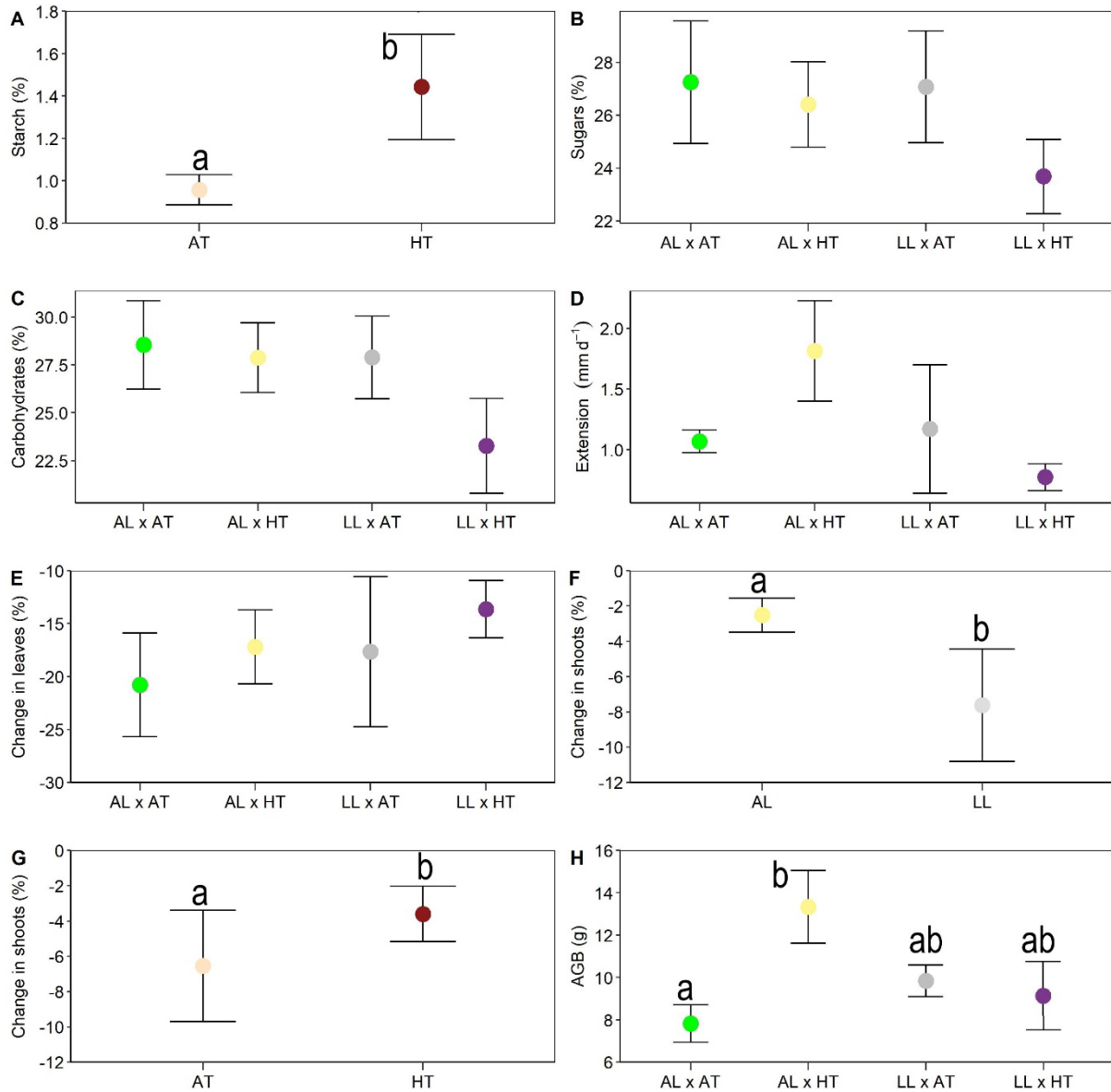
Figure 2 Effects of light and temperature on physiology and meadow-scale responses of *Posidonia sinuosa*. Letters denote the significant pairwise comparisons for factor(s) or interactions determined by two-way PERMANOVA analyses for the factors of light (AL- Ambient Light; LL- Low Light) and temperature (AT- ambient temperature; HT- heatwave temperature) on variables including rhizome starch (A), rhizome sugars (B), carbohydrates (C), extension (D), change in leaves (E), change in shoots (F, G) and aboveground biomass (H).

