2023

Impact of marine heatwaves on the physiological health of two fucoid species

Burnet, L.

The Plymouth Student Scientist
University of Plymouth

Impact of marine heatwaves on the physiological health of
two fucoid species

Lily Burnet

Project Advisor: Dr Simon Ingram, School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA

Abstract

Marine Heatwaves (MHWs) are periods of high-water temperature that have become an increasingly significant threat to marine ecosystem biodiversity in recent decades with rising anthropogenic carbon driving greater severity of MHW events. The two intertidal fucoid species, *Fucus serratus* and *Fucus vesiculosus*, are keystone primary producers supporting an extensive biodiverse community of associated flora and fauna. As intertidal species, fucoids are adapted to cope with high atmospheric temperatures during exposure at low tide, however, are prone to changes in abundance, distribution, and life cycles during MHW events. Changes to fucoid communities resulting in reduced primary production and habitat biomass will have knock-on impacts to higher trophic levels. This study aims to identify the impact of MHWs of varying intensity on the eco-physiology of *F. serratus* and *F. vesiculosus* in the South-West (SW) of the United Kingdom (UK). The objectives were to conduct MHW experiments on *F. serratus* and *F. vesiculosus* taken from Firestone Bay, Plymouth, under two MHW intensities chosen based on realistic MHW temperatures for the region. These intensities were the control (14°C), as ambient seawater temperature for the region, a moderate MHW treatment (18°C) and an extreme MHW treatment (22°C), over a duration of one month. Results showed healthy Fv/Fm values and significant growth for both species throughout the experiment period. Overall, no clear evidence of physiological stress induced by the MHW treatments was found, showing a high tolerance to temperature over a one-month duration. The findings from this study contribute to the growing understanding of how MHW events have the capacity to impact key marine species in an intertidal environment, building knowledge on a topic with still limited scientific understanding.

Keywords: Marine Heatwaves (MHWs), *Fucus serratus*, *Fucus vesiculosus,* Climate Change, Temperature, Latitudinal distribution

Introduction

MHW events are anomalously high periods of sea surface temperature (SST), above the 90th percentile of a 30-year baseline which persist for five days or longer (Oliver et al, 2018; Hobday et al, 2016). The physical drivers of MHWs are driven by a combination of oceanic and atmospheric processes including heat transport changes in water, changes in atmospheric conditions and alterations in air-sea circulation, for example during El Nino/Nina events (Holbrook et al, 2019; Sen Gupta et al, 2020; Eric et al, 2020). The frequency, duration, and intensity of MHW events have increased over the past few decades and are projected to continue to increase under the acceleration of climate change (Eric et al, 2020; Frolicher et al, 2018). Climate change has already been identified as the key driver behind 87% of MHWs over the past four decades, with a prediction for this number to rise to 100% as global temperatures increase (Frolicher et al, 2018). The increasing severity and frequency of MHWs will result in detrimental ecological consequences as species' thermal thresholds are exceeded. Therefore, understanding the extent of these effects is an important goal for climate change ecologists in coming years (Smale et al, 2019; Frolicher et al, 2018).

To date, current MHW research has focussed on coral bleaching and associated phase shifts and ecosystem collapses post MHW, particularly on the Great Barrier Reef with major MHW bleaching events in 2016 bleaching 91% of coral communities (Stuart-Smith et al, 2018). Other habitat formers, such as kelp, have also been documented to be detrimentally impacted by MHWs resulting in severe impacts to the local ecosystem. An example of this was observed in local extinctions of kelp forests on the western coast of Australia where kelp devastation gave way to a phase shift from kelp forest to turf algae (Wernberg, 2021). Similarly, impacts also span to seagrass bed damage and decreased primary production with knock-on impacts to higher trophic levels, alongside societal impacts on fishing and trade (Laufkotter et al, 2020; Oliver et al, 2018). The impact of MHWs on other key seaweed species is currently largely unknown, which creates difficulty when anticipating and mitigating MHW impacts to these species in the future (Piñeiro-Corbeira et al, 2018; Straub et al, 2019).

Geographical distribution of seaweed species is largely governed by temperature boundaries (Smith et al, 2023; Straub et al, 2019; Breeman, 1988). The latitudinal range of each species begins at the cool trailing edge where assemblages live at their coolest possible temperatures in the Northern latitudes down to their thermal heat tolerance limit in Southern latitudes towards the equator (Smith et al, 2023; Jueterbock et al, 2013b). The area within this region where temperatures are at their optimum for ecological function and performance is referred to as the range centre (Smith et al, 2023). Efficiency of ecological function tends to decrease with increasing distance from the range centre with heat/cool temperature stress induced closer to the range margins (Smith et al, 2023). At the warm trailing edge of their distribution, assemblages are most vulnerable to MHW warming events on top of warmer ambient temperatures (Smith et al, 2023; Graiff et al, 2015). At the cool trailing edge however, MHWs could have a positive impact on increasing ecological function and performance whilst alleviating stress from sub optimal temperatures (Smith et al, 2023). At the range centre, assemblages have a greater tolerance to temperature than the warm trailing edge as ambient temperatures are lower and, therefore, MHW temperatures of a couple of degrees above the ambient temperature

could have a positive impact on assemblages with enhanced physiological performance (Smith et al, 2023).

