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RESEARCH ARTICLE

Marine Heatwaves

The influence of pre-exposure to marine heatwaves on the critical thermal maxima (CT_{max}) of marine foundation species

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Abstract

1. Marine foundation species underpin some of the world's most diverse ecosystems but they are increasingly threatened by intensification of marine heatwaves (MHWs). Where MHWs exceed critical thermal maxima (CT_{max}), increased mortality and population declines can occur. CT_{max} is increasingly used to assess MHW population vulnerability but studies estimating CT_{max} across species, range edges and thermal histories in a comparable manner remain lacking.
2. We determined the impact of MHWs on subsequent CT_{max} estimates of matched cool/warm affinity pairs of marine foundation species (kelp, seagrass and bivalves) in the Western English Channel. Following a 4-week MHW simulation, individuals were subjected to a CT_{max} trial, where temperatures were raised by 2°C day^{-1} until physiological end points were reached.
3. We found no positive effect of MHWs on CT_{max} but clear negative impacts were observed for some groups of foundation species. Increased MHW intensity had a stepwise negative impact on the physiology of both warm (*Laminaria ochroleuca*) and cool water (*L. digitata*) kelp species that manifested in significant reductions in CT_{max}. Surprisingly, this was most marked in the warm water species, which runs opposite to the assumed safety of leading-edge populations. The physiology of warm (*Zostera noltii*) and cool (*Z. marina*) seagrasses was negatively impacted by increasing MHW intensity but no significant decrease in CT_{max} was observed. Both bivalve species (*Mytilus edulis* and *Magallana gigas*) showed marked resistance to exposure to MHWs, which was unexpected given the observed vulnerability of these species to stressful summertime conditions.
4. Our results show pre-exposure to realistic MHWs can influence CT_{max} values but generalities are difficult to make across groups or based on assumed thermal safety margins. We show CT_{max} is a labile trait and exposure to MHWs, can erode the resilience of an individual or population to subsequent thermal challenges. This leaves uncertainty within frameworks built to understand where and when MHWs will be most impactful.
5. Further experimentation across a wider range of species and thermal challenges is needed to better understand the dynamic nature of CT_{max} and field validation

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is needed to determine the responses of individuals and populations within complex natural systems.

KEYWORDS
adaptation, climate change, plasticity, thermal limits, thermotolerance

1 | INTRODUCTION

Anthropogenic climate change is driving reconfigurations of entire ecosystems, as species shift their distributions to track favourable thermal environments (Lenoir et al., 2020). This pattern is particularly strong for marine ectotherms, which generally occupy most of their thermal niche so that their distributions are strongly constrained by temperature (Sunday et al., 2012). Studies on the dynamics of species range shifts have typically focussed on responses to decadal-scale gradual increases in mean temperatures, which manifest through changes in demography and fitness over multiple generations (Parmesan & Yohe, 2003; Poloczanska et al., 2013; Root et al., 2003). However, significant increases in marine heatwave (MHWs or discrete periods of anomalously warm water; see Hobday et al., 2016) activity over the past few decades (Oliver et al., 2018) have been linked with widespread ecological impacts, as extreme temperatures can exceed physiological thresholds, causing decreased fitness, increased mortality, population declines and even local extinctions (Breshears et al., 2021; Brodribb et al., 2020; Smale et al., 2019; Smith et al., 2023; Teskey et al., 2015).

Losses of foundation species (e.g. bivalves, kelps, seagrasses and corals) in response to MHWs can drive stepwise shifts in ecosystem structure and functioning due to the number of associated organisms that rely on them (Smith et al., 2024; Wernberg et al., 2023). Indeed, this can lead to reduced biogenic habitat availability, altered environmental conditions, decreased associated biodiversity, disruption to food webs and reduced resource supply (Montie & Thomsen, 2023; Wernberg et al., 2023). Consequently, predicting where, when and why populations of marine foundation species are vulnerable to MHW stress is becoming increasingly important for the conservation and management of wider ecosystems and the services they underpin (Harvey et al., 2022; Smith et al., 2023).