Table 2 Summary of PERMANOVA mains test outcomes examining the effects of factors (light, temperature or day) on response variables of adult *Posidonia sinuosa*. Significant comparisons are indicated in bold text (p < 0.05, unless otherwise stated).

Source	Maximum quantum yield (F_v/F_m)			Electron transport rate (ETR)		
	df	SS	p-value	df	SS	p-value
Light (L)	1	0.0006	n.s.	1	32868	**0.0001**
Temperature (T)	1	0.002	n.s.	1	0.610	n.s.
Day (D)	7	0.026	**0.0001**	5	6296	**0.0001**
L x T	1	0.002	n.s.	1	33.16	n.s.
L x D	7	0.011	**0.0263**	5	7804	**0.0001**
T x D	7	0.003	n.s.	5	224	n.s.
L x T x D	7	0.005	n.s.	5	219	n.s.
Residual	96	0.063		48	2990	
Total	127	0.112		71	50435	

Source	Maximum electron transport rate (ETR_{max})			Saturating irradiance (E_k)		
	df	SS	p-value	df	SS	p-value
Light (L)	1	54.1	n.s.	1	4335	**0.016**
Temperature (T)	1	540.35	**0.0151**	1	4794.5	**0.0121**
Day (D)	5	978.07	n.s.	5	12634	**0.0088**
L x T	1	0.17	n.s.	1	73.38	n.s.
L x D	5	330.84	n.s.	5	3494.3	n.s.
T x D	5	324.22	n.s.	5	4053.6	n.s.
L x T x D	5	266.57	n.s.	5	996.13	n.s.
Residual	48	3948.4		48	34154	
Total	71	6441.5		71	64535	

Source	Photosynthetic efficiency (α)		
	df	SS	p-value
Light (L)	1	0.007	n.s.
Temperature (T)	1	0.0008	n.s.
Day (D)	4	0.007	n.s.
L x T	1	0.001	n.s.
L x D	4	0.011	n.s.
T x D	4	0.022	**0.0368**
L x T x D	4	0.009	n.s.
Residual	39	0.076	
Total	58	0.134	

Source	Sugars			Starch		
	df	SS	p-value	df	SS	p-value
Light (L)	1	16.73	n.s.	1	0.013	n.s.
Temperature (T)	1	35.80	n.s.	1	0.061	**0.0513**
L x T	1	12.98	n.s.	1	0.010	n.s.
Residual	28	820.97		28	0.414	
Total	31	886.48		31	0.497	

Source	Total carbohydrates			Shoot extension rate		
	df	SS	p-value	df	SS	p-value
Light (L)	1	55.14	n.s.	1	390.89	n.s.
Temperature (T)	1	55.78	n.s.	1	54.08	n.s.
L x T	1	31.33	n.s.	1	577	n.s.
Residual	28	954.23		12	2500.70	
Total	31	1096.50		15	3522.70	

	Change in leaves			Change in shoots		
Source	df	SS	p-value	df	SS	p-value
Light (L)	1	37.95	n.s.	1	225.85	**0.0012**
Temperature (T)	1	66.46	n.s.	1	114.21	**0.0107**
L x T	1	0.99	n.s.	1	14.23	n.s.
Residual	12	1048.30		12	156.70	
Total	15	1153.70		15	149.19	
	Aboveground biomass			Total biomass		
Source	df	SS	p-value	df	SS	p-value
Light (L)	1	4.69	n.s.	1	0.42	n.s.
Temperature (T)	1	23.13	n.s.	1	47.63	n.s.
L x T	1	38.70	**0.0351**	1	31.08	n.s.
Residual	12	82.66		12	430.64	
Total	15	149.19		15	509.77	