The intertidal fucoids, *Fucus serratus* and *Fucus vesiculosus,* are important ecosystem engineers in temperate coastal intertidal environments providing a habitat for the diverse associated community (Jackson, 2008; Piñeiro-Corbeira et al, 2018). Their global distribution and life cycle (early life-history, reproductive cycle and development) is largely controlled by temperature, making them susceptible and responsive to MHW temperatures (Bartsch et al, 2013; Straub et al, 2019; Andrews et al, 2014; Breeman, 1988). Global distributions of *F. serratus* and *F. vesiculosus* are similar latitudinally in range from the Arctic, at their cool trailing edge, down to the Atlantic coast of Portugal, at their warm trailing edge (Jackson, 2008; White, 2008; Jueterbock et al, 2013a) (Figure.1). UK assemblages fall within the mid latitudes of distribution, making thermal conditions near the optimum for the species (Atkinson et al, 2020). In previous studies, the relationship between fucoids and temperature showed increasing temperature as having a positive effect on photosynthetic performance of cool trailing edge *F. vesiculosus* from the Baltic Sea and UK *F. serratus* up to a maximum threshold level (Graiff et al, 2015; Atkinson et al; 2020). Beyond this threshold temperature, which differed depending on latitudinal location of the assemblage and species, rapid decrease in rate of photosynthesis and health was observed as physiological stress was induced (Graiff et al, 2015; Piñeiro-Corbeira et al, 2018).
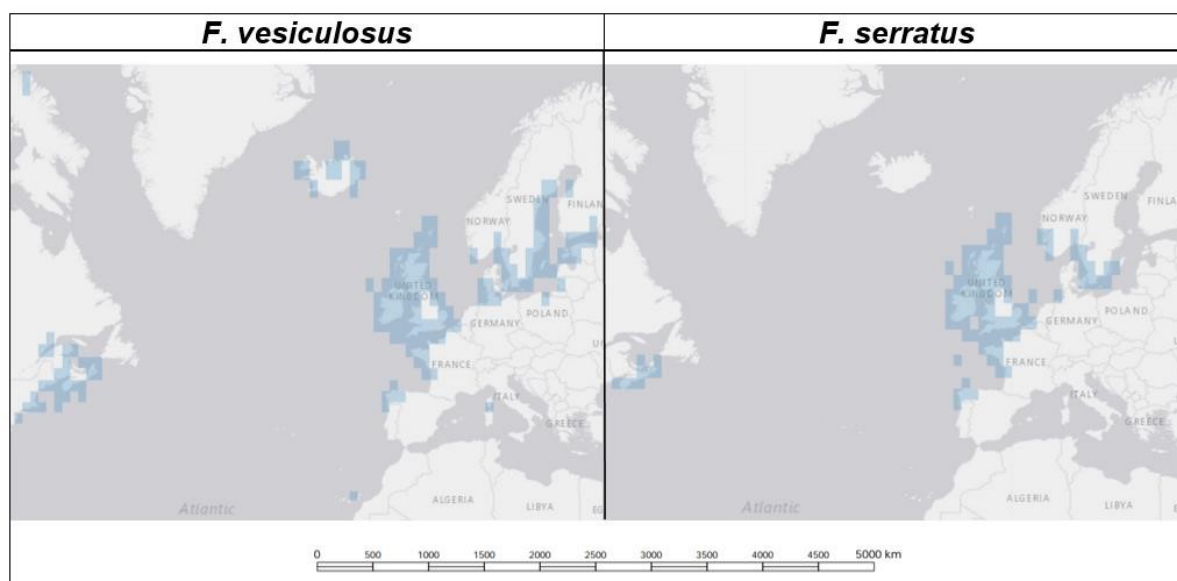

Figure 1: Blue shading shows global distribution of F. vesiculosus (left) and F. serratus (right) Distribution data supplied by the Ocean Biodiversity Information System (OBIS) accessed using the Marine Biological Association, UK, MarLIN website. (www.iobis.org Accessed on 15/10/2022)(https://www.marlin.ac.uk/species/detail/1326 Accessed on 15/10/2022).

In terms of vertical distribution along the shore, *F. serratus* is found on the low shore and *F. vesiculosus* occupies the mid shore (Jackson, 2008; White, 2008). Within the tidal cycle, both species are exposed to atmospheric temperatures at low tides, especially F. vesiculosus which is exposed for longer durations particularly during springs (Graiff et al, 2015; Somero, 2010). Fucoid species have adapted to

exposure to high atmospheric temperatures with high heat tolerances, however, this ability to tolerate high atmospheric temperature depends on the latitudinal distribution of the species (Smith et al, 2023; Breeman, 1988; Jueterbock et al, 2013b; Straub et al, 2019). High atmospheric temperatures at low tide push fucoid species living at the warm trailing edge towards their heat limit, making them highly susceptible to stress during periods of warmer than average sea temperatures (Straub et al, 2019; Smith et al 2023). However, at the cool trailing edge, warmer sea temperatures can alleviate cool stress from atmospheric temperatures and have a positive impact on ecological performance (Straub et al, 2019). In general, physiological stress of fucoid species due to MHWs is typically observed over long durations and periods of extreme warming (Weitzman et al, 2021; Saha et al, 2020).

In this investigation, the influence of two MHW temperature treatments (18°C moderate MHW and 22°C extreme MHW) and one control treatment (14°C) were investigated in temperature regulated seawater tanks over a one-month period using samples of *F. serratus* and *F. vesiculosus*. Changes during the experiment to sample biomass (percentage change in growth from the MHW start), appearance (bleaching) and physiological stress (as a value of Fv/Fm) were monitored as the response variables. The aim of this study was to assess the impact of moderate and extreme MHW temperature treatments on the physiological health of the two fucoid species. The objectives of the investigation were to; i) set up and run two MHW treatments at 18°C and 22°C and one control at 14°C, reflecting moderate and extreme MHW conditions in SW UK waters as predicted under current climate change scenarios by Hobday et al (2018) and greenhouse gas emission scenarios (Oliver et al, 2019) against the ambient water temperature for the autumn season, ii) monitor physiological change to samples (photosynthetic capability, bleaching and percentage change in biomass) over a one-month period, iii) statistically analyse and compare sample responses to the two main effects of the temperature treatments and key time points alongside the interaction between the two factors, iv) Analyse and draw conclusions from the results on the influence of MHW temperatures on the physiological health, photosynthetic capability, and growth rates of *F. serratus* and *F. vesiculosus*.

Methodology

Sample Collection

Samples of *F. serratus* and *F. vesiculosus* were collected from Firestone Bay, Plymouth, at low tide on the 14th of October 2022. Thirty non-reproductive apical tips (15cm in length) were cut from different individual plants on the shore for each species and transported back to the laboratory to be kept in seawater tanks in cool, dark conditions. The samples remained in tanks for a four-day acclimation period at 14 °C, before apical were cut to an equal length of 10cm and assigned to a treatment temperature.

MHW Experiment Setup

Each individual apical tip was placed into independent 2L seawater tanks and individually aerated using air stones. These 2L tanks were placed into 64L water baths, eight 2L tanks in each of the six 64L baths, which were used to create the three experiment treatment temperatures. Light was provided to the baths through LED lighting tiles (AquaRay), under a photosynthetic flux density of ~120µmol m-2 s-1 on a 12:12 light-dark regime. To prevent nutrient limitation, the water in the 2L

tanks was changed every three days throughout the experiment. Daily checks on salinity and temperature ensured treatments remained within ± 0.5 °C of the desired temperature and salinity between 33-35ppt.

After the four-day sample acclimation period at 14°C, water bath temperatures were increased by 1°C per day until the desired treatment temperature was reached (18°C Moderate and 22°C Extreme), the MHW temperature was maintained for 28 days. At the end of the MHW period, temperatures were then lowered at a rate of 1°C per day until the control temperature of 14°C, after which the recovery period at 14°C began for five days. Final measurements for the experiment were taken at the end of this recovery period.

MHW temperature treatments were chosen from Representative Concentration Pathway (RCP) emission scenarios for greenhouse gas emissions by 2100 based on the CMIP5 global climate model projections (Oliver et al, 2019). RCP8.5 describes a high emission scenario, set to be the case if significant change is not made to reduce greenhouse gas emissions, and RCP4.5 describes a lower emissions scenario (Alexander et al, 2018; Oliver et al, 2019). These scenarios significantly impact the intensity of future MHW events with RCP8.5 set to double the frequency of extreme MHW days compared to RCP4.5 (Oliver et al, 2019). The moderate MHW treatment represents RCP4.5 scenario at a 4°C above the seasonal average, and the extreme MHW represents RCP8.5 as a future extreme increase of 8°C above the seasonal average. Classifications of moderate and extreme MHWs were also set by Hobday et al (2018), in which four categories of MHW extremity were determined based off the extent of warming above the local average temperatures. These categories are based on the percentile above the 90th percentile threshold used to categorise MHWs in the definition set by Hobday et al (Hobday et al, 2016; Hobday et al, 2018). Moderate MHWs were determined as 1-2 times the local difference in temperature and extreme MHWs as >4 times (Hobday et al, 2018).

