



WESTERN AUSTRALIAN  
MARINE SCIENCE  
INSTITUTION

WESTPORT

Better science **Better decisions**

# Seagrass thermal tolerance varies between species and within species across locations

**Theme:** Benthic Habitats and Communities  
WAMSI Westport Marine Science Program



# WAMSI WESTPORT MARINE SCIENCE PROGRAM



WESTERN AUSTRALIAN  
MARINE SCIENCE  
INSTITUTION



WESTPORT



## 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.

## OWNERSHIP OF INTELLECTUAL PROPERTY RIGHTS

Unless otherwise noted, any intellectual property rights in this publication are owned by the State of Western Australia.

Unless otherwise noted, all material in this publication is provided under a Creative Commons Attribution 4.0 Australia License.

(<https://creativecommons.org/licenses/by/4.0/deed.en>)



## FUNDING SOURCES

The \$13.5 million WAMSI Westport Marine Science Program was funded by the Western Australian Government, Department of Transport. WAMSI partners provided significant in-kind funding to the program to increase the value to >\$22 million.

## 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).

## LEGAL NOTICE

The Western Australian Marine Science Institution advises that the information contained in this publication comprises general statements based on scientific research. The reader is advised and needs to be aware that such information may be incomplete or unable to be used in any specific situation. This information should therefore not solely be relied on when making commercial or other decisions. WAMSI and its partner organisations take no responsibility for the outcome of decisions based on information contained in this, or related, publications.

## YEAR OF PUBLICATION

October 2024

This report is part of the project: Pressure-response relationships, building resilience and future proofing seagrass meadows.

## CITATION

Said, N., Webster, C., Dunham, N., Strydom, S., McMahon, K. (2024). Seagrass thermal tolerance varies between species and within species across locations. Prepared for the WAMSI Westport Marine Science Program. Western Australian Marine Science Institution, Perth, Western Australia. 26 pp.

## 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

- SEAGRASS THERMAL TOLERANCE VARIES BETWEEN SPECIES AND WITHIN SPECIES ACROSS LOCATIONS ..... I**
- 1 INTRODUCTION ..... 1**
- 2 MATERIALS AND METHODS ..... 3**
  - 2.1 SEAGRASS SPECIES AND DISTRIBUTION..... 3
  - 2.2 PLANT COLLECTION AND ACCLIMATION ..... 4
  - 2.3 PHOTOSYNTHESIS-TEMPERATURE DETERMINATIONS ..... 4
  - 2.4 PHOTOSYNTHESIS-TEMPERATURE CURVE FITTING ..... 5
- 3 RESULTS..... 7**
  - 3.1 THERMAL PERFORMANCE BETWEEN DIFFERENT SPECIES ..... 7
  - 3.2 THERMAL PERFORMANCE ACROSS LOCATIONS FOR EACH SPECIES ..... 7
  - 3.3 TEMPERATURE DEPENDENCE OF PRODUCTIVITY..... 9
- 4 DISCUSSION ..... 10**
  - 4.1 THERMAL TOLERANCE..... 10
    - 4.1.1 Seagrass thermal tolerance varies between species ..... 10
    - 4.1.2 Seagrass thermal tolerance varies within a species across locations ..... 10
  - 4.2 PRODUCTIVITY ..... 11
    - 4.2.1 Productivity varies across species life history strategies ..... 11
    - 4.2.2 Productivity varies across locations and increases with latitudinal gradient ..... 11
  - 4.3 MANAGEMENT RECOMMENDATIONS..... 12
    - 4.3.1 Management to protect existing habitat ..... 12
    - 4.3.2 Seagrass resilience building opportunities..... 14
- 5 CONCLUSION ..... 14**
- 6 ACKNOWLEDGEMENTS ..... 14**
- 7 REFERENCES..... 15**
- 8 APPENDICES..... 19**
  - 8.1 APPENDIX 1..... 19

## Figures

- Figure 1.** Typical photosynthesis-temperature dependent relationship. Productivity increases to a point of maximum net productivity ( $P_{max}$ ), where the intercept of  $P_{max}$  with a temperature defines thermal optima ( $T_{opt}$ ) as temperature increases, productivity decreases to a carbon-balance of zero, defining thermal maxima ( $T_{max}$ ). Figure credit Collier et al. (2017). .....1
- Figure 2.** Seagrass species distribution in Australia overlaid with average summer ocean temperatures (December to March 10 year average). The six locations represent those assessed in this study: Coral Bay as tropical, Shark Bay sub-tropical, and Geraldton, Jurien Bay, Perth and Geographe Bay as temperate.....3
- Figure 3.** Net photosynthesis-temperature curves for seagrass species within and across locations at temperatures ranging from 15-45 C (n=5). Modelled fits are shown by the coloured lines, with the shading representative of the 95% CI in the model fits. Note the different scales on the Y-axes. ....8

## Tables

- Table 1.** For each seagrass species, geographic region, collection location and time (month), average temperature range for each location (summer and winter), water temperature and salinity at time of plant collection and water depth. ....4
- Table 2.** For photosynthesis:  $T_{opt}$ ,  $T_{max}$ ,  $Q_{10}$ , and maximum net productivity ( $NP_{max}$ ) at  $T_{opt}$  raw values from Yan & Hunt model, and for respiration: the maximum respiration rate and at which temperature this rate was observed, and  $Q_{10}$  for seagrass species and locations assessed. Average summer temperature, ocean warming (average summer + 2.2 °C; RCP 6.0) and 2010/11 marine heatwave data for each species location combination, where for each scenario green is low concern = >2 °C below  $T_{opt}$ , yellow is moderate concern = within 0-2 °C of  $T_{opt}$ , and orange is high concern = above  $T_{opt}$ . .....9
- Table 3.** Concern rating, and cause of concern (ocean warming or marine heatwave) for seagrass species and location sampled. Concern ratings are based on an ocean warming (summer ambient + RCP6.0 2.2 C) or MHW event (based on 2010/11), being higher or equal to optimum = high concern; <2 °C below optimum = moderate concern; and ≥2 °C + below optimum = low concern. Where populations have higher thermal tolerances than other populations these have been recognised as options for resilience building. Refuge areas are those with high thermal tolerances in cooler regions. Blank squares indicate a species does not grow in a location, and dashed lines indicate the species grows in a location but was not sampled. ....13

*The WAMSI Westport Marine Science Program is a \$13.5 million body of research that is designed to fill knowledge gaps relating to the Cockburn Sound region. It was developed with the objectives of improving the capacity to avoid, mitigate and offset environmental impacts of the proposed Westport container port development and increase the WA Government's ability to manage other pressures acting on Cockburn Sound into the future. Funding for the program has been provided by Westport (through the Department of Transport) and the science projects are being delivered by the Western Australian Marine Science Institution.*

# Seagrass thermal tolerance varies between species and within species across locations

Nicole E. Said<sup>a\*</sup>, Chanelle Webster<sup>a</sup>, Natasha Dunham<sup>a</sup>, Simone Strydom<sup>ab</sup>, and Kathryn McMahon<sup>a</sup>

<sup>a</sup>Centre for Marine Ecosystems Research, School of Science, Edith Cowan University, Joondalup, WA 6027, Australia

<sup>b</sup>Marine Science Program, Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia

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

## Executive Summary

Proactive strategies are increasingly being considered to conserve threatened species in the face of global climate change (Caruso et al. 2021). Understanding the thermal tolerance across a range of seagrasses will help identify species vulnerable to thermal stress and provide justification for prioritising restoration efforts. Further, assessing the thermal tolerance of multiple populations within a single species provides insights for thermal resilience building opportunities to future-proof vulnerable seagrass meadows (Caruso et al. 2021, Coleman & Bragg 2021). Cockburn Sound is an industrialised embayment south of Perth, Western Australia (WA), where seagrass has been heavily impacted (~75% decrease; Kendrick et al. 2002). Future dredging activities are currently being proposed, and restoration and resilience building options for seagrasses in Cockburn Sound and Owen Anchorage are likely to be a critical component of Environmental Impact Assessment and Management (EIA&M). This report presents findings from controlled experiments for six dominant seagrass species in Cockburn Sound and Owen Anchorage.

To inform restoration and thermal resilience building options for management of Westport dredging operations in Cockburn Sound and Owen Anchorage, thermal performance was assessed for five predominantly temperate seagrass species (*Posidonia sinuosa*, *Posidonia australis*, *Amphibolis antarctica*, *Amphibolis griffithii* and *Zostera nigricalis*) and one globally distributed species (*Halophila ovalis*) in the coastal waters of Perth where the development is proposed. Further, this study assessed populations of four species (*P. sinuosa*, *P. australis*, *A. antarctica* and *H. ovalis*) across two to four locations spanning 10° in latitude. Thermal tolerances were generated by measuring oxygen evolution in closed incubation chambers at temperatures ranging from 15-45 °C for seagrass productivity ( $P_{max}$ ), optimum temperature ( $T_{opt}$ ) at which maximum photosynthesis occurred, and thermal maximum temperature ( $T_{max}$ ).

The key findings of importance to Westport are:

- *Z. nigricalis* in Perth coastal waters is already growing in conditions outside of its thermal optima and is therefore of high concern. As there are no known populations growing further north of the Perth region (no sightings from Jurien Bay northwards), focusing management efforts to build resilience for *Z. nigricalis* is challenging.