Discussion

Understanding the interactions between local and global stressors is important for generating effective conservation outcomes for ecosystems (Dawson, 2011). In this study, we investigated the effects of light reduction to simulate a dredging scenario, and high temperatures to mimic a marine heatwave on the response of the seagrass *P. sinuosa*. Most response variables, except for above ground biomass, were affected by light or temperature independently, reflecting the findings of a similar study on *Z. muelleri* (York et al., 2013). Responses to low light were as expected and indicated that plants were trying to optimise photosynthesis by lowering their light requirements (E_k) and reduce respiratory load through losing shoots (Collier et al., 2016). These findings confirmed that light reduction induced by dredging (2 mols m^{-2} d^{-1}) can negatively impact *P. sinuosa* even over a short duration (2 weeks). However, shoot reductions were of a relatively small magnitude (< 10 %) and we predict meadows would likely be able to recover if operations were stopped after two weeks. In relation to temperature, there was some benefit of exposure to heatwave conditions. For instance, plants became more productive with higher E_k leading to a higher potential maximum electron transport rate. These responses are known to assist plants in maintaining a positive carbon balance and likely accounts for why these plants also lost fewer shoots (Lee et al., 2007). Under the heatwave conditions, above-ground biomass values were significantly higher for plants subjected to ambient light (i.e. no dredging) but this positive response was not realised when the plants were growing under low light conditions. Plants in the low light-heatwave treatment, although the interactive effects were non-significant, had slightly lower carbohydrates and growth. Taken together, our results demonstrate *P. sinuosa* can tolerate the cumulative effects of a short-term heatwave and low light. However, exposure to warming under low light disturbances has the potential to compromise the long-term resilience of meadows and make them vulnerable to further disturbance.

3.4   Light reduction negatively impacts P. sinuosa even over a short duration

The physiological adjustments under reduced light levels known to impact *P. sinuosa* (Collier et al., 2009) such as a lower saturating irradiance (E_k) are indicative of photoacclimatory responses to increase photosynthetic efficiencies (Ralph, 1999; Yaakub et al., 2014). Despite these adjustments, productivity was reduced under low light conditions, as indicated by an 80 % reduction in ETR and after three weeks, plants lost more shoots under low light, compared to plants under ambient light conditions, irrespective of temperature. Shoot loss is a common plant response to reduce respiratory load, and generally reflects that photosynthesis is no longer sufficient to maintain a positive carbon balance (Lee and Dunton, 1997). The number of shoots lost in our study were far below levels expected

to cause delayed meadow recovery; Collier et al. (2009) recorded shoot reductions of between 69 to 82 % under light levels similar to those imposed in this experiment (2 mols m^{-2} d^{-1}) over a three-month period and estimated recovery would take 3.5 to 5 years. However, in this study shoot losses were lower (8 ± 3%) which may be due to the shorter duration low light (three weeks total with two of these weeks at heatwave conditions), but the response occurred by three weeks of low light conditions, indicating that meadow scale responses can occur quite rapidly. Shoot declines are indicative of declining meadow condition which can affect ecosystem services e.g. reduced habitat complexity that can influence faunal abundance (Bostrom and Bonsdorff, 2000; Horinouchi and Sano, 2001). The differences in the magnitude of shoot reduction between our study and that of Collier et al. (2009) is likely explained by differences in the experimental duration; 21 versus 105 days respectively. Overall, *P. sinuosa* is likely to tolerate light reduction from dredging over a two-week period and although some shoot losses occurred, the magnitude of the loss was not so large as to be expected to result in damage that is either irreversible or would take > 5 years to recover. However, longer exposure to low light has been shown to degrade resilience, emphasising that the duration of low light exposure is an important factor to consider when managing dredging campaigns and especially considering *P. sinuosa* is a slow-growing species with limited or very slow recovery (Marbá and Walker, 1999).