Response Variables
The experiment response variables were the following: 1. Growth (% increase in biomass), 2. Physiological stress (maximum quantum yield Fv/Fm) and 3. Bleaching (semi quantitative index). Measurements used in the statistical analysis and results were collected at four experiment timepoints: the Acclimatisation period at the experiment start, the MHW start, MHW end and recovery end.

1. *% Change in Biomass* - Change in biomass to indicate sample growth was measured using the wet weight of each sample and calculating biomass change in relation to its initial mass at the MHW start time point using the following equation:

$$\% \ \Delta \ in \ biomass = \frac{(current \ mass - initial \ mass)}{initial \ mass} \ X \ 100$$

2. *Photosynthetic Capability (Fv/Fm)-* To identify changes in photosynthetic capability of the samples, the quantum efficiency of photosystem II was

measured using a Pocket PEA chlorophyll fluorimeter recording values as
Fv/Fm. Fv/Fm values are used as an indicator of physiological stress in
macroalgae, Fv is the photochemical quenching and Fm is the total fluorescence
of PSII when the reactions centres are closed (Jueterbock et al, 2013a; Atkinson
et al, 2020). The value shows the ratio between the two with a healthy value
considered to be between 0.6-0.8 Fv/Fm and stress identified as a value <0.6
(Jueterbock et al, 2013a). To test for physiological stress, clips were placed on
the longest point of each sample to block out light for ten minutes, causing the
oxidation of PSII in the area under the clip without the influence of light. After ten
minutes, the PEA meter attached to the clip sends an LED beam of 3,500 molm-
2s-1 through the sample to generate an Fv/Fm value.

3. *Bleaching* – Visible degradation and bleaching of the samples were recorded
using a semi-quantitate scale of 0-5 from no change (0%) to major bleaching
(100%). Observations included discoloration/bleaching, sections of the sample
broken off and loss of rigidity.

Table 1: Semi-quantitative scale from 0 – 5 to determine the severity of bleaching and
degradation of *F. serratus* and *F. vesiculosus* at the 18°C and 22°C MHW temperatures and
the control.

0	1	2	3	4	5
No change	Minor bleaching	Clear bleaching	Significant bleaching	Bleaching and clear degradation	Major bleaching and degradation
0%	0-10%	10-30%	30-60%	60-90%	90-100%

MHW Data Collection
Starting measurements for the experiment of biomass and Fv/Fm were taken on the
18th of October 2022. The temperature of the 18°C and 22°C baths were increased
from the 14°C control temperature by 1°C each day until the MHW temperature
treatment was reached for each. Once at the MHW temperature, the MHW time
period began, and response variable measurements were taken for each sample
twice a week for a one-month period. After the MHW treatment period was complete,
the 18°C and 22°C samples decreased in temperature by one degree a day until the
14°C control temperature was resumed. A recovery period at 14°C for five days was
the final phase of the experiment with response measurements taken at the start and
the end of this period. During the experiments there were four significant time points;
the MHW start, the MHW end, the recovery start, and the recovery end. The data
used in the statistical analysis and results was taken from these four experiment
timepoints.

Statistical Analysis
Variability in the response variables for each species was analysed with two-way
repeated measures Analysis of Variance using the anova_test function in the R
studio "rstatix". A Shapiro Wilks test was conducted first to test the normality of the
results. Tests consisted of two factors both with three levels, these were: Treatment
(14°C control, 18°C moderate and 22°C extreme) and Time point (MHW Start, MHW

End and Recovery End). Where significance was found (p < 0.05) in these results, *post hoc* analysis was conducted to identify where it lay in the data.

Results

Percentage Change in Biomass
For *F. serratus*, significant difference was found between the Time point x Treatment factors (Table.2). Treatments were similar at the MHW start, however were significantly different by the MHW end. Here, the control had an average biomass of 177% ± 84% which was significantly higher than the extreme (68% ± 75%) (*post hoc*, p = 0.035), and significantly higher than the moderate (73% ± 31%) (*post hoc*, p = 0.021). By the recovery end, there was no significant difference between treatments. Overall percentage biomass increase was greatest in the control, (155% ± 69%), followed by the moderate (142% ± 63%*)* and finally the extreme (86% ± 72%)(Figure.2)*.*

For *F. vesiculosus*, no significance was found between the Time point x Treatment factors, however there was a significant main effect of the Time point factor (Table.2). Percentage change in biomass was significantly different at all three time points throughout the experiment period: MHW start to MHW end (*post hoc*, p = <0.001), MHW end and recovery end (*post hoc*, p = 0.005), and the MHW start to recovery end (*post hoc*, p = <0.001). By the recovery end, the moderate showed the greatest increase (190% ± 58%), then the control (169% ± 41%) and lowest in the extreme (115% ± 46%) (Figure.2).

Table 2: Two-way repeated ANOVA test results for *F. serratus* and *F. vesiculosus* % change in biomass response to the two main experiment factors: Treatment (control, moderate and extreme MHW temperatures) and Timepoint (MHW start, MHW end, recovery end). The Time point x Treatment shows interaction between the two main effect factors. Significance indicated as p<0.05, significant results shown in bold.