- *H. ovalis* in the Perth region had a thermal optima of 32 °C, which is considerably higher than predicted ocean warming and marine heatwaves (MHWs) for Perth for 2050 and 2100 projections. Therefore, it is likely that under ocean warming the productivity of *H. ovalis* will increase, making this species of low concern.
- *Amphibolis* and *Posidonia* genera in the Perth region had thermal optima (26-27 °C) close to that of the 2010/11 MHW that impacted the WA coastline. Based on the 2010/11 MHW data these species are of moderate concern in this area. However, the water temperature in Perth coastal waters during the 2010/11 MHW was +3 °C, and future predictions estimate potential MHW severity of +5 °C. Therefore, under future conditions these species in Perth could be of high concern and it is recommended that restoration and resilience building efforts focus on *Amphibolis* and *Posidonia* genera as the priority.
- Contrary to previous assumptions, thermal performance does not necessarily reflect thermal geography of a seagrass species range. This finding is important from a management perspective when assessing future climate scenarios and emphasises that investigating local thermal performance data is important to identify which populations can be used for thermal resilience building opportunities.
- This study identified populations across multiple species (*P. australis*, *P. sinuosa*, and *A. antarctica*) that may be 'better equipped' (i.e. more resilient) at resisting thermal stress. For these species there was a population within a warmer region which had a higher thermal tolerance which could be considered appropriate for building thermal resilience. For example, individual adult *P. sinuosa* plants from Jurien Bay could be transplanted into Cockburn Sound to assist gene flow for higher thermal tolerance to future warming.

### Future Work

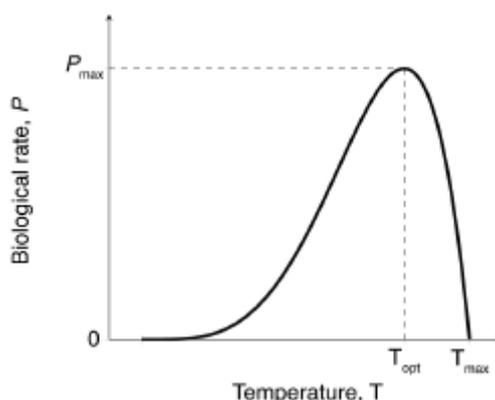
Overall, this study has been able to identify which seagrass species EIA proponents and environmental management bodies should focus management efforts on from a thermal resilience building perspective (*Amphibolis* and *Posidonia*), especially under ocean warming and provides insights of the potential impacts from MHWs on specific populations. One limitation of this study is the capacity to understand the effects of duration on thermal sensitivity. This has implications for accurately predicting impacts of MHWs, which can rapidly warm ocean temperatures by 5 °C and persist for weeks to months. The data generated from this study progresses our understanding of the variation in thermal tolerance within and between seagrass species, however, further research is recommended to test thermal optima over longer periods of time mimicking heatwave conditions.

# 1 Introduction

Global changes in temperature is a leading cause of biodiversity loss and ocean warming is already having unprecedented ecological impacts on marine ecosystems, with immobile benthic habitats, such as corals and seagrasses, particularly vulnerable to extreme events e.g. marine heatwaves (MHWs; Halpern et al., 2019; Trisos et al., 2020). With the increased intensity and frequency of MHWs occurring worldwide (Oliver et al. 2018), widespread ecological impacts have been observed, such as mass die-offs, range shifts, changes in community structure and reduced performance of populations due to species experiencing temperatures outside of their thermal range (Wiens 2016, Feeley et al. 2020). Understanding the thermal tolerance range of species is essential to predict potential ecological impacts of warming.

Seagrasses are the only flowering plants in the ocean, and are highly valued for their ecosystem services which contribute to a multitude of environmental and socio-economic benefits (Orth et al. 2006). Despite their recognised importance, seagrasses are among the most threatened ecosystems globally, with approximately 19% to 29% of monitored seagrass area lost since the 1940s (Waycott et al. 2009, Dunic et al. 2021). Our understanding of the effects of warming-induced mortality on seagrasses lags behind that of other marine organisms such as corals, likely due to the relatively few studies linking mass seagrass mortality with extreme climate events (Lough et al. 2018, Strydom et al. 2020). Ocean warming increases of less than 3 °C have resulted in seagrass mortality in both subtropical (Fraser et al. 2014, Strydom et al. 2020) and temperate regions (Diaz-Almela et al. 2007, Marbà & Duarte 2010). With rising ocean temperatures and increased frequency of MHW events, climate change poses a growing threat to seagrass meadows and their resilience globally (Jordà et al. 2012).

Temperature is a key factor influencing most plant processes such as respiration, photosynthesis and reproduction. Temperature varies both spatially and temporally, which affects plant distribution and productivity (Berry & Bjorkman 1980). Seagrasses can broadly be split into tropical, sub-tropical and temperate varieties, and can survive across a wide range of temperatures (0-45 °C; Collier et al. 2017) due to thermoprotection and repair mechanisms (e.g. rubisco activase, lipid permeability, heat shock proteins) that buffer plants against heat stress (Sharkey & Schrader 2006). Temperature affects the balance between carbon uptake (photosynthesis) and carbon consumption (respiration; Bulthuis, 1987). As temperature increases, the rate of photosynthesis initially increases to a point of physiological optimum, the optimum temperature ( $T_{opt}$ ) being where net photosynthesis is at its highest. An increase in temperature past  $T_{opt}$  results in a decline in productivity, and can invoke physiological stress, growth inhibition, and prolonged exposure may result in mortality (Collier & Waycott 2014; Figure 1). Understanding the thermal tolerance of multiple seagrass species can aid in identifying vulnerable species and habitats to climate impacts (Foden et al. 2019).



**Figure 1.** Typical photosynthesis-temperature dependent relationship. Productivity increases to a point of maximum net productivity ( $P_{max}$ ), where the intercept of  $P_{max}$  with a temperature defines thermal optima ( $T_{opt}$ ) as temperature increases, productivity decreases to a carbon-balance of zero, defining thermal maxima ( $T_{max}$ ). Figure credit Collier et al. (2017).

Accurately predicting seagrass thermal sensitivity is crucial for the effective management of seagrasses in the face of environmental change and anthropogenic impacts (Collier et al. 2017). To date, broad-scale thermal assessments have focused on a seagrass species realised thermal niche (the temperature range over the distribution of a species) or localised thermal performance data has been extrapolated across a species range (Araujo & Peterson 2012). These methods overlook differences in local-scale thermal physiology. Within a species, populations can grow across temperature gradients, with populations growing in the warmest area (warm-edge), core (middle of range), and coolest area (cool-edge). From the limited work to date, the thermal tolerance of a seagrass species is not always homogeneous across these gradients, nor is there necessarily a trend of increased tolerance with higher water temperature (Bennett et al., 2022; Collier et al., 2017). Seagrass populations, like all sexually reproducing organisms, can adapt (particular genes are selected to provide an individual with an advantage and over generations these genotypes become more common) to a set of environmental conditions such as different temperature ranges, or through phenotypic plasticity, acclimate to different environmental conditions (Quigley 2024). Therefore, a species' ability to tolerate changes in temperature across their distribution can be attributed to their adaptive capacity, which can affect the optimum temperature for net productivity across a species distribution (Bennett et al. 2019). For example, if populations across a species range display a similar  $T_{opt}$ , this would signify a limited ability to tolerate changes in temperature and warm-edge populations already growing close to their thermal limits will likely be more vulnerable than the cool edge-populations. Alternatively, if  $T_{opt}$  varies across populations, then warm-edge populations may display plasticity that affords physiological adjustments to improve photosynthesis under warmer temperatures. Therefore, in addition to thermal threshold performance data for species, data across an individual species range are also critical for accurate predictions under current and future climate conditions.

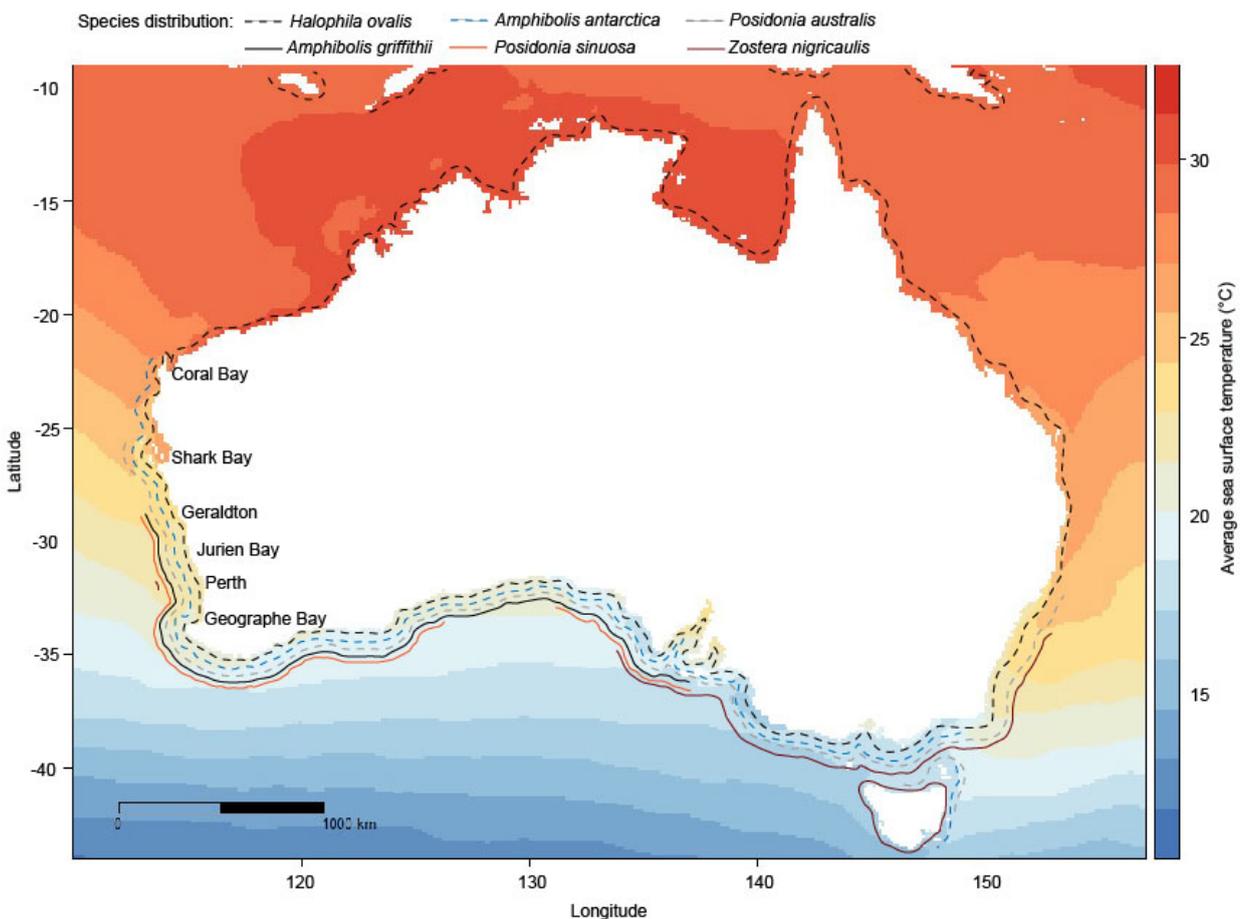
Compiling photosynthetic temperature (P-T) threshold data for seagrasses is important at the global scale to aid predictions. Currently there are physiological tolerance estimates for four seagrass species which occur in Australia (Collier et al. 2017, Kong et al. 2020), two of which have been assessed at multiple locations (Collier et al. 2017), but there is no P-T data across both temperate and tropical regions. Western Australia (WA) is an ideal region for studying thermal thresholds due to the occurrence of species across a large thermal gradient (temperate to tropical; 16° latitude), and there is no P-T data. There is a critical need for this data due to WA's designation as a global hotspot for marine climate impacts, where there has been substantial warming at a rate faster than other regions, and where MHWs are intensifying (Hobday & Pecl 2014, Kajtar et al. 2021). The objective of this study is to identify which species may be vulnerable to future climate scenarios based on physiological thermal optima, as well as to provide insight into geographical variation in thermal optima which can inform thermal resilience building opportunities, with a focus on species that have a broadly temperate distribution. Therefore, the aims of this study were to (1) determine the temperature tolerances of different seagrass species, and (2) assess thermal tolerance between populations of single species across a thermal latitudinal gradient.