Whilst the reductions in shoot density were not substantial, shoot loss can make meadows more susceptible to other stressors. For example, sulphide is toxic to seagrasses unless they can produce enough oxygen to oxidise sulphide into non-toxic compounds like sulphur (Pedersen et al., 2004). Meadows with fewer shoots have less overall leaf surface area available for photosynthesis and lower resilience to sulphide intrusion. Additive effects on seagrass have been reported in relation to low light and sulphide stress (Goodman et al., 1995). Plants under the low light conditions simulated in our experiment were photosynthesising at a lower rate (ETR), and therefore, these plants are producing less oxygen and may be more susceptible to sulphide intrusion. This is a relevant consideration in Cockburn Sound given the high levels of sediment sulphide recorded in some meadows (Fraser et al., 2023). The occurrence of sulphide intrusion in seagrasses is likely to be further compounded by the increased intensity and frequency of marine heatwaves. Plants respire more under higher temperatures, and therefore, may produce inadequate amounts of oxygen such that the interaction between warming and sulphide stress becomes synergistic (García et al., 2012; Koch et al., 2007). Therefore, minimising light reduction impacts from dredging may be warranted for meadows which, due to pre-existing stressors, may be declining or less tolerant of additional stressors. For instance, although future dredging is not proposed for Warnbro Sound area, these meadows are already in decline and one of the reasons is intrusion of sulphides into seagrass tissue (Fraser et al., 2017).

3.5 *Elevated temperatures over two weeks had a positive effect on productivity but negative implications for long-term resilience*

Exposure to heatwave temperatures for a two-week period, positively affected plant productivity as shown by an increase in the maximum photosynthetic rate (ETR$_{max}$). Higher E$_k$ under heatwave conditions suggests that plants needed more light to saturate photosynthesis and that plants had the potential to be more productive (Berry and Bjorkman, 1980). Plants also lost fewer shoots under the heatwave indicating plants were able to meet their respiratory load and the likely explanatory mechanism could be the increase in the ETR, indicating plants were more productive under these conditions (Zhang et al., 2017). In contrast, plants under the dredging scenario (LL) could not take 'advantage' of the benefits of higher temperatures, because the light they were receiving was insufficient to increase photosynthesis and counteract the warming-induced increase in respiration (Masini and Manning, 1997). The midday light received by the plants under experimental low light conditions (95 μmol m^{-2} s^{-1}) was well below the estimated E$_k$ irrespective of light or temperature treatment. Moreover, rhizome sugars trended downwards, in the low light heatwave treatments, although not statistically significant, indicating that these plants were not able to meet their energy demands via photosynthesis alone. This point was further supported by the trends in growth rates; which also not statistically significant, growth was lower in plants exposed to low light and heatwave

conditions. Trends in both these parameters support the known response pathway of seagrasses under stress. Reduced growth rates can make meadows less resistant to stress (Brun et al., 2003) and decelerate their recovery (Olsen et al., 2012), with implications for long-term resilience. Plants under ambient light conditions received higher levels of light (midday averages of irradiance of 214 µmol m^{-2} s^{-1}), well above the estimated E_k for the ambient light and heatwave treatments. Plants under these conditions had adequate light, and with heatwaves conditions showed a trend of increased growth and significantly higher aboveground biomass. Overall, it appears that plants can benefit from exposure to heatwaves by being more productive, but only if light is available in sufficient quantities and if the heatwave temperature is not above their thermal optima. This implies that water quality is likely to be an influential factor in our ability to increase the likelihood of seagrass persistence under climate change. Thus, we predict that plants undergoing prolonged light reduction from dredging are more likely to have carbon deficits and eventually experience impacts to growth and survival during a heatwave and may be worse off than plants under ambient light.