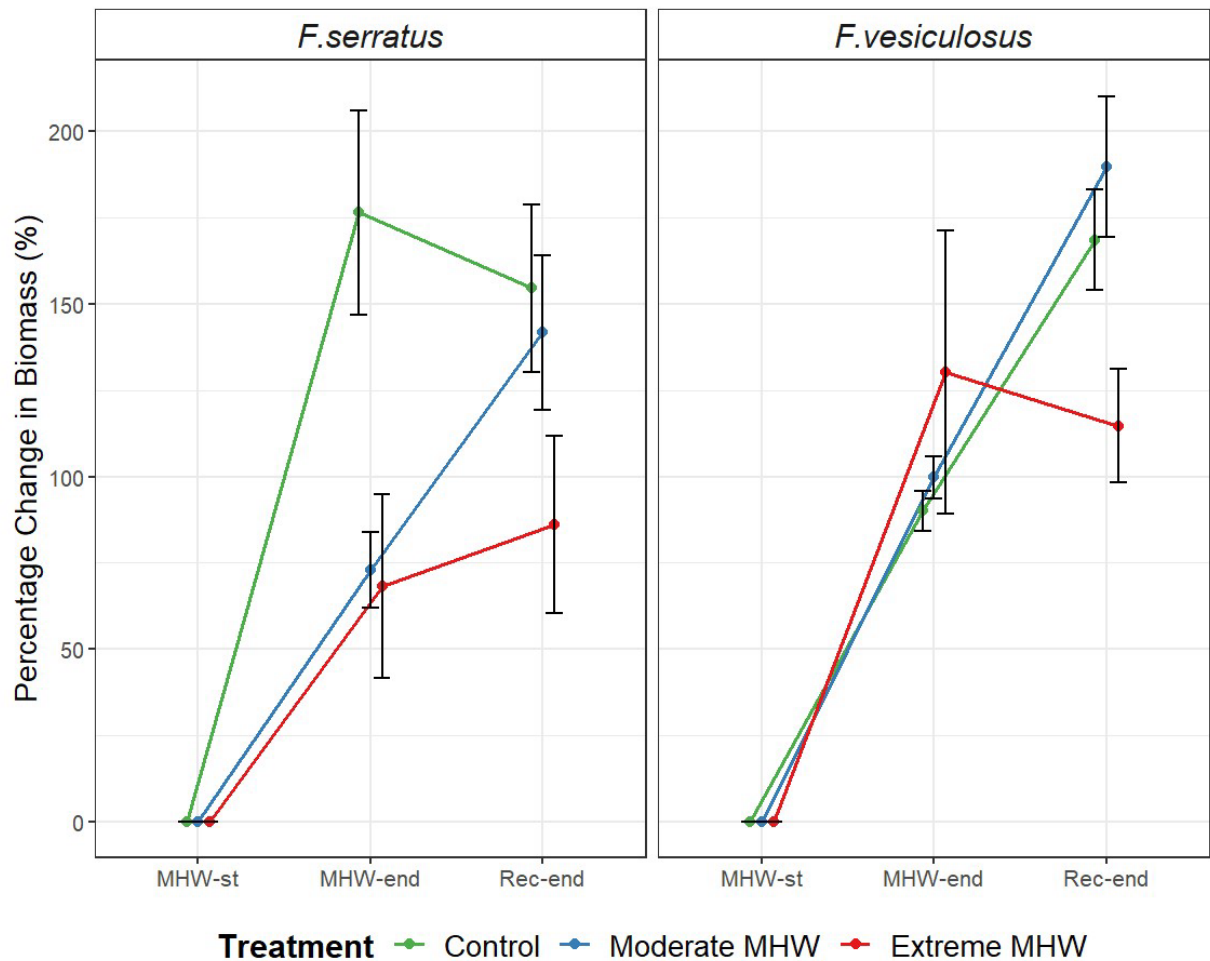|		F. serratus		F. vesiculosus	
	Df	*F*	*P*	*F*	*p*
Time point	2	85.523	<0.001	89.810	<0.001
Treatment	2	3.244	0.070	0.708	0.443
Time point x Treatment	5	4.830	0.004	3.524	0.080

Figure 2: Percentage change in biomass calculated from the MHW start biomass for the *F. serratus* and *F. vesiculosus* samples at the two MHW treatments (Moderate 18°C MHW and extreme 22°C MHW) and control treatment (14°C) over the key experiment time point (MHW start, MHW end and the Recovery end). Error bars show the standard deviation within the results for the eight samples at each treatment temperature.

Fv/Fm

F. serratus showed a significant difference in the Time point x Treatment factors (Table.3). At the MHW start, there was no statistical significance between the three treatments, however, by the MHW end and recovery end there was statistical significance. At the MHW end, this significance was found between the control (0.65 ± 0.08 Fv/Fm) which was significantly lower than the moderate (0.75 ± 0.02 Fv/Fm) (*post hoc*, p = 0.015), and between the extreme (0.70 ± 0.02 Fv/Fm) which was significantly lower than the moderate (*post hoc*, p = 0.002). At the recovery end, the control (0.59 ± 0.08 Fv/Fm) was significantly lower than the moderate (0.71 ± 0.04 Fv/Fm) (*post hoc*, p = 0.007). The greatest decrease between the acclimatisation and recovery end was in the control (0.75 ± 0.01 Fv/Fm to 0.59 ± 0.08), followed by the extreme (0.74 ± 0.02 Fv/Fm to 0.66 ± 0.04 Fv/Fm), and the moderate (0.74 ± 0.01 Fv/Fm to 0.71 ± 0.04 Fv/Fm) (Figure.3).

F. vesiculosus showed no significant difference in the Time point x Treatment factors, however, there was significance in the Treatment and Time point main effects

(Table.3). For the treatment main effect, significance was identified between all three treatments: the control and extreme (*post hoc*, p = 0.004), the control and moderate (*post hoc*, p = 0.024), and the extreme and moderate (*post hoc*, p = <0.001). In the Time point main effect, significance was also identified between all three time points:

MHW start to MHW end (*post hoc*, p = 0.018), MHW end to recovery end (*post hoc*, p = 0.037), and MHW start to recovery end (*post hoc*, p = <0.001). Between the acclimatisation and recovery end, the extreme treatment decreased the most (0.72 ± 0.02 Fv/Fm to 0.68±0.03 Fv/Fm), then the control (0.74 ± 0.02 Fv/Fm to 0.69 ± 0.03 Fv/Fm), and the least in the moderate (0.73 ± 0.02 Fv/Fm to 0.71 ± 0.03 Fv/Fm) (Figure.3).

Table 3: Two-way repeated ANOVA test results for *F. serratus* and *F. vesiculosus* Fv/Fm response to the two main experiment factors: Treatment (control, moderate and extreme MHW temperatures) and Timepoint (MHW start, MHW end, recovery end). The Time point x Treatment shows interaction between the two main effect factors. Significance indicated as p<0.05, significant results shown in bold.

		F. serratus		*F. vesiculosus*	
	Df	*F*	*P*	*F*	*P*
Time point	*2*	*30.819*	*<0.001*	*17.113*	*<0.001*
Treatment	*2*	*12.245*	*<0.001*	*13.914*	*<0.001*
Time point x Treatment	*5*	*4.850*	*0.021*	*2.223*	*0.092*

Bleaching
For *F. serratus*, no significantly different interaction was found between the Time point x Treatment factors, however, significance was found in the Time point main effect (Table.4). Here, there was significant increase between the MHW start and MHW end (*post hoc*, p = 0.035), and between the MHW start and recovery end (*post hoc*, p = 0.021). Between the MHW start and recovery end, greatest bleaching increase was observed in the extreme (0.12 ± 0.35 to 0.38 ± 1.06), followed by the moderate (0.25 ± 0.46 to 1.25 ± 0.89), then the control (0.13 ± 0.35 to 0.38 ± 1.06) (Figure.4).