## 2 Materials and Methods

### 2.1 Seagrass species and distribution

This study focused on assessing the thermal tolerance of predominantly temperate species, although the geographic range for some of these species extends into sub-tropical and tropical regions (Figure 2). We assessed five temperate species (*Posidonia sinuosa*, *Posidonia australis*, *Amphibolis antarctica*, *Amphibolis griffithii*, and *Zostera nigricaulis*), and one globally distributed species, *Halophila ovalis*. Hereafter, we will refer to locations as temperate (Geraldton, Jurien Bay, Perth and Geographe Bay), sub-tropical (Shark Bay) and tropical (Coral Bay). All of these species were assessed in Perth coastal waters and four of these six species were assessed at 2-4 sites over a latitudinal gradient (Table 1).

The seagrass species selected can be classified as colonising, opportunistic and persistent, based on life history traits that influence their ability to resist and recover from pressures (Kilminster et al. 2015). The smaller, faster growing colonising genera (e.g. *Halophila*) have a low physiological resistance (duration) to pressures (e.g., heatwaves), however they have the ability to rapidly recover. Comparatively, the larger, persistent genera (e.g. *Posidonia* and *Amphibolis*) have a greater ability to withstand pressures but are slower to recover (Kilminster et al. 2015). The opportunistic genera (e.g. *Zostera*) is intermediate between the colonising and persistent genera and combines elements of both resistance and recovery strategies.



**Figure 2.** Seagrass species distribution in Australia overlaid with average summer ocean temperatures (December to March 10 year average). The six locations represent those assessed in this study: Coral Bay as tropical, Shark Bay sub-tropical, and Geraldton, Jurien Bay, Perth and Geographe Bay as temperate.

## 2.2 Plant collection and acclimation

To assess 1) if the P-T relationship varied between different species, six seagrass species were collected from a temperate region (Perth), and 2) to determine whether the P-T relationship varied for four of these species over a latitudinal gradient (4° to 10° latitude) an additional, two to four locations were assessed depending on the species (Table 1), two species in the sub-tropical region and two species in the tropical region (Table 1). Whole plants were collected by gently fanning the sediment to expose rhizomes and placed in a cooler box filled with seawater and aeration for transportation to the laboratory. At each collection time, temperature and salinity were recorded to determine initial laboratory acclimation conditions.

In the laboratory, the experimental plants were gently cleaned to remove epiphytes. Plants were then planted into 50 L aquaria containing a ~10 cm layer of unsorted, washed, quartz river sand overlaid by aerated seawater. Water temperature and salinity mimicked field collection conditions (Table 1). Water temperature was controlled using aquarium heaters. Plants were provided with ~180  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (above approximating saturating irradiance; Lee et al. 2007) using marine aquarium Light Emitting Diode modules with a full spectrum light (MarinTech™ Pty Ltd) on a 12/12 light: dark cycle. Light intensity at the base of the canopy was measured using a micro-PAR sensor (In-Situ Marine Optics™). Plants were left for two days to acclimate after which dark adapted maximum quantum yields were taken on five separate plants to assess their acclimation. Plants were considered healthy and acclimated if they had a dark-adapted yield of 0.73–0.75 (Ralph & Burchett 1995).

**Table 1.** For each seagrass species, geographic region, collection location and time (month), average temperature range for each location (summer and winter), water temperature and salinity at time of plant collection and water depth.

Species	Dominant geographic region	Collection location	Latitude	Longitude	Collection month	Location water temp range (°C)*	Water temp at collection (°C)	Salinity at collection (ppt)	Water Depth (m)**
<i>P. sinuosa</i>	Temperate	Geraldton	-28.748°	114.610°	June	17-24	21	33.4	8
		Jurien Bay	-30.330°	115.031°	June	17-24	19	33.6	4
		Perth	-32.272°	115.690°	June	15-23	18	33.6	2
		Geographe Bay	-33.616°	115.128°	August	15-23	15	35-36**	4
<i>P. australis</i>	Temperate	Shark Bay	-25.824°	113.463°	August	17-26	17.5	39.5	2
		Perth	-32.136°	115.746°	July	15-23	16	33.6	2
<i>A. antarctica</i>	Temperate	Coral Bay	-22.723°	113.710°	September	22-26	19	34.0	8
		Shark Bay	-25.824°	113.463°	August	17-26	17.5	39.5	2
		Perth	-32.272°	115.690°	June	15-23	18	33.6	2
<i>A. griffithii</i>	Temperate	Perth	-32.272°	115.690°	June	15-23	18	33.6	2
<i>Z. nigricaulis</i>	Temperate	Perth	-32.136°	115.746°	June	15-23	17	33.6	2
<i>H. ovalis</i>	Global	Coral Bay	-23.168°	113.762°	September	22-26	21	34.0	2
		Perth	-32.272°	115.690°	August	15-23	15	33.6	2

\*Water temperature data 10-year average from NOAA Coral Reef Watch Daily Global 5 km Satellite Data, corrected with benthic logger data provided by DBCA, Mid-West Ports and Busselton Jetty.

\*\*Salinity not collected at site for Geographe Bay location, range provided from Port Geographe Bay Water Quality Report (O2 Marine 2021).

\*\*\*Water depth at time of collection

## 2.3 Photosynthesis-temperature determinations

For each seagrass species and location combination, data was generated to examine seagrass productivity, optimum temperature ( $T_{\text{opt}}$ ) at which maximum photosynthesis occurred, and thermal maximum temperature ( $T_{\text{max}}$ ) where photosynthesis is zero. Seagrass photosynthesis and respiration were measured via production or consumption of  $\text{O}_2$ . Five replicate plant chambers, and a sixth 'blank' chamber (containing no plant material) were established and placed into the temperature-controlled tank. Multiple whole plants (4-5 leaf pairs with an apical meristem for *H. ovalis*, and 3+ shoots/stems for other species) were incubated in sealed transparent, acrylic chambers, with the size (15-45 cm), and orientation (vertical or horizontal to mimic natural plant orientation) of the chamber dependent on the

species being assessed. Water within the chambers was circulated using small submersible pumps. Dissolved oxygen concentrations within the chambers were measured using FireSting™ 3 mm robust REDFLASH technology sensors (PyroScience) inserted through the chamber wall and connected through a 4-channel meter to a computer recording mg of O<sub>2</sub>. Oxygen electrodes were calibrated using the manufacturer's 2-point method (0% and 100% air saturated water).

To maintain a stable temperature ( $\pm 0.25$  °C), chambers were submerged in a tank with 200-450 L of seawater which was circulated through a chiller-heater unit set to the appropriate experimental temperature. Temperatures ranged from 15-43 °C, where cooler temperatures were reached using the chiller function, and warmer temperatures were reached using the heater function as well as additional titanium heaters. The internal temperature of the chamber was also measured using a submersible temperature sensor (accuracy  $\pm 0.5$  °C) connected to the FireSting O<sub>2</sub> meter, and this was the temperature which was relied upon for experiments. As the accuracy of the temperature sensor used was  $\pm 0.5$  °C, in text we have reported thermal tolerance data to the nearest 0.5 °C. For each temperature treatment, oxygen concentrations (measured every second) were first measured in the dark for seagrass respiration, and then the plants were illuminated by full spectrum lights (MarinTech™ Pty Ltd) above a saturating light level of 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for photosynthesis and respiration measurements. This was repeated at 8-10 temperature steps (15, 18, 21, 24, 27, 30, 33, 36, 38/39, 42/43 °C) depending on the species. Experiments were 8 to 12 hours in length with the time to reach each experimental temperature taking 30 to 65 minutes.

Each dark and light step was 10 minutes from when the oxygen reading was stable at each temperature. Seawater within the chambers was refreshed if the oxygen level fell below 2 mg O<sub>2</sub>/L to prevent oxygen toxicity. At the end of the experiment, plants were removed from the chambers and separated into above-ground and below-ground tissue. Plants were dried for 48 h at 60 °C and then weighed.