There was an interesting response with carbohydrate allocation for *P. sinuosa* in the high temperature treatments, whereby plants, albeit only slightly, increased starch storage in the rhizome. Starch is often involved in a stress response where it is broken down to soluble sugars to support growth during stress or conversely, and less common, is the preferential storage of starch in organs to build resilience to future stress events (Thalmann and Santelia, 2017). The importance of starch accumulation in rhizomes to confer future resilience has been demonstrated in seagrass species (e.g. Govers et al., 2015). Locally generated data from WAMSI Project 2.2 estimated the thermal optimum (T_{opt}) of *P. sinuosa* in Shoalwater was at 26.4 °C under saturating light conditions (Said et al., 2024a). The heatwave conditions of 28 °C imposed in this study were slightly above the estimated thermal optimum, providing support that the increased starch could be a stress response to build resilience to future events. Costa et al. (2021) also found increased starch but in the leaves, not rhizomes of the seagrass *Cymodocea nodosa* and attributed this to higher assimilation of CO_2 due to higher temperatures. In terrestrial plants, starch accumulation in response to abiotic stress has been observed for salinity and cold stress (Kanai et al., 2007; Kaplan and Guy, 2004) but not high temperature stress. Further research on the mechanisms of carbon dynamics and starch accumulation in seagrasses is warranted and can be explored through 'omics' approaches (e.g. Jung et al., 2023).

3.6 *Importance of identifying relationships between cumulative stressors for management*

Our results do not suggest that the current light thresholds for *P. sinuosa* need to be modified if a dredging proposal was to co-occur with a short-term heatwave, as there were no synergistic effects of increased shoot loss under cumulative pressures. However, trends of reduced carbohydrate storage and growth suggested plants under low light and heatwave conditions would have lower resilience to prolonged or future events, so if the low light event continued beyond three weeks, with or without the heatwave, then reducing the low light pressure, including intensity and duration of operations, could be considered. This study has contributed to the body of knowledge on cumulative impacts and highlighted that determining the 'lethal' combination of light, temperature and other stressors is complex, and interactions are not always synergistic as recognised by Côté et al. (2016). Clearly, there is a need to continue multi-stressor research and we recommend future experiments investigate a greater number of light and temperature combinations and over longer durations. Such studies will provide much-needed information for improving ecosystem management given management actions in single-stressor settings may need to be reconsidered in multiple-stressor settings. For instance, water quality management is widely accepted as a strategy that can enhance seagrass resilience (Cullen-Unsworth and Unsworth, 2016). If we consider water quality in the context of this study – higher water clarity could enable plants to counteract increases in respiration in warmer waters. Under high light, thermal thresholds for photosynthesis and respiration are expected to be higher (Berry and Bjorkman, 1980) and the significant increase in aboveground biomass we documented is suggestive of this. However, a recent study on *Enhalus acoroides* showed that high light can worsen the effects of temperature stress due to damage of PSII resulting in photoinhibition, implying there are scenarios

where turbid waters are better for seagrasses during a heatwave (Zhang et al., 2023). Going forward, management options may need to be developed on a case-by-case basis and such 'tailoring' can be achieved provided efforts to collect location-specific information is prioritised and ongoing (Collier et al., 2020). For example, timing of dredging could be planned to minimise coinciding with marine heatwave events. Timing of dredging to avoid sensitive periods has been demonstrated as a suitable strategy in Western Australia and other jurisdictions (Fraser et al 2017, Wu et al 2017).