For *F. vesiculosus*, there was also no significant difference in the Time point x Treatment factor, but there was significance in the Time point main effect (Table.4). Significant increase in bleaching was identified between all timepoints throughout the experiment period: MHW start to MHW end (*post hoc*, p = 0.005), MHW end to recovery end (*post hoc*, p = 0.017), and the MHW start to recovery end (*post hoc*, p = <0.001). Between the MHW start and recovery end, the control showed the greatest increase in bleaching (0.13 ± 0.35 to 1.38 ± 0.74), followed by the extreme (0.38 ± 0.52 to 1.25 ± 0.89), then the moderate (0.13 ± 0.35 to 1.25 ± 0.89) (Figure.4).
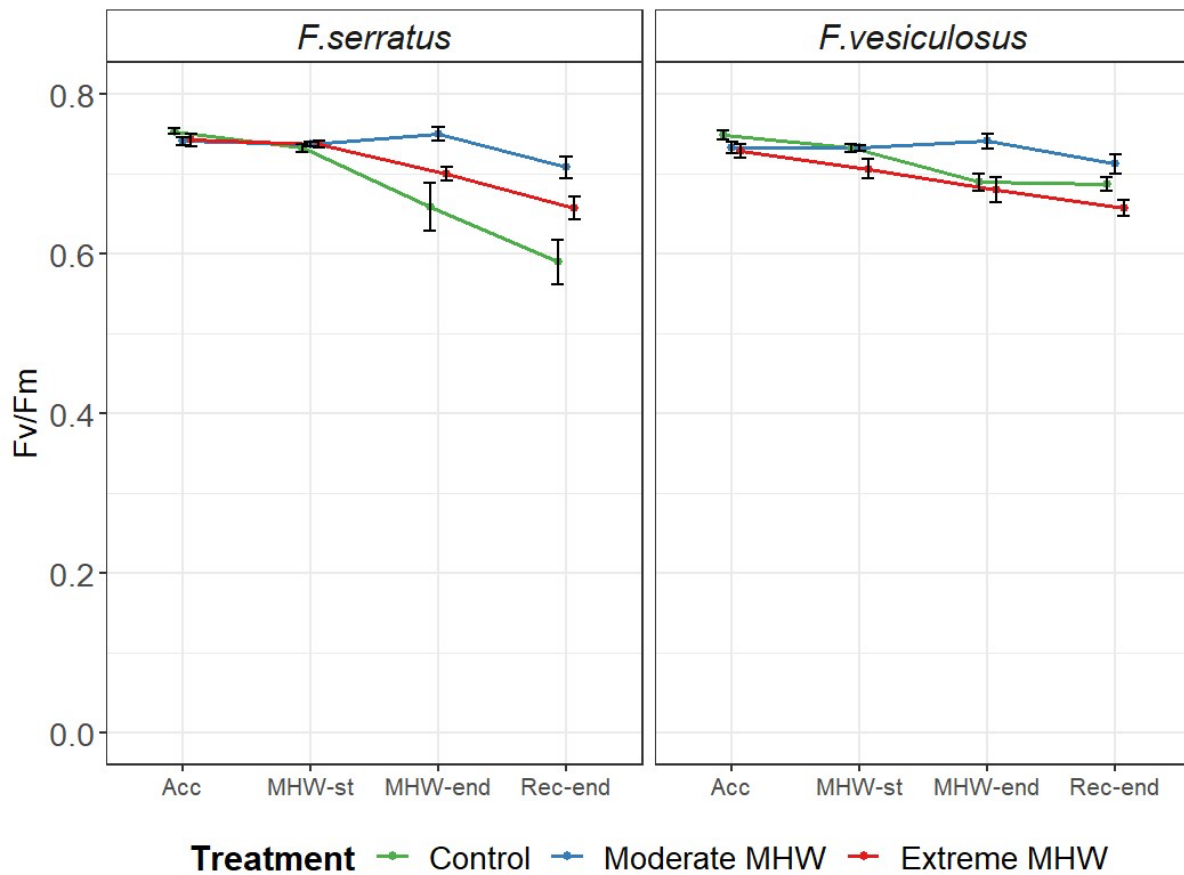
Figure 3: Mean Fv/Fm values for the *F. serratus* and *F. vesiculosus* samples at the two MHW treatments (Moderate 18°C MHW and extreme 22°C MHW) and control treatment (14°C) over the key experiment time points (Acclimatisation, MHW start, MHW end and the Recovery end). Error bars show the standard deviation within the results for the eight samples at each treatment temperature.

Table 4: Two-way repeated ANOVA test results for *F. serratus* and *F. vesiculosus* bleaching response to the two main experiment factors: Treatment (control, moderate and extreme MHW temperatures) and Timepoint (MHW start, MHW end, recovery end). The Time point x Treatment shows interaction between the two main effect factors. Significance indicated as $p < 0.05$, significant results shown in bold.

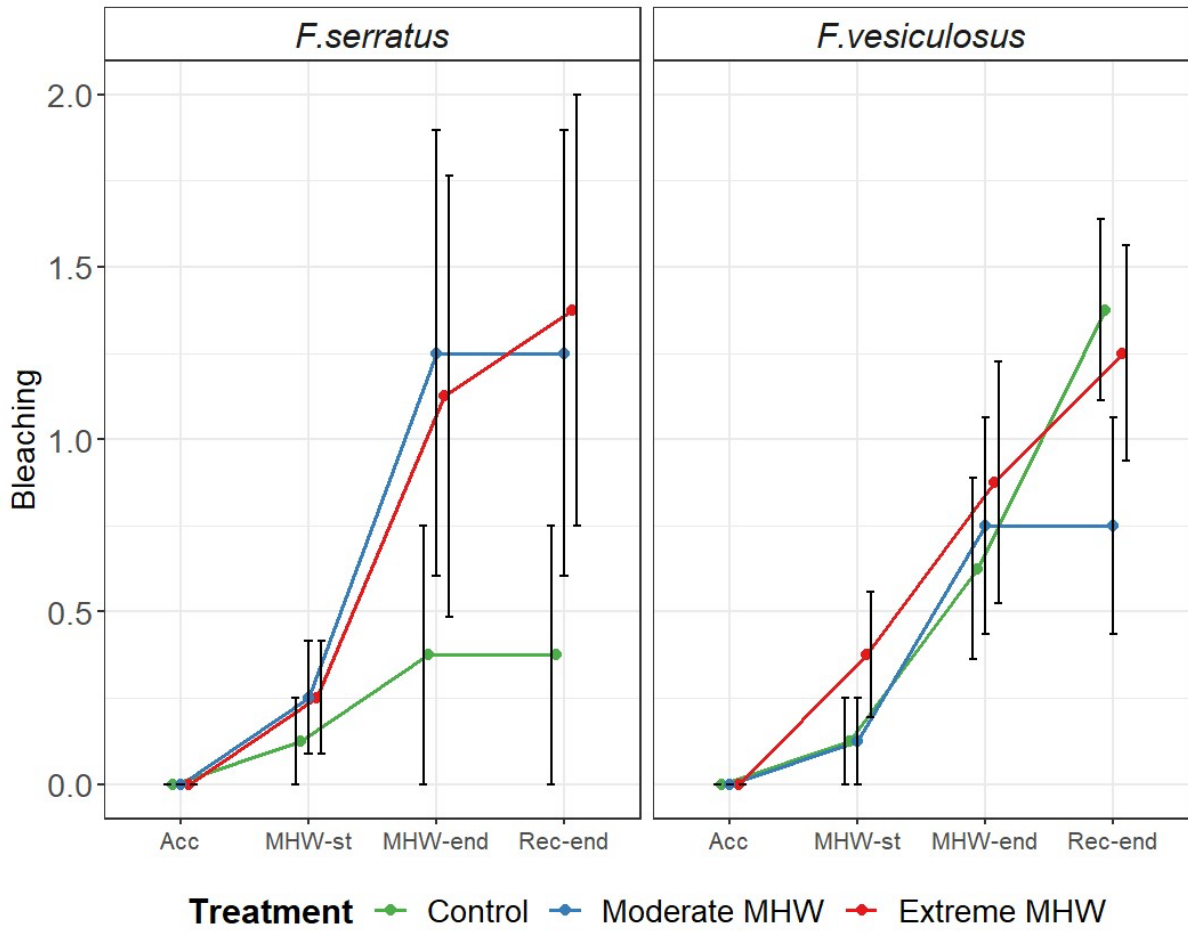|		*F. serratus*		*F. vesiculosus*	
	Df	*F*	*P*	*F*	*p*
Time point	2	*14.217*	*<0.001*	*14.926*	*<0.001*
Treatment	2	*0.591*	*0.567*	*0.467*	*0.637*
Time point x Treatment	5	*0.773*	*0.552*	*1.167*	*0.347*