#### 2.4 Photosynthesis-temperature curve fitting

For each replicate incubation (and control) and for all temperatures, oxygen concentration was plotted against time after discarding the first two minutes of data, which was considered a stabilisation period. The portion of the remaining data used to determine the rate was confined to that where the R<sup>2</sup> value was greater than 0.9. Rates of oxygen exchange were normalised to mg O<sub>2</sub>. g<sup>-1</sup> DW<sup>-1</sup>. hr<sup>-1</sup> of whole plant material. Oxygen concentration within the control chamber (containing no seagrass) was measured throughout the experiment and experimental units were only used if there was no significant change in control chamber oxygen concentration.

Photosynthetic rates were expected to follow the general trend of a gradual increase to thermal optima, followed by a steep decline past T<sub>opt</sub> (Figure 1. Typical photosynthesis-temperature dependent relationship **Table 2** Adams et al. 2017), and respiration was expected to show an increase with increasing temperature. For each incubation, productivity-temperature data were fitted to the Yan and Hunt model (Yan & Hunt 1999) to obtain maximum metabolic rates and thermal thresholds. This model is the most appropriate for this type of data (Adams et al. 2017, Collier et al. 2017) to extract thermal optima (T<sub>opt</sub>), thermal maxima (T<sub>max</sub>), productivity at T<sub>opt</sub>, which were extracted for photosynthesis, and Q<sub>10</sub> was extracted for both photosynthesis and respiration.

$$P(T) = P_{\max} \left( \frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \right) \left( \frac{T}{T_{\text{opt}}} \right)^{T_{\text{opt}} / (T_{\max} - T_{\text{opt}})} \quad (1)$$

In this equation, P (T) is the biological rate P at temperature T (°C) and can represent either photosynthesis or respiration (mg O<sub>2</sub>. g DW<sup>-1</sup>. hr<sup>-1</sup>), P<sub>max</sub> is the maximum rate (mg O<sub>2</sub>. g DW<sup>-1</sup>. hr<sup>-1</sup>) which occurs at the optimum temperature T<sub>opt</sub> (°C), and T<sub>max</sub> (°C) is the temperature greater than the optimum at which the biological rate drops to zero (Collier et al., 2017). Using non-linear regression (MATLAB Statistics and Machine Learning Toolbox R2022a), equation (1) was fitted to seagrass net photosynthesis of whole plants (which takes both leaf respiration and below-ground respiration into consideration), for the six species and location combinations.

Below the optimum temperature, the  $Q_{10}$  coefficient is used to predict rate of metabolic change, which is the factor by which there is an increase in the biological rate due to a temperature increase of 10 °C (John et al. 1988, Atkin & Tjoelker 2003). Following methods from Collier et al., (2017) a second model was fitted to estimate  $Q_{10}$  values by fitting the temperature-dependence of seagrass net photosynthesis and respiration for all species and location combinations. Based on the P-T model (equation 1), only data that was predicted to fall below  $T_{opt}$  was used to within equation 2. The second model was an exponential function of the form.

$$P(T) = P_0 Q_{10}^{(T - T_0)/10} \quad (2)$$

where  $P_0$  ( $\text{mg O}_2 \cdot \text{g DW}^{-1} \cdot \text{hr}^{-1}$ ) is the biological rate at a reference temperature  $T_0$  (°C). We set  $T_0 = 20$  °C, following the protocol of (Baird et al. 2016).

### 3 Results

All species followed a temperature-dependent relationship (**Error! Reference source not found.**), showing a gradual increase in photosynthesis with temperature to  $T_{opt}$ , generally followed by a rapid decline to  $T_{max}$  (Figure 3). For all species, respiration increased with temperature and was generally highest at the highest temperature tested (Table 2).

Overall, there was a larger variation between different species for  $T_{opt}$  (1-10 °C) and  $T_{max}$  (0-5 °C), than across locations for the same species ( $T_{opt}$  1-4 °C,  $T_{max}$  0-2 °C). At temperatures below  $T_{opt}$  there was a gradual rise in net  $P_{max}$  with an increase in temperature, which was characterised by the  $Q_{10}$  parameter. In general, there was no substantial differences in the  $Q_{10}$  coefficient (Figure A1), so we have not gone into detail for this parameter (except for *P. sinuosa* at Geographe Bay).

#### 3.1 Thermal performance between different species

In the temperate location (Perth), there was a clear difference in thermal tolerances between different species, varying by almost 10 °C across the six species assessed (Table 2). For the larger species in Perth (*P. sinuosa*, *P. australis*, *A. antarctica*, *A. griffithii*)  $T_{opt}$  and  $T_{max}$  varied by ~1 °C, ranging from 26-27 °C for  $T_{opt}$  and 38-39 °C for  $T_{max}$ . *Z. nigricaulis*, had the lowest  $T_{opt}$  (22.5 °C) and  $T_{max}$  (35 °C). *H. ovalis*, a globally distributed species, had the highest  $T_{opt}$  of 32 °C and highest  $T_{max}$  of 40 °C.

In the sub-tropical location (Shark Bay), *A. antarctica* and *P. australis* had similar thermal tolerances,  $T_{opt}$  was 30 °C and 30.5 °C, respectively.  $T_{max}$  was 38 °C for *A. antarctica* and 39 °C for *P. australis*.

In the tropical location (Coral Bay),  $T_{opt}$  varied by ~4 °C, with *H. ovalis* having a higher thermal tolerance than *A. antarctica*, 31.5 °C and 27 °C, respectively.  $T_{max}$  across the two species had a lower variation (than  $T_{opt}$ ), varying by ~2 °C, with *H. ovalis* having a higher  $T_{max}$  than *A. antarctica*, 40 °C and 38 °C, respectively.

#### 3.2 Thermal performance across locations for each species

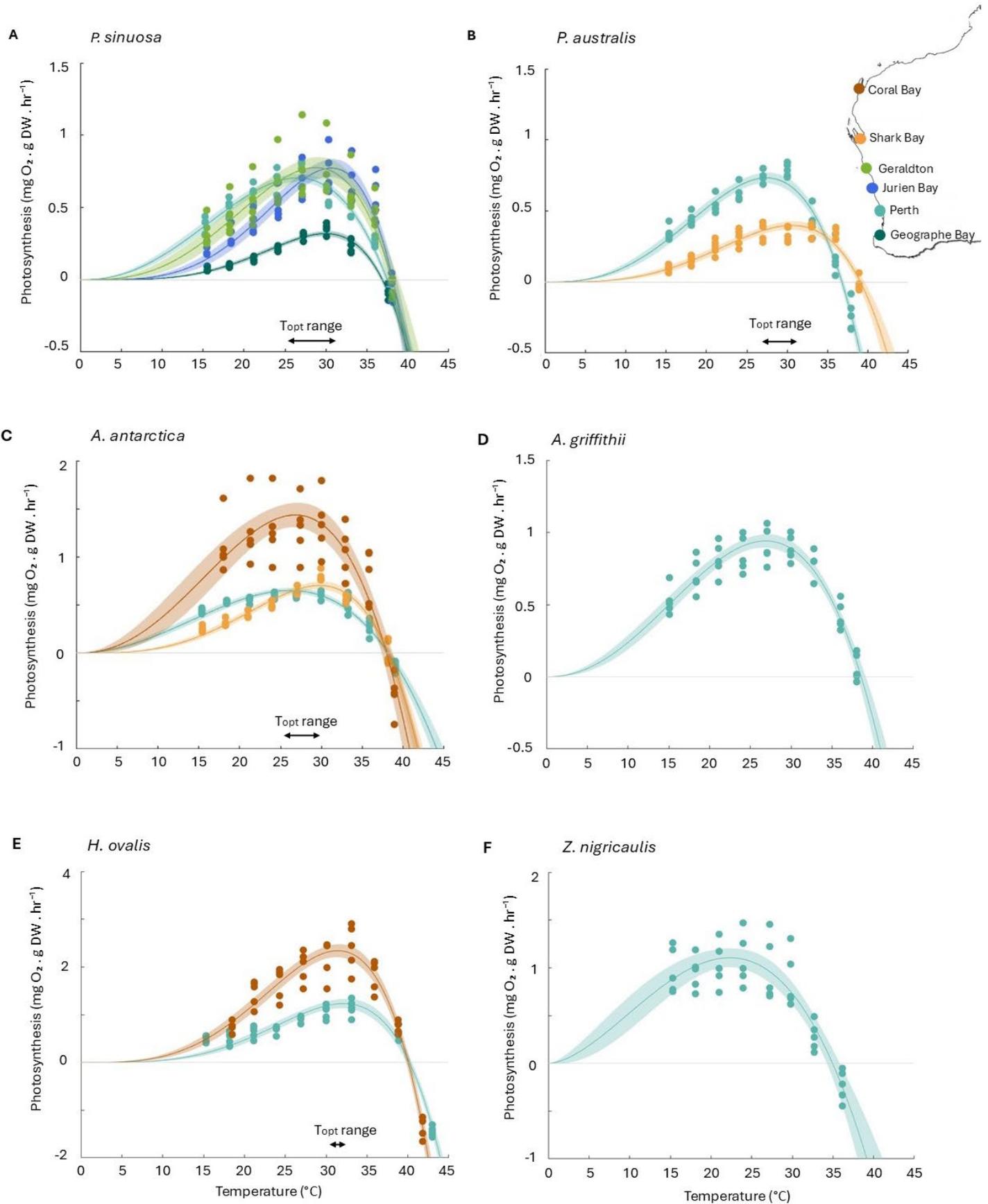
Thermal optima varied across locations for a single species, but the amount of variation was species dependent (~1-4 °C; Table 2). The variation in  $T_{opt}$  showed no consistent trend across geographical regions (temperate, sub-tropical, tropical).

*P. sinuosa*  $T_{opt}$  varied by ~4 °C across the four temperate locations (Geraldton, Jurien Bay, Perth, Geographe Bay) assessed, spanning ~500 km. There was no consistent pattern in  $T_{opt}$  along the latitudinal gradient tested (Figure 3A). Geographe Bay, the most southern (and coolest) population, had a similar  $T_{opt}$  (30 °C) to Jurien Bay ( $T_{opt}$  31 °C), and the most northern (and warmest) population in Geraldton had a 2 °C lower  $T_{opt}$  (29 °C) than Jurien Bay. Thermal optima was lowest in Perth (26 °C; Figure 3). In contrast, there was a trend of increased  $T_{max}$  from Geographe Bay, 37 °C, to Geraldton, 38 °C. The rate of  $Q_{10}$  at most locations was not substantially different (1.9 to 2.2), except for at Geographe Bay which had a  $Q_{10}$  of 3.3 (Table 2, Figure A1).