4 Conclusions

Under a simulated dredging and heatwave scenario, the effects of light and temperature on *Posidonia sinuosa* were predominantly independent rather than synergistic, but where there was an interactive effect, it was positive with higher biomass under adequate light and heatwave conditions. This is positive from a management perspective because it implies that adverse effects on seagrass could be minimised via management of light stress associated with dredging. Overall, our results did not provide evidence to suggest the current light thresholds that are used for EIA of *P. sinuosa* during marine dredging proposals need to be changed if dredging operations lead to light levels of 2 mols m^{-2} d^{-1} and coincide with a short-term heatwave (2 weeks at 28°C). However, declines in seagrass photochemical efficiency and electron transport rates under low light with subsequent trends for reduced growth and carbohydrate storage with low light and heatwave conditions could be considered early warning signs of reduced resilience. Based on our findings and previous work, we predict that irreversible impacts to *P. sinuosa* may be induced by a greater intensity and / or duration of reduced light, temperature or a combination of these. We recommend future experiments be conducted over a longer duration to determine appropriate temporal thresholds for significant synergistic impacts. As dredging operations and MHWs can create unique combinations of light and temperature conditions, we urge stakeholders to collect and share data to inform experimental design and increase the specificity of thresholds to maximise the effectiveness of EIA and management. This information and ongoing multi-stressor research are important for mitigating the risk of seagrass mortality associated with dredging under a changing climate.

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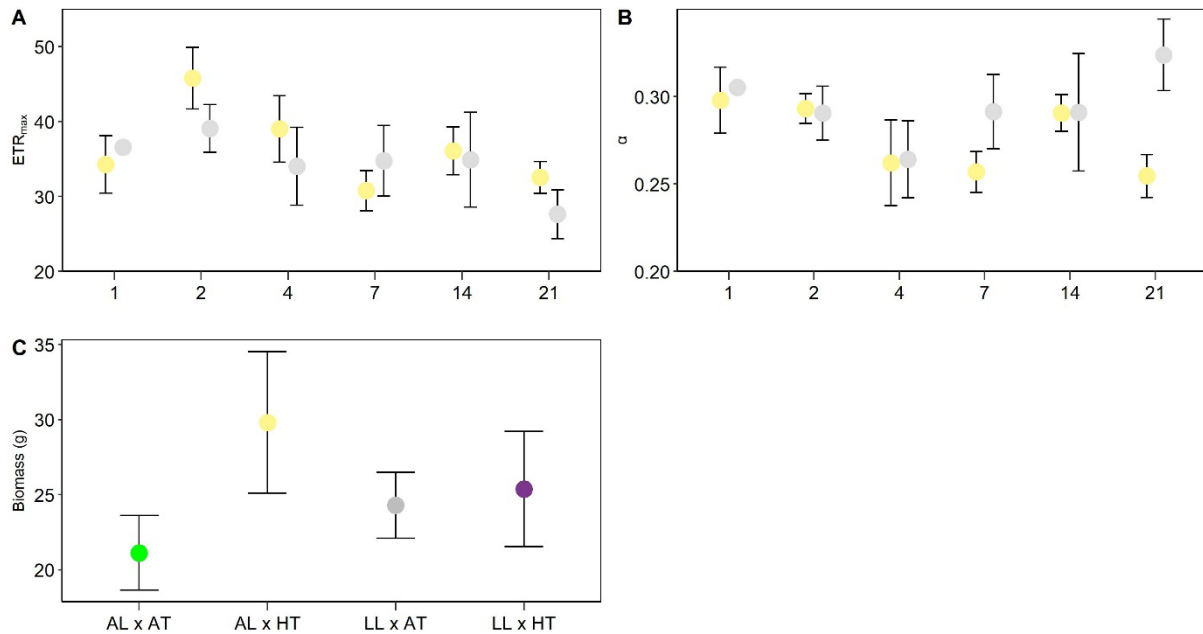
6 Appendices

Figure 3 Effects of Light, Temperature and Day tested on the response of *Posidonia sinuosa* across photophysiological and meadow-scales. Graphs represent the significant factor(s) or interactions determined by PERMANOVA analyses for maximum electron transport rates (A), photosynthetic efficiency (B) and total biomass (C).

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