Figure 4: Mean bleaching values from a visible scale of 0-5 (0 – no bleaching observed, 5 – 100% bleaching) for the F. serratus and F. vesiculosus samples at the two MHW treatments (Moderate 18°C MHW and extreme 22°C MHW) and control treatment (14°C) over the key experiment time point (Acclimatisation, MHW start, MHW end and the Recovery end). Error bars show the standard deviation within the results for the eight samples at each treatment temperature.

Discussion

This study investigated the influence of moderate and extreme MHW scenarios in UK waters on the physiological health of two fucoid species, *F. serratus* and *F. vesiculosus*, growing near their range centre. Previous studies have shown fucoids to have a high resilience to temperature evolving from their regular exposure to atmospheric temperatures at low tides (Graiff et al, 2015; Piñeiro-Corbeira et al, 2018; Atkinson et al, 2020). This ability to tolerate thermal stress is linked to their geographic distribution (Smith et al, 2023). Assemblages living near to their heat limit at the warm trailing edge are more vulnerable to MHW heat stress than those living in the range centre and cool trailing edge which could, in some cases, benefit from elevated temperature (Smith et al, 2023; Straub et al, 2019; Breeman, 1990). Despite high temperature tolerance, the projected rise in MHW severity and duration under climate change poses an increased risk of thermal stress to SW UK assemblages in coming decades, hence the need to understand its potential impact to physiological health of fucoids (Eric et al, 2020; Frolicher et al, 2018; Oliver et al, 2019).

In this study, both species demonstrated a high physiological resilience to the moderate and extreme MHW temperatures over a one-month duration despite the seasonal autumnal water temperatures being exceeded by 8°C. No clear physiological stress or mortality was observed in either species or treatments. In the three response variables, the statistical analysis showed the Treatment main effect to have less significance than the Time point main effect, indicating little or no significant difference in effect between treatment temperatures. Mean Fv/Fm values remained above 0.6 Fv/Fm, indicating healthy quantum efficiency of photosystem II throughout the experiment period. Samples continued to grow significantly at each experiment time point, ending the recovery period with greater biomass than the MHW start, indicating efficient ecological function and performance despite the moderate and extreme temperatures. Bleaching values showed less significance, however, remained on the lower end of the semi-quantitative scale with no samples showing 100% bleaching.

As intertidal species, both *F. serratus* and *F. vesiculosus* have high thermal tolerances and wide ecological temperature ranges as demonstrated in the results of this study (Smith et al, 2023; Jueterbock et al, 2013a; Jueterbock et al, 2013b). Previous studies by Graiff et al (2015) and Saha et al (2020) showed the wide ecological temperature range of range centre *F. vesicuolsus* from the western Baltic Sea with growth and survival between 5-26°C. Within this range, 15-20°C was optimal for growth, 24°C was optimal for photosynthesis and temperatures exceeding 27°C became lethal to the species (Graiff et al, 2015; Jueterbock et al, 2013b). For *F. serratus*, a 25°C thermal limit was identified for range centre assemblages (Atkinson et al, 2020; Jueterbock et al, 2013a; Figueroa et al, 2019). In the Western Baltic Sea, warm summer temperatures in the upper decimetre of shallow water, where thalli of *F. vesiculosus* extend to, can reach up to 30°C during the day before dropping to 18°C at night, a significant daily change in temperature (Saha et al, 2020). These temperature changes are natural, relatively predictable diurnal and seasonal variations that fucoids are adapted to tolerate, unlike MHW temperature anomalies which have only begun to occur more frequently in recent decades (Graiff et al, 2015; Jueterbock et al, 2013b; Oliver et al, 2019). The temperature treatments used in this study fall within the growth and survival range for the species, hence no mortality or severe declines in physiological health of the samples were observed (Graiff et al, 2015; Atkinson et al, 2020; Saha et al, 2020).

Intertidal species also deal with several other stressors from both the marine and terrestrial environment, these include desiccation stress during low tide, terrestrial heatwaves, grazing pressure, water quality, bacterial infection, and wave action (Straub et al, 2019; Saha et al, 2020; Graiff et al, 2015). The variety of stressors in an intertidal environment can create difficulty when distinguishing impacts solely from MHWs, hence why there is little long term field data on the influence of MHWs on fucoid assemblages (Straub et al, 2019). MHWs that exacerbate stressors and or coincide with increased pressures from other sources will have more lethal effects on fucoid assemblages (Saha et al, 2020). A study by Saha et al (2020) investigated whether late spring and summer MHWs impair *F. vesiculosus* ability to defend against bacterial infection. The results, however, showed that the MHW treatments had no effect on defence ability (Saha et al, 2020). In terms of terrestrial heatwaves, the increasing trend in frequency and intensity of events under climate change is set to add further stress to fucoid species with greater risk of desiccation alongside

elevating water temperatures over long periods (Straub et al, 2019; Perkins-Kirkpatrick and Lewis, 2020). Fucoid species have been found to be more susceptible to MHWs when atmospheric temperatures are greater during summer months, pushing assemblages towards their thermal limit (Atkinson et al, 2020). In a study by Atkinson et al (2020) on the impact of summer and winter MHWs on range centre *F. serratus*, samples under summer MHWs of 2°C and 3.5°C increases had significantly lower growth values as well as a greater decrease in Fv/Fm values than the control samples. Winter MHW temperatures of 1.5°C and 2°C had no effect on growth and temperatures of 3.5 degrees had a positive effect by alleviating cool stress (Atkinson et al, 2020). Therefore, summer terrestrial heatwaves and or summer MHWs pose a greater potential for heat stress at the range centre than during autumn months as used in this study (Atkinson et al, 2020). The influence of terrestrial temperatures and other intertidal stressors alongside MHWs was not accounted for in this study as samples were submerged for the duration of the experiment without other natural stressors. This could be explored in a future experiment or closely observed on a rocky shore assemblage.