*P. australis* was assessed in temperate Perth and sub-tropical Shark Bay, ~700 km apart. Both  $T_{opt}$  and  $T_{max}$  were higher at the sub-tropical location, compared to the temperate location (Figure 3B).  $T_{opt}$  varied by ~4 °C, 31 °C in the sub-tropical location and 27 °C in the temperate location, and  $T_{max}$  varied by ~2 °C; 39 °C and 37 °C, respectively.

*A. antarctica* was assessed across three regions, temperate (Perth), sub-tropical (Shark Bay) and tropical (Coral Bay), spanning ~1,000 km. There was no clear trend for  $T_{opt}$  along the latitudinal gradient.  $T_{opt}$  was lowest in the temperate location (26 °C) and highest at the sub-tropical location (30 °C), with the tropical location  $T_{opt}$  (27 °C) more similar to the temperate location (Figure 3C). *A. antarctica* had a  $T_{max}$  of 38 °C for all locations.

*H. ovalis* showed the least variation in  $T_{opt}$  across locations, varying by less than 1 °C (Figure 3E). The temperate location (Perth) had a slightly higher  $T_{opt}$  than the tropical location (Coral Bay), 32 °C and 31.5 °C, respectively.  $T_{max}$  for *H. ovalis* was the same across both locations tested (40 °C).



**Figure 3.** Net photosynthesis-temperature curves for seagrass species within and across locations at temperatures ranging from 15-45 °C (n=5). Modelled fits are shown by the coloured lines, with the shading representative of the 95% CI in the model fits. Note the different scales on the Y-axes.

### 3.3 Temperature dependence of productivity

Following the same trend as the thermal tolerance data, the net productivity at the optimum temperature also had greater variation between different species than within the same species.

When assessing the maximum net productivity ( $NP_{max}$ ) at  $T_{opt}$  across species in the temperate region (Perth), the smaller species, *Z. nigricaulis* and *H. ovalis* had a ~2-fold higher  $NP_{max}$  per g DW<sup>-1</sup> plant material than the larger persistent species (*Posidonia* and *Amphibolis*). The productivity for the smaller species ranged from 1.11 and 1.23 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup> and for the larger species from 0.65 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup> for *A. antarctica* to 0.94 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup> for *A. griffithii* (Table 2). For the sub-tropical location (Shark Bay), *A. antarctica* had the highest  $NP_{max}$  and *P. australis* had the lowest  $NP_{max}$ , 0.70 and 0.39 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>, respectively. The tropical location (Coral Bay) followed the same trend as the temperate location (small vs large persistent species), with *H. ovalis* having a ~1.5 -fold higher  $NP_{max}$  compared to *A. antarctica*, 2.34 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup> and 1.44 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>, respectively.

When comparing seagrass species (*P. australis*, *A. antarctica*, *P. sinuosa*, *H. ovalis*) across locations,  $NP_{max}$  at  $T_{opt}$  generally increased at the warmest location assessed, except for *P. australis*. For *P. sinuosa*,  $NP_{max}$  was generally two-fold higher in the warmest locations (0.77-0.78 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>), compared to the cooler location (Geographe Bay; 0.32 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>). *A. antarctica* showed the same trend as *P. sinuosa*, showing a ~2-fold increase in  $NP_{max}$  at  $T_{opt}$  from the temperate region (Perth; 0.65 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>) to the tropical region (Coral Bay; 1.44 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>). *H. ovalis* also followed this trend with a ~2-fold increase in productivity in the tropical location (Coral Bay; 2.34 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>), compared to the temperate location (Perth; 1.23 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>). Conversely, *P. australis* showed the opposite trend to the other species assessed, having almost a ~2-fold higher  $NP_{max}$  in the temperate location (Perth) compared to the sub-tropical location (Shark Bay), 0.73 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup> and 0.39 mg O<sub>2</sub>.g DW<sup>-1</sup>. hr<sup>-1</sup>, respectively.

**Table 2.** For photosynthesis:  $T_{opt}$ ,  $T_{max}$ ,  $Q_{10}$ , and maximum net productivity ( $NP_{max}$ ) at  $T_{opt}$  raw values from Yan & Hunt model, and for respiration: the maximum respiration rate and at which temperature this rate was observed, and  $Q_{10}$  for seagrass species and locations assessed. Average summer temperature, ocean warming (average summer + 2.2 °C; RCP 6.0) and 2010/11 marine heatwave data for each species location combination, where for each scenario green is low concern = >2 °C below  $T_{opt}$ , yellow is moderate concern = within 0-2 °C of  $T_{opt}$ , and orange is high concern = above  $T_{opt}$ .

Species	Location	Temperature (°C)			Photosynthesis				Respiration		
		Summer average	Summer average +2.2	2010/11 heatwave	$T_{opt}$ (°C)	$T_{max}$ (°C)	$Q_{10}$	$NP_{max}$ at $T_{opt}$ (mg O <sub>2</sub> · g <sup>-1</sup> DW · h <sup>-1</sup> )	Temperature at maximum R (°C)*	$Q_{10}$	Maximum R (mg O <sub>2</sub> · g <sup>-1</sup> DW · h <sup>-1</sup> )
<i>P. australis</i>	Shark Bay	26	28.2	31	30.5 ± 0.3	39.1 ± 0.1	1.9 ± 0.2	0.39 ± 0.01	39	1.5 ± 0.3	-0.26 ± 0.01
	Perth	23	25.2	26	27.4 ± 0.3	36.7 ± 0.2	1.8 ± 0.1	0.73 ± 0.02	38	1.8 ± 0.1	-0.78 ± 0.01
<i>A. antarctica</i>	Coral Bay	26	28.2	29	26.8 ± 0.7	37.9 ± 0.3	1.3 ± 0.3	1.44 ± 0.06	39	1.6 ± 0.1	-0.71 ± 0.05
	Shark Bay	26	28.2	31	29.8 ± 0.3	38.2 ± 0.2	2.2 ± 0.1	0.70 ± 0.02	33*	1.5 ± 0.6	-0.37 ± 0.01
	Perth	23	25.2	26	26.2 ± 0.4	38.2 ± 0.2	1.4 ± 0.1	0.65 ± 0.01	39	1.6 ± 0.1	-0.48 ± 0.02
<i>P. sinuosa</i>	Geraldton	24	26.2	28	28.7 ± 0.5	38.1 ± 0.3	2.0 ± 0.3	0.78 ± 0.04	38	1.6 ± 0.1	-0.69 ± 0.05
	Jurien Bay	24	26.2	29	30.7 ± 0.3	38.1 ± 0.2	2.2 ± 0.2	0.77 ± 0.03	38	1.7 ± 0.1	-0.68 ± 0.07
	Perth	23	25.2	26	26.5 ± 0.3	37.5 ± 0.1	1.9 ± 0.2	0.70 ± 0.02	38	1.9 ± 0.1	-0.69 ± 0.02
	Geographe Bay	23	25.2	26	29.9 ± 0.3	36.9 ± 0.1	3.3 ± 0.2	0.32 ± 0.01	39	1.5 ± 0.1	-0.33 ± 0.02
<i>A. griffithii</i>	Perth	23	25.2	26	26.9 ± 0.4	38.6 ± 0.2	1.6 ± 0.2	0.94 ± 0.02	36*	1.7 ± 0.1	-0.58 ± 0.01
<i>Z. nigricaulis</i>	Perth	23	25.2	26	22.3 ± 0.9	34.9 ± 0.4	1.1 ± 0.3	1.11 ± 0.05	36	1.7 ± 0.1	-3.11 ± 0.18
<i>H. ovalis</i>	Coral Bay	26	28.2	29	31.4 ± 0.3	40.0 ± 0.1	2.0 ± 0.2	2.34 ± 0.07	42	1.5 ± 0.1	-4.26 ± 0.23
	Perth	23	25.2	26	32.1 ± 0.4	40.2 ± 0.2	1.8 ± 0.1	1.23 ± 0.05	43	1.5 ± 0.4	-4.16 ± 0.13

All respiration rates increased with temperature and had the highest respiration at the maximum temperature tested, except rows with \*.

## 4 Discussion

Understanding variation in thermal tolerance for different species and populations within the same species is critical for accurately predicting climate change impacts (Araujo & Peterson 2012, Bennett et al. 2019). This study assessed the thermal tolerance of six different seagrass species, predominantly found in temperate regions, across a range of life history strategies (colonising, opportunistic and persistent). Additionally, thermal tolerance was assessed within the same species (four out of six) across multiple locations from temperate to tropical regions. Two of the major findings were that 1) thermal optima varied by almost 10 °C between the six species, and 2) thermal optima for the same species differed by up to 4 °C across locations but there was not a consistent pattern with latitude.

### 4.1 Thermal tolerance

#### 4.1.1 Seagrass thermal tolerance varies between species

A major gap in our knowledge to inform future climate predictions is our understanding of temperature response for multiple species (Donelson et al. 2019). This study has highlighted clear differences between seagrass species' thermal tolerances, which broadly coincided with their geographic thermal distributions. *Halophila ovalis* has a global distribution and was the species with highest thermal optima in this study. *Zostera nigricaulis*, the species with the most restricted distribution in this study to only temperate waters, had the lowest thermal optima. This finding is consistent with results from Collier et al. (2017), that tropical species, *Cymodocea serrulata* and *Halodule uninervis* had a higher thermal tolerance (35 °C) than *Zostera muelleri* (31 °C), a predominantly temperate species which extends into tropical waters in eastern Australia. Further, this concept seems to hold true for seagrasses in the Mediterranean, where Bennett et al. (2022) found thermal optima differences of up to 10 °C for *Cymodocea nodosa* (Mediterranean, broad thermal range) compared to *Posidonia oceanica* (exclusively temperate, restricted thermal range), which was also consistent with the species thermal distributions. This suggests that species may have adapted their thermal optima to the water temperature across their distributional range. Understanding individual seagrass species tolerances and responses in relation to temperature is critical information that will allow for more focused management of vulnerable species as climate change impacts continue to intensify.