Under climate change and increasing frequency of extreme MHW events, the population structure of *F. serratus* and *F. vesiculosus* communities are predicted shift northward (Jueterbock et al, 2013a; Figueroa et al, 2019; Breeman, 1990). Moderate and extreme MHW events of 4°C and 8°C increases above the average will pose a significant threat to fucoid assemblages living close to their thermal heat limit at the warm trailing edge along the Portuguese coastline and in southern regions of their latitudinal distribution (Jueterbock et al, 2013a; Jueterbock et al, 2013b). A migration to cooler regions in northern latitudes and population declines in southern distribution latitudes is the predicted response of fucoids to climate change (Jueterbock et al, 2013a; Breeman, 1990). Shifts have already been observed in Australian populations which were documented to move 2° poleward under warmer conditions (Wernberg et al, 2021). This shift will subsequently make the SW UK closer to the warm trailing edge and could result in temperatures being further from optimal at the range centre in coming decades. **Jueterbock et al (2013)** predict that *F. serratus* and *F. vesiculosus* will disappear from North-Atlantic Ocean shores extending south of 45° latitude by 2200 under current climate change predictions (Graiff et al, 2015; Jueterbock et al, 2013a). The results from this study indicate that extreme temperature increases of 8°C above the ambient temperature under extreme category MHW events and RCP8.5 warming scenarios will not be lethal to UK assemblages, therefore, shifts are unlikely to be observed in this region. Moderate and extreme MHWs will have a more severe impact on the warm trailing edge than lower temperature, less stressful range centre conditions (Alexander et al, 2018; Smith et al, 2023). However, this does not go to say that under increasing severity, frequency and duration of MHWs and terrestrial heatwaves due to climate change in coming decades that heat stress and population change will not be observed at the range centre (Smale et al, 2019; Frolicher et al, 2018; Eric et al, 2020). Future MHW events could make SW UK waters warmer and less optimal for ecological function, resulting in changes to fucoid assemblages (Smith et al, 2023; Straub et al, 2019; Breeman, 1990).

The ecological implications of declines in fucoid communities will have knock-on impacts to higher trophic levels, particularly invertebrates, that rely on algal canopies to regulate and buffer against extreme temperature and salinity fluctuations, as well

as protection against desiccation and wave action and as a ground for growth and reproduction (Jueterbock et al, 2013b; Piñeiro-Corbeira et al, 2018; Straub et al, 2019). Observations have also seen phase shifts in seaweed assemblages from fucoids and kelp to invasive turf-forming algae post MHW events, resulting in major shifts away from functional fucoid ecosystems (Straub et al, 2019; Wernberg et al, 2013). Declines in fucus assemblages will in turn result in declines in invertebrate species and other benthic organisms with knock-on impacts to bird communities and the wider marine ecosystem (Straub et al, 2019; Piñeiro-Corbeira et al, 2018; Graiff et al, 2015). SW UK assemblages should avoid the worst of these impacts as the results have demonstrated the high temperature tolerance of *F. serratus* and *F. vesiculosus*. Severe population declines in assemblages are unlikely in this region, however, pose a greater threat to assemblages at the warm trailing edge.

To identify the impact of moderate and extreme MHWs on warm trailing edge assemblages, a similar study could be conducted on, for example Portuguese fucoid samples, to investigate their tolerance to the treatments. To find the lethal limit of range centre assemblages and observe greater change in the physiological health of both species, higher treatment temperatures would have been required (Graiff et al, 2015; Piñeiro-Corbeira et al, 2018). The extreme 22°C temperature treatment used in the experiment was not hot enough to induce physiological stress, as seen in previous studies where higher, more extreme temperatures up to 30°C were used (Graiff et al, 2015; Piñeiro-Corbeira et al, 2018). In these experiments, clear signs of stress and mortality were shown by the end of the MHW period at temperatures exceeding 26°C (Graiff et al, 2015; Piñeiro-Corbeira et al, 2018). The ecological relevance, however, of temperatures over 22°C does not reflect MHW predictions in SW UK range centre waters under current warming trends and emission scenarios (Hobday et al, 2018; Oliver et al, 2019). Temperature anomalies in the Western English Channel were observed as MHW SSTs at 3.5 to 4.7°C above the long-term average for the season over durations of 5-78 days (Atkinson et al, 2020; Joint and Smale, 2017). This makes the results from the treatments used in this experiment relevant for understanding the ecological impacts of future MHWs in SW UK waters, despite not showing physiological change and pushing the samples to a lethal limit. Instead of increasing the treatment temperatures to find the mortality point of the samples, MHW duration and frequency could be tested in a future experiment to find the point at which the treatments become lethal.

Conclusion

F. serratus and *F. vesiculosus* both demonstrated a high affinity to tolerate moderate and extreme MHW temperature anomalies above autumn season SW UK water temperatures in this study. Results showed healthy Fv/Fm values and significant growth with overall no clear evidence of physiological stress induced by the MHW treatments over the one-month period. This high physiological resilience is attributed to the evolution of intertidal fucoids to cope with fluctuating temperatures during the tidal cycle alongside the UK study region being near the fucoid species range centre. Despite having a high tolerance to heat, increasing MHW frequency and duration under climate change in coming decades will pose an increased threat of thermal stress to fucoids and the associated ecosystem. This will be apparent at the warm trailing edge and possibly the range centre if extremes persist and other intertidal stressors increase. Increasing MHWs are predicted to result in population declines at the warm trailing edge and a northward distributional shift to cooler regions. This

could shift the UK away from the range centre, possibly making assemblages more vulnerable to higher temperatures in coming decades.

However, overall, UK fucoid assemblages will tolerate and not be detrimentally impacted by MHWs under current climate change predictions. The results from this study build on limited existing knowledge of the impact of MHWs on the physiological health of keystone fucoid species, aiding the understanding and drive for mitigation efforts against MHWs in years to come.

Acknowledgements

References

Alexander, M.A., Scott, J.D., Friedland, K.D., Mills, K.E., Nye, J.A., Pershing, A.J. and Thomas, A.C., 2018. Projected sea surface temperatures over the 21st century: Changes in the mean, variability and extremes for large marine ecosystem regions of Northern Oceans. *Elementa: Science of the Anthropocene*, **6.**

Andrews, S., Bennett, S. and Wernberg, T., 2014. Reproductive seasonality and early life temperature sensitivity reflect vulnerability of a seaweed undergoing range reduction. *Marine Ecology Progress Series*, **495**, pp.119-129.

Atkinson, J., King, N., Wilmes,S., Moore, P., 2020. Summer and winter marine heatwaves favor an invasive over native seaweeds, *Journal of Phycology*, **56**(6), pp. 1591–1600.

Bartsch, I., Vogt, J., Pehlke, C. and Hanelt, D., 2013. Prevailing sea surface temperatures inhibit summer reproduction of the kelp *Laminaria digitata* at Helgoland (North Sea). *Journal of Phycology*, **49**(6), pp.1061-1073.

Breeman, A.M., 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgoländer Meeresuntersuchungen*, **42**(2), pp.199-241.