#### 4.1.2 Seagrass thermal tolerance varies within a species across locations

In the era of global change, it is critical that we not only understand and predict multiple species responses, but also the amount of variation within a single species (intra-specific variation). This study has shown that thermal optima can vary across locations within a species and the change in  $T_{opt}$  does not necessarily increase along a latitudinal gradient from populations growing in cooler to warmer waters, even for populations growing at their warm-edge. Three species, *P. sinuosa*, *P. australis* and *A. antarctica* were all collected from their warm-edge growing limit and further south in cooler waters (but not at their cool-edge). *Posidonia australis* was the only species assessed in this study to have a higher thermal optimum at the warm-edge, where both *A. antarctica* and *P. sinuosa* had a lower thermal optimum at the warm-edge of their range. Interestingly, *P. australis* at its warm-edge in Shark Bay is abundant and grows in both shallow and deep waters, whereas *A. antarctica* and *P. sinuosa* plants at their warm-edge were restricted to deeper waters. Further south (cooler) where these two species are more prevalent, they inhabit both shallow and deep waters. As deeper waters have a more consistent temperature and are generally cooler than shallow waters, it is possible that these warm-edge populations of *P. sinuosa* and *A. antarctica* can only persist at deeper depths where it is cooler (Giraldo-Ospina et al. 2020), and could explain the lower thermal tolerances seen at the warm-edge for these species. Only *P. sinuosa* was collected at the coolest location in this study, Geographe Bay, which is not the cool-edge for this species, but experiences similar temperatures to the Southern-Australian region (*P. sinuosa* cool-edge). At the coolest location tested, *P. sinuosa* had a thermal optimum higher than that of the warm-edge and more similar to the warmer location (Jurien Bay) where *P. sinuosa* is more abundant. Previous hypotheses suggest that warm-edge populations would have the highest thermal

tolerance where a species has reached its maximum adaptation and/ or plasticity potential (Donelson et al. 2019). This study contradicts this assumption and further, is consistent with Bennett et al. (2022a), where *Posidonia oceanica* at its cool-edge had a higher tolerance to warming than the core-population, and was more similar to that of the warm-edge population, suggestive of niche conservatism (Wiens et al. 2010, Bennett et al. 2022a). This is an important finding as it suggests that thermal performance does not necessarily reflect the thermal geography of a species range, and therefore, this needs to be taken into consideration when predicting future climate scenarios.

Contrasting to the temperate species assessed in this study, the globally distributed *H. ovalis*, showed little variation in  $T_{opt}$  across the two locations assessed ( $10^\circ$  latitude, tropical and temperate). This result supports Collier et al., (2017) who assessed tropical species *Halodule uninervis* and *Cymodocea serrulata* across multiple tropical locations and found little variation in  $T_{opt}$ . Generally, tropical ocean temperatures are more seasonally stable than temperate waters, where the greater climate variability displayed in temperate regions has been hypothesised to favour increased acclimation potential (Moore et al. 2023). Further, it has been proposed that species with higher thermal tolerances may have a reduced ability to acclimate (Janzen 1967, Gunderson et al. 2015), and therefore, it is possible that tropical seagrass species have ‘traded-off’ their ability to thermally acclimate in order to grow in warmer climates. A greater number of tropical seagrass species and spatial replication is needed to test this theory. Nonetheless, these results are seemingly positive for *H. ovalis* under future climate conditions, where a higher thermal optimum is potentially more advantageous than the ability to acclimate to a warming ocean. Further, these results show for *H. ovalis*, a species with a much larger thermal distribution, there is potential to extrapolate thermal optima across locations, but this is not the case for the temperate seagrass species. However, due to only two locations assessed here for *H. ovalis* and *P. australis* increased spatial replication is warranted to improve understanding of this variability.

## 4.2 Productivity

### 4.2.1 Productivity varies across species life history strategies

Maximum net productivity ( $\text{mg O}_2 \cdot \text{g DW}^{-1} \cdot \text{hr}^{-1}$ ) also varied among species, but unlike  $T_{opt}$ , productivity differed amongst species based on the life history strategy. Smaller colonising/opportunistic species (*Halophila* and *Zostera*) had a two-fold higher net productivity at  $T_{opt}$  compared to the larger persistent species (*Posidonia* and *Amphibolis*), following the same trend found by Lee et al. (2007). The higher net plant productivity for the smaller species may reflect the life history strategy of allocating a high amount of energy into growth and relatively smaller proportion of non-photosynthetic tissues. In contrast the larger species are slow growing and invest more in non-photosynthetic tissues and hence have a lower productivity. Under future ocean warming and MHWs, thermal tolerance is an importer qualifier in the bid for survival to maintain productivity, but the sizeable difference in productivity for the smaller species suggests that if they suffer loss, there is greater potential for a quicker recovery than the larger persistent species if the temperatures remain at or below their thermal optima. Further, there is potential for increased negative implications on ecosystem services (i.e. habitat for fish, carbon storage) in losing large, structurally complex seagrasses compared to the smaller species. This reinforces high priority conservation towards persistent seagrass species, which once lost are difficult or take much longer to recover.

### 4.2.2 Productivity varies across locations and increases with latitudinal gradient

Populations of plants that inhabit thermally different habitats can show considerable differences in their response to temperature, enabling them to function efficiently within their temperature growing range (Yamori et al. 2014). If populations are adapted or acclimated to their local temperature range, then we might expect  $NP_{max}$  to occur at or near the highest temperature they usually grow under (Collier et al. 2011). In contrast to  $T_{opt}$ , all species examined across a latitudinal gradient (*P. sinuosa*, *A. antarctica*, *H. ovalis*) had the highest productivity in the warmest location tested (two-fold increase), except for *P. australis*. Results for *H. ovalis* from this study are consistent with results from Said et al., (2021), also finding an increase for *H. ovalis* in the tropical region compared to the temperate region, and is further

supported by findings for other angiosperms (Berry & Bjorkman 1980). These results are reflective of acclimation or adaptation to the temperature regimes of their respective habitats. Interestingly, *P. australis* was the only species to have a lower productivity at the warm-edge of its location assessed despite having a higher  $T_{opt}$ . This finding for *P. australis* supports the species-generalist trade-off hypothesis for temperate species adapted to colder environments having a greater tolerance to colder temperatures with a lower performance in warmer temperatures (Moore et al. 2023). Of course, this hypothesis does not hold for the other temperate species tested in this study, and therefore other explanations such as past exposure to warming (Somero 2010) from the 2010/11 MHW (Strydom et al. 2020), or limited genetic variation (single hybrid plant spanning 180 km; Edgeloe et al. 2022) could be contributing to the physiological anomaly of this species at this location.

### 4.3 Management recommendations

#### 4.3.1 Management to protect existing habitat

The assessment and approval for coastal developments generally require an evidence-based prediction of potential impacts and benefits from a range of design scenarios. Decisions on the final design are generally informed by a range of criteria including environmental data which also considers cumulative pressures and more recently future climate change. We used the thermal threshold information generated in this study to assess seagrass vulnerability to ocean warming. This vulnerability assessment can be used to inform decisions on management of coastal development.

Thermal optima ( $T_{opt}$ ) denotes temperature for maximum productivity, and therefore temperatures greater than thermal optima will result in negative declines in productivity. We interpret temperatures  $>T_{opt}$  as the temperature threshold to which species would likely be vulnerable to ocean warming or MHWs. It is also important to take into consideration that the thermal tolerance for photosynthesis is higher than that for seagrass growth (See Lee et al. 2007). Therefore, whilst temperatures at  $T_{opt}$  may afford the plants buffering capacity at the physiological scale, under a prolonged MHW event, it is possible that at the plant-scale carbohydrates stores will be reduced and the overall resilience to further stressors compromised. We do not advocate for thermal maxima ( $T_{max}$ ) to be used in a management context, as this is likely to lead to complete mortality. For example photosynthesis-temperature experiments (up to  $T_{max}$ ) undertaken on *P. oceanica* showed no recovery of individuals when they were re-acclimated to ambient conditions following exposure to the maximum temperatures (Rinaldi et al., 2023).

We compare the location and species specific  $T_{opt}$  to three different temperature scenarios: 1. The current summer ambient temperature of that location; 2. The 2010/2011 MHW temperature from that location; and 3. A future summer temperature scenario of an increase in 2.2 °C above current conditions (2.2 °C is based on an average effort to curb emissions globally, RCP scenario 6.0 in 2100; IPCC 2023). A ‘concern’ of vulnerability rating was defined as Low where water temperature of either scenario was more than 2 °C below  $T_{opt}$ , Moderate where water temperature was equal to or near  $T_{opt}$ , or High where the water temperature was above  $T_{opt}$ . At locations and for species with Moderate or High concern we recommend that the cumulative impacts from coastal development and climate change be explicitly considered in the environmental assessment.

#### Low concern

In Table 3 a low concern ranking has been attributed to populations (species/location) where the thermal optima was 2 °C or higher than all scenarios (summer ambient conditions, ocean warming scenario and the 2010/11 MHW event). *Posidonia sinuosa* from Geographe Bay ( $T_{opt}$  30 °C) as well as *H. ovalis* at both locations collected (Coral Bay;  $T_{opt}$  31.5 °C and Perth;  $T_{opt}$  32 °C) can be considered populations of low concern (Table 3). For these populations it is unlikely that they will reach their maximum net productivity under ambient conditions (23-26 °C) and plant productivity will likely increase under the RCP6.0 ocean warming scenario (26-28 °C). When looking at current summer ambient temperatures alone, almost all species and location combinations can be attributed a rating of low concern, except for *Z. nigricaulis* in Perth (colour gradient in Table 2).