Breeman, A.M., 1990. Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. *Expected effects of climatic change on marine coastal ecosystems*, pp.69-76.

Eric C.J. Oliver, Jessica A. Benthuysen, Sofia Darmaraki, Markus G. Donat, Alistair J. Hobday, Neil J. Holbrook, Robert W. Schlegel, Alex Sen Gupta. 2020. Marine Heatwaves. *Annual Review of Marine Science 2021* **13:1**, 313-342

Figueroa, F.L., Celis-Plá, P.S., Martínez, B., Korbee, N., Trilla, A. and Arenas, F.,

2019. Yield losses and electron transport rate as indicators of thermal stress in Fucus serratus (Ochrophyta). *Algal Research*, **41**, p.101560.

Frolicher, T., Fischer, E. and Gruber, N., 2018. Marine heatwaves under global warming. *Nature*, **560**(7718), pp.360-364.

Graiff, A., Liesnerab,D., Karsten,U., Bartsch,A., 2015. Temperature tolerance of western Baltic Sea fucus vesiculosus – growth, photosynthesis and survival. *Journal of Experimental Marine Biology and Ecology*, **471**, pp. 8–16.

Hobday,A.,Alexander,L.,Perkins,S.,Smale.D.,Straube,S.,Oliver,E.,Benthuyseng,J.,Burrows, M.,Donat,M., Ming,F., Holbrook,N., Moore,P., Scannell,H.,Sen Gupta,A., Wernberg,T., 2016. A hierarchical approach to defining marine heatwaves, *Progress in Oceanography*, **141**, pp. 227–238.

Hobday, A., Oliver,E., Sen Gupta, A., Benthuysen, J., Burrows, M., Donat, M., Holbrook, N., Moore,P., Thomsen, M., Wernberg.,T and Smale,D., 2018. Categorizing and naming Marine Heatwaves, *Oceanography*, **31**(2).

Holbrook, N., PerkinsKirkpatrick, S., Scannell,H., Sen Gupta, A., Payne,B & Moore,P., 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Chang*. **9**, 306–312.

Joint, I. and Smale, D.A., 2017. Marine heatwaves and optimal temperatures for microbial assemblage activity. *FEMS Microbiology Ecology*, **93**(2).

Jackson, A. 2008. Fucus serratus Toothed wrack. Marine Biological Association, UK. https://www.marlin.ac.uk/species/detail/1326 . Accessed on 15/10/2022.

Jueterbock, A., Kolliasa,S., Smolina,I., Fernandes,J.,Coyerb,J., Olsen,J.,Hoaraua,G., 2013a. Thermal stress resistance of the brown alga Fucus serratus along the north Atlantic Coast: Acclimatization potential to climate change, *Marine Genomics*, **13**, pp. 27–36

Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L. and Hoarau, G., 2013b. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and evolution*, **3**(5), pp.1356-1373.

Laufkotter, C., Zscheischler, J. and Frölicher, T.L., 2020. High-impact marine heatwaves attributable to human-induced global warming. *Science*, **369**(6511), pp.1621-1625.

OBIS, 2023. Global map of species distribution using gridded data. Available from: Ocean Biodiversity Information System. www.iobis.org. Accessed: 15/10/2022

Oliver, E., Donat, M., Burrows, M., Moore, P., Smale, D., Alexander, L., Benthuysen, J., Feng, M., Sen Gupta, A., Hobday, A., Holbrook, N., Perkins-Kirkpatrick, S., Scannell, H., Straub, S. and Wernberg, T., 2018. Longer and more frequent marine heatwaves over the past century. *Nature Communications*, **9**(1).

Oliver, E.C., Burrows, M.T., Donat, M.G., Sen Gupta, A., Alexander, L.V., Perkins-Kirkpatrick, S.E., Benthuysen, J.A., Hobday, A.J., Holbrook, N.J., Moore, P.J. and Thomsen, M.S., 2019. Projected marine heatwaves in the 21st century and the potential for ecological impact. *Frontiers in Marine Science*, **6**, p.734.

Perkins-Kirkpatrick, S.E. and Lewis, S.C., 2020. Increasing trends in regional heatwaves. *Nature communications*, **11**(1), p.3357.

Piñeiro-Corbeira, C., Barreiro, R., Cremades, J. and Arenas, F., 2018. Seaweed assemblages under a climate change scenario: Functional responses to temperature of eight intertidal seaweeds match recent abundance shifts. *Scientific reports*, **8**(1), p.12978.

Saha, M., Barboza, F.R., Somerfield, P.J., Al-Janabi, B., Beck, M., Brakel, J., Ito, M., Pansch, C., Nascimento-Schulze, J.C., Jakobsson Thor, S. and Weinberger, F., 2020. Response of foundation macrophytes to near-natural simulated marine heatwaves. *Global change biology*, **26**(2), pp.417-430.

Sen Gupta, A., Thomsen, M., Benthuysen, J., Hobday, A., Oliver,E ., Alexander,L ., Burrows, M., Donat,M., Feng,M., Holbrook, N., Perkins-Kirkpatrick,S., Moore, P., Rodrigues, R., Scannell,H., Taschetto,A., Ummenhofer, C., Wernberg,T & Smale ,D., 2020. Drivers and impacts of the most extreme marine heatwave events, *Scientific Reports*, **10**(1).

Smale, D., Wernberg, T., Oliver, E., Thomsen, M., Harvey,B., Straub,S .,Burrows,M., Alexander,L., Benthuysen, J., Donat, M., Feng, M., Hobday, A.,Holbrook, N., Perkins-Kirkpatrick, S., Scannell,H., Sen Gupta, A., Payne,B & Moore,P., 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Chang*. **9**, 306–312.

Smith, K.E., Burrows, M.T., Hobday, A.J., King, N.G., Moore, P.J., Sen Gupta, A., Thomsen, M.S., Wernberg, T. and Smale, D.A., 2023. Biological impacts of marine heatwaves. *Annual Review of Marine Science*, **15**, pp.119-145.

Somero, G.N. 2010. The Physiology of Climate Change: How Potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*, **213**(6), pp. 912–920

Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M. and Edgar, G.J., 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature*, **560**(7716), pp.92-96.

Straub, S., Wernberg,T ., Thomsen, M., Moore ,P., Burrows, M., Harvey, B., and Smale, D., 2019. Resistance, extinction, and everything in between – the diverse responses of seaweeds to marine heatwaves, *Frontiers in Marine Science*, **6**.

Weitzman, B. Brown, C., Ceccarelli,D & Edgar,G., 2021. Changes in rocky intertidal community structure during a marine heatwave in the northern Gulf of Alaska. Frontiers in Marine Science, **8**.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., De Bettignies, T., Bennett, S. and Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3**(1), pp.78-82.

Wernberg, T., 2021. Marine heatwave drives collapse of kelp forests in Western Australia, *Ecosystem Collapse and Climate Change*, pp. 325–343.

White, N. 2008. Fucus vesiculosus Bladder wrack. Marine Biological Association, UK. https://www.marlin.ac.uk/species/detail/1330 .Accessed on 15/10/2022