Moderate concern ranking has been attributed to populations where thermal optima was equal to or less than 2 °C (0-1.99 °C) below the summer ambient, ocean warming scenario or the 2010/11 MHW event temperatures. The larger persistent genera in Perth, *Posidonia* and *Amphibolis* ( $T_{opt}$  26-27 °C), are of moderate concern to MHWs (Table 3). While this location has currently been designated as moderate concern, it is worth noting that the 2010/11 MHW was only 3 °C warmer than summer ambient conditions and should a MHW of higher intensity impact Perth (+4 °C) waters in the future, then these species would escalate to high concern in Perth. *Posidonia sinuosa* from its warm-edge (Geraldton;  $T_{opt}$  29 °C) where there are isolated patches growing in deeper waters are of moderate concern to MHWs. *Posidonia sinuosa* meadows in Jurien Bay are also of moderate concern to MHWs but is bordering on low concern. Even though the *P. sinuosa* population in Jurien Bay is of moderate concern to MHWs, this population can be used for building resilience into populations of lower thermal resilience e.g. transplanting plants from Jurien Bay to Perth (see Section 4.3.2 below).

### High concern

High concern ranking has been attributed to populations where thermal optima was equal to or fell below the summer ambient, ocean warming scenario or the 2010/11 MHW event. *Z. nigricaulis* in Perth (temperate) and *A. antarctica* in Coral Bay (tropical) are of high concern due to already experiencing conditions above their thermal optima (Table 3). Both of these species/location combinations were found in one isolated patch, and it is likely that ocean warming and MHWs could lead to further decreases in net plant productivity and potentially loss of these populations at these locations. Apart from *Z. nigricaulis*, the overall trend was for temperate species in the sub-tropical and tropical regions to be of highest concern. In the sub-tropical region (Shark Bay), both *P. australis* ( $T_{opt}$  31 °C) and *A. antarctica* ( $T_{opt}$  30 °C) both had their highest thermal optima in this region, and whilst ocean warming may increase plant productivity, MHWs within this region are of high concern. On a more positive note, because these species within Shark Bay have high thermal optima, they are ideal candidates for resilience building in areas of concern with lower thermal optima e.g. transplant adult plants or seedlings from Shark Bay to Perth.

**Table 3.** Concern rating, and cause of concern (ocean warming or marine heatwave) for seagrass species and location sampled. Concern ratings are based on an ocean warming (summer ambient + RCP6.0 2.2 °C) or MHW event (based on 2010/11), being higher or equal to optimum = high concern; <2 °C below optimum = moderate concern; and ≥2 °C + below optimum = low concern. Where populations have higher thermal tolerances than other populations these have been recognised as options for resilience building. Refuge areas are those with high thermal tolerances in cooler regions. Blank squares indicate a species does not grow in a location, and dashed lines indicate the species grows in a location but was not sampled.

Location	Seagrass species						Key
	<i>P. sinuosa</i>	<i>P. australis</i>	<i>A. antarctica</i>	<i>A. griffithii</i>	<i>H. ovalis</i>	<i>Z. nigricaulis</i>	
Coral Bay			HC			LC	
Shark Bay		HC	HC	-	-		
Geraldton	MC	-	-	-	-		
Jurien Bay	MC	-	-	-	-		
Perth	MC	MC	MC	MC	LC	HC	
Geographe Bay	LC	-	-	-	-	-	Refuge

### 4.3.2 Seagrass resilience building opportunities

To date, seagrass science has focused on protection and restoration in a bid to conserve seagrass, and whilst this is important, our thinking needs to extend to consider how we build resilience under climate change where different strategies may be required (e.g. Coleman et al. 2020). There are a range of actions that can be taken to build resilience to future pressures, such as genetic rescue, assisted gene flow and assisted evolution using breeding or biotechnology (e.g. Caruso et al. 2021, Coleman & Bragg 2021) but to our knowledge, none of these have been trialed for seagrasses. This study revealed that for multiple species (*P. australis*, *P. sinuosa*, and *A. antarctica*) there are populations that have a higher thermal tolerance ( $T_{opt}$ ) which could make them ‘better equipped’ to deal with thermal pressures. Even though there was not a clear pattern for higher thermal tolerance at the warmest-edge of species range (*P. australis*, *P. sinuosa*, and *A. antarctica*), for all species there was an adult population within a warmer region which had a higher thermal tolerance (Table 2 **Table 3**). Assuming the differences in  $T_{opt}$  are adaptive, the resilience building strategy of assisted gene flow could be employed where these ‘pre-adapted individuals’ are introduced to areas within the existing distributional range to facilitate adaptation to future conditions. These populations could be targeted as source populations for restoration or assisted migration locations further south, to future-proof these meadows to warming (Pickup et al. 2012, Aitken & Whitlock 2013). This approach could be incorporated into existing restoration programs such as *Seeds for Snapper* or *Operation Posidonia*. Opportunities for this type of resilience building based on the results of this study are identified in Table 3. To be confident that populations will retain these higher thermal optima when translocated into cooler waters further trials are required to test this. Another important consideration is the genetic connectivity between source and translocated populations, which for *P. sinuosa* in this study, is assessed in Whale et al. (2024).

## 5 Conclusion

Overall, we conclude that it is crucial to understand seagrass species thermal tolerances both across species and within species (populations of the same species) to be able to accurately predict and manage for future climate impacts. This understanding has the potential to inform EIA and enable quantitative cumulative impact assessment. Further, thermal performance does not necessarily reflect thermal geography of a seagrass species range. This finding is important from a management perspective when assessing future climate scenarios and using thermal tolerance data within models. Further, this study implies thermal performance data collected for the same species from multiple locations can aid in identifying populations which can be used for thermal resilience building.

## 6 Acknowledgements

We acknowledge the traditional owners on which this research was conducted: Nynggulu (Ningaloo-Coral Bay) the Baiyungu, Thalanyji and Yinigurdira people; Gutharraguda (Shark Bay) the Malgana people; Jambinu (Geraldton) the Yamatji People; Derbal Nara (Cockburn Sound) and Jurien Bay the Whadjuk people; and Quedjinup (Geographe Bay) the Wadandi People. We would also thank Matthew Adams for providing script to extract thermal tolerance parameters, the Department of Biodiversity, Conservation and Attractions (DBCA) for vessel support, and the Minderoo Foundation for support and funding to conduct research in Coral Bay.

## 7 References

- Adams MP, Collier CJ, Uthicke S, Ow YX, Langlois L, O'Brien KR (2017) Model fit versus biological relevance: Evaluating photosynthesis-temperature models for three tropical seagrass species. *Sci Rep* 7:39930.
- Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. *Annu Rev Ecol Evol Syst* 44:367–388.
- Araujo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modelling. *Ecology* 93:1527–1539.
- Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *8:343–351*.
- Baird ME, Adams MP, Babcock RC, Oubelkheir K, Mongin M, Wild-Allen KA, Skerratt J, Robson BJ, Petrou K, Ralph PJ, O'Brien KR, Carter AB, Jarvis JC, Rasheed MA (2016) A biophysical representation of seagrass growth for application in a complex shallow-water biogeochemical model. *Ecol Modell* 325:13–27.
- Bennett S, Alcoverro T, Kletou D, Antoniou C, Boada J, Cucala L, Jorda G, Kleitou P, Roca G, Santanagarcon J, Savva I, Verg A (2022a) Resilience of seagrass populations to thermal stress does not reflect regional differences in ocean climate. 1657–1666.
- Bennett S, Duarte CM, Marbà N, Wernberg T (2019) Integrating within-species variation in thermal physiology into climate change ecology.
- Bennett S, Vaquer-sunyer R, Jordá G, Forteza M, Roca G, Marbà N, Donelson JM (2022b) Thermal Performance of Seaweeds and Seagrasses Across a Regional Climate Gradient. 9:1–11.
- Berry J, Bjorkman O (1980) Photosynthetic Response and Adaptation to Temperature in Higher Plants. *Annu Rev Plant Physiol* 31:491–543.
- Brodersen KE, Hammer KJ, Schrammeyer V, Floytrup A, Rasheed MA, Ralph PJ, Kühl M, Pedersen O (2017) Sediment resuspension and deposition on seagrass leaves impedes internal plant aeration and promotes phytotoxic H<sub>2</sub>S intrusion. *Front Plant Sci* 8.
- Bulthuis DA (1987) Effects of Temperature on Photosynthesis and Growth of Seagrass. *Aquat Bot* 27:27–40.
- Caruso C, Hughes K, Drury C (2021) Selecting Heat-Tolerant Corals for Proactive Reef Restoration. 8.
- Coleman MA, Bragg JG (2021) A decision framework for evidence-based climate adaptation interventions. *Glob Chang Biol* 27:472–474.
- Coleman MA, Wood G, Filbee-Dexter K, Minne AJP, Goold HD, Vergés A, Marzinelli EM, Steinberg PD, Wernberg T (2020) Restore or Redefine: Future Trajectories for Restoration. *Front Mar Sci* 7:1–12.
- Collier CJ, Ow YX, Langlois L, Uthicke S, Johansson CL, O'Brien KR, Hrebien V, Adams MP (2017) Optimum temperatures for net primary productivity of three tropical seagrass species. *Front Plant Sci* 8:1–14.
- Collier CJ, Uthicke S, Waycott M (2011) Thermal tolerance of two seagrass species at contrasting light levels: Implications for future distribution in the Great Barrier Reef. *Limnol Oceanogr* 56:2200–2210.
- Collier CJ, Waycott M (2014) Temperature extremes reduce seagrass growth and induce mortality. *Mar Pollut Bull* 83:483–490.
- Diaz-Almela E, Marbà N, Duarte CM (2007) Consequences of Mediterranean warming events in seagrass

(*Posidonia oceanica*) flowering records. *Glob Chang Biol* 13:224–235.

- Donelson JM, Sunday JM, Figueira WF, Gaitán-Espitia JD, Hobday AJ, Johnson CR, Leis JM, Ling SD, Marshall D, Pandolfi JM, Pecl G, Rodgers GG, Booth DJ, Munday PL (2019) Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. *Philos Trans R Soc B Biol Sci* 374.
- Dunic JC, Brown CJ, Connolly RM, Turschwell MP, Côté IM (2021) Long term declines and recovery of meadow area across the world ' s seagrass bioregions. 4096–4109.
- Edgeloe JM, Severn-Ellis AA, Bayer PE, Mehravi S, Breed MF, Krauss SL, Batley J, Kendrick GA, Sinclair EA (2022) Extensive polyploid clonality was a successful strategy for seagrass to expand into a newly submerged environment. *Proc R Soc B Biol Sci* 289.
- Feeley K, Martinez-villa J, Perez T, Duque AS (2020) The Thermal Tolerances , Distributions , and Performances of Tropical Montane Tree Species. 3:1–11.
- Foden WB, Young BE, Stein BA, Carr JA, Akçakaya HR, Thomas CD (2019) Climate change vulnerability assessment of species. 1–36.
- Fraser MW, a. Kendrick G, Statton J, Hovey RK, Zavala-Perez A, Walker DI (2014) Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. *J Ecol* 102:1528–1536.
- Giraldo-Ospina A, Kendrick GA, Hovey RK (2020) Depth moderates loss of marine foundation species after an extreme marine heatwave: could deep temperate reefs act as a refuge? *Proc R Soc B Biol Sci* 287.
- Gunderson AR, Stillman JH, Gunderson AR (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming.
- Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, Hara CO, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world ' s ocean. 1–8.
- Hobday AJ, Pecl GT (2014) Identification of global marine hotspots : sentinels for change and vanguards for adaptation action. 415–425.
- IPCC (2023) : : Summary for Policymakers. In: *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.
- Janzen DH (1967) WHY MOUNTAIN PASSES ARE HIGHER IN THE TROPICS. 101:233–249.
- John BY, Nd AR, Biology P, Box PO, Birmingham B (1988) Temperature and algal growth.
- Jordà G, Marbà N, Duarte CM (2012) Mediterranean seagrass vulnerable to regional climate warming. *Nat Clim Chang* 2:821–824.
- Kajtar JB, Holbrook NJ, Hernaman V (2021) A catalogue of marine heatwave metrics and trends for the Australian region. *J South Hemisph Earth Syst Sci* 71:284–302.
- Kendrick GA, Aylward MJ, Hegge BJ, Cambridge ML, Hillman K, Wyllie A, Lord DA (2002) Changes in seagrass coverage in Cockburn Sound, Western Australia between 1967 and 1999. *Aquat Bot* 73:75–87.
- Kilminster K, McMahon K, Waycott M, a. Kendrick G, Scanes P, McKenzie L, O'Brien KR, Lyons M, Ferguson A, Maxwell P, Glasby T, Udy J (2015) Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Sci Total Environ*.
- Kong E, Ow YX, Lai S, Yaakub SM, Todd P (2020) Effects of shading on seagrass morphology and thermal optimal of productivity. *Mar Freshw Res* 71:913–921.

- Lee KS, Park SR, Kim YK (2007) Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *J Exp Mar Bio Ecol* 350:144–175.
- Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs : 1871 – 2017. *Sci Rep*:1–8.
- Marbà N, Duarte CM (2010) Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Glob Chang Biol* 16:2366–2375.
- Moore NA, Morales-Castilla I, Hargreaves AL, Olalla-Tárraga MÁ, Villalobos F, Calosi P, Clusella-Trullas S, Rubalcaba JG, Algar AC, Martínez B, Rodríguez L, Gravel S, Bennett JM, Vega GC, Rahbek C, Araújo MB, Bernhardt JR, Sunday JM (2023) Temperate species underfill their tropical thermal potentials on land. *Nat Ecol Evol* 7:1993–2003.
- O2 Marine (2021) Port Geographe Marina Monitoring Program (2016 – 2021). Close-out Report.
- Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander L V, Benthuyssen JA, Feng M, Gupta A Sen, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Straub SC, Wernberg T (2018) Longer and more frequent marine heatwaves over the past century. *Nat Commun* 9:1–12.
- Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, a. Randall Hughes, a. Kendrick G, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A Global Crisis for Seagrass Ecosystems. *Bioscience* 56:987.
- Pedersen O, Binzer T, Borum J (2004) Sulphide intrusion in eelgrass (*Zostera marina* L.). *Plant, Cell Environ* 27:595–602.
- Pickup M, Field DL, Rowell DM, Young AG (2012) Predicting local adaptation in fragmented plant populations: Implications for restoration genetics. *Evol Appl* 5:913–924.
- Quigley KM (2024) Breeding and Selecting Corals Resilient to Global Warming. 1–24.
- Ralph PJ, Burchett MD (1995) Photosynthetic responses of the seagrass *Halophila ovalis* (R. Br.) Hook. f. to high irradiance stress, using chlorophyll a fluorescence. *Aquat Bot* 51:55–66.
- Rinaldi A, Martinez M, Badalamenti F, Anna GD, Mirto S, Mar L, Procaccini G, Montalto V (2023) The ontogeny-specific thermal sensitivity of the seagrass *Posidonia oceanica*. 1–11.
- Said NE, McMahon K, Lavery PS (2021) Accounting for the influence of temperature and location when predicting seagrass (*Halophila ovalis*) photosynthetic performance. *Estuar Coast Shelf Sci* 257:107414.
- Shah AA, Chris Funk W, Ghalambor CK (2017) Thermal acclimation ability varies in temperate and tropical aquatic insects from different elevations. *Integr Comp Biol* 57:977–987.
- Sharkey TD, Schrader SM (2006) CHAPTER 4 HIGH TEMPERATURE STRESS. 101–129.
- Somero GN (2010) The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *J Exp Biol* 213:912–920.
- Strydom S, Murray K, Wilson S, Huntley B, Rule M, Heithaus M, Bessey C, Kendrick GA, Burkholder D, Fraser MW, Zdunic K (2020) Too hot to handle: Unprecedented seagrass death driven by marine heatwave in a World Heritage Area. *Glob Chang Biol* 26:3525–3538.
- Trisos CH, Merow C, Pigot AL (2020) The projected timing of abrupt ecological disruption from climate change. *Nature* 580:496–501.
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, a Randall Hughes, a Kendrick G, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci U S A*

106:12377–12381.

Whale JW, Webster CL, Said NS, Field DL, Sinclair EA, McMahon KM (2024) Population Genomics in *Posidonia sinuosa*. Prepared for the WAMSI Westport Marine Science Program. Western Australian Marine Science Institution, Perth, Western Australia.

Wiens JJ (2016) Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLoS Biol* 14:1–18.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell H V., Damschen EI, Jonathan Davies T, Grytnes JA, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol Lett* 13:1310–1324.

Yamori W, Hikosaka K, Way DA (2014) Temperature response of photosynthesis in C3, C4, and CAM plants: Temperature acclimation and temperature adaptation. *Photosynth Res* 119:101–117.

Yan W, Hunt LA (1999) An Equation for Modelling the Temperature Response of Plants using only the Cardinal Temperatures. *Ann Bot* 84:607–614.

## 8 Appendices

### 8.1 Appendix 1

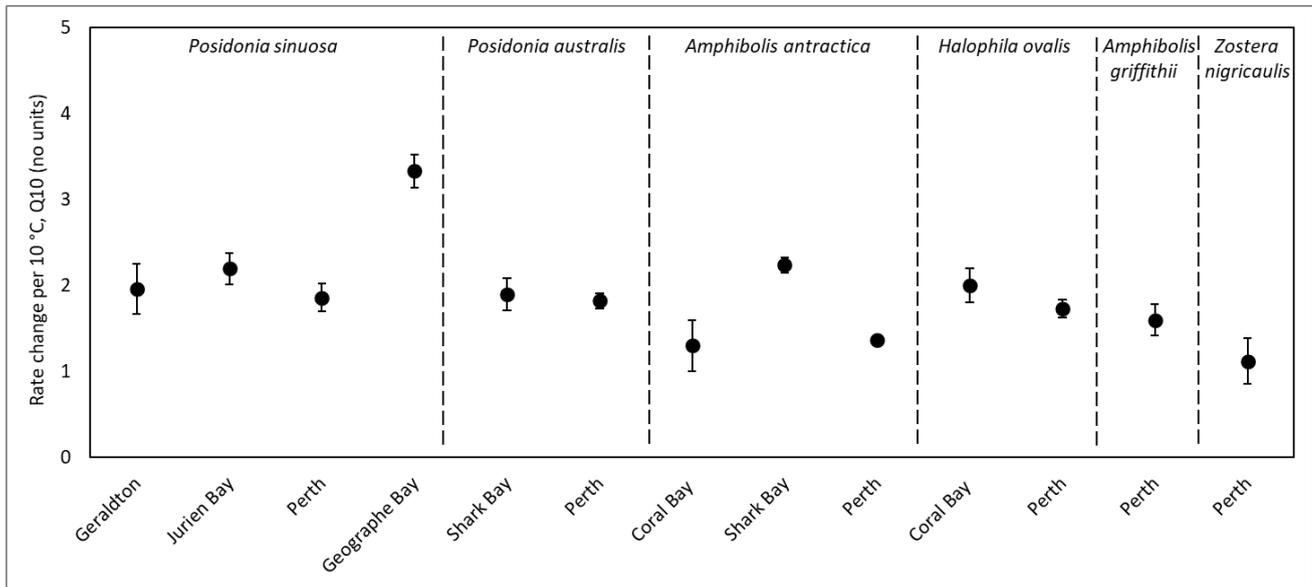


Figure A1. The rate of metabolic change (photosynthesis Q<sub>10</sub>) below the optimum temperature for seagrass species across and within locations.

Submitted as draft	13/2/2024
Review completed	29/5/2024
Submitted as revised draft	5/6/2024
Approved by Science Program Leadership Team	11/7/2024
Approved by WAMSI CEO	15/10/2024
Final report	



WESTERN AUSTRALIAN  
**MARINE SCIENCE  
INSTITUTION**