Some of the greatest impacts of MHWs are associated with the exceedance of critical thermal limits (i.e. CT_{max}) as mortality may ensue with potential consequences for the wider population, community or ecosystem. Whilst CT_{max} has been widely explored in thermal physiology studies (Cowles & Bogert, 1944; Lutterschmidt & Hutchison, 1997), climate change ecologists increasingly apply CT_{max} to predict current and future population vulnerability to thermal extremes (Sunday et al., 2012). However, CT_{max} values are generally ascertained from thermal physiology experiments that are often designed and conducted in different ways, hindering comparisons between studies and limiting broad-scale predictive power (Lutterschmidt & Hutchison, 1997; Ørsted et al., 2022; Rezende et al., 2014; Vinagre et al., 2015). To improve population vulnerability assessments, there is a need for multi-species studies conducted within a consistent experimental framework. Moreover, most historical estimates of CT_{max} ignore previous thermal history (Deutsch et al., 2008), despite strong evidence that recent exposure to stressful temperatures can both enhance or reduce thermal tolerance (Morley et al., 2019; Peck et al., 2014). As such, approaches that utilise CT_{max} to assess population vulnerability may perform poorly, with local extinctions potentially occurring at lower or higher temperatures than predicted. This also means MHWs themselves may have knock on consequences for subsequent resilience and resistance to thermal extremes (Hughes et al., 2019; Pansch et al., 2018). Both issues present challenges for developing reliable predictions of current and future responses to ocean warming.

The strength and direction of responses to MHWs will largely depend on where any given population sits within the wider geographic distribution of the species (Harvey et al., 2022; Smith et al., 2023). Whilst regional and local scale factors can overwhelm latitudinal patterns of stress intensity in intertidal systems (Helmuth et al., 2006; Kuo & Sanford, 2009), physiological tipping points are most often exceeded at trailing (equatorward) range edges, due to the lower thermal safety margins (difference between CT_{max} and experienced temperatures) found in these populations (Sunday et al., 2014; Wiens, 2016). Here, MHWs may cause severe physiological damage to the macromolecular machinery or deplete energy reserves upon which stress mechanisms rely (Somero, 2020). Conversely, populations at cooler parts of a species' range (i.e. range centre and leading edges) are often less vulnerable and temperatures experienced during MHW events may 'harden' or 'prime' these populations, increasing their CT_{max} and in turn raising thermal resilience (Hackerott et al., 2021; Jueterbock et al., 2021; Nguyen et al., 2020). However, whilst both lowering and raising of thermal tolerance has been observed in a range of marine foundation species, direct assessments across taxa and at populations at differing parts of their range are rare (but see Bennett et al., 2022).

The Western English Channel (WEC) represents an important biogeographic transition zone that supports marine species with both Boreal (cool) and Lusitanian (warm) distributions (Amelot et al., 2023; Forbes et al., 1853; Smale et al., 2013). This region also experiences strong summertime MHWs, which have intensified in recent decades (Simon et al., 2023), and a number of marine foundation species have exhibited range shifts in response to

ocean warming trends (King et al., 2021; Salland et al., 2023; Smale et al., 2015). Here, we used the WEC as a model system to determine how pre-exposure to realistic MHWs affects subsequent estimates of CT_{max} in a range of marine foundation species. In doing so, we aim to understand how labile CT_{max} is and if this is impacted by the position of a population within its wider species range.

2 | MATERIALS AND METHODS

2.1 | Study species

We conducted a series of realistic simulations to test the responses of foundation species to MHWs in the WEC. We selected paired species of three types of foundation organism (kelps, seagrasses and bivalves), with one being more cool-adapted and having a more northerly distribution, and the other being warm-adapted with a more southerly distribution. All study species were collected from sites in southwest England across the summers of 2021, 2022 and 2023 (Table 1; detailed context on thermal physiology of each species can be found in the Supporting Information S1). No permission for fieldwork was required in this study, and ethics approval was not required as manipulations only involved non-cephalised invertebrates.

2.2 | MHW conditions

Average monthly sea temperatures in the WEC range from ~9°C in February to ~17°C in August but maximum temperatures of >20°C are occasionally experienced under summertime MHW conditions (Simon et al., 2023). We applied a widely adopted MHW definition (Hobday et al., 2016), which states that temperatures must exceed the upper 90th percentile relative to a baseline climatology of the region for more than five consecutive days. MHW intensity categories were defined according to Hobday et al. (2018), which is based on multiples of the difference between the 90th percentile and the 30-year climatological mean. To examine previous MHW profiles in our study region, we extracted metrics for the period 1983–2022 in the WEC (between 49°N to 51°3′N and 3°2′W to 6°W) using the r package 'HeatwaveR' (Smit et al., 2018). This returned a climatological mean summertime (July–September) sea temperature of 16.0°C, with an upper 90th percentile threshold for an MHW of 17.3°C. Therefore, multiples of 1.3°C above the climatological mean of 16.0°C were used to assign MHW categories. Our experimental intensities consisted of a Control (14°C: ambient, annual average seawater temperature), Moderate (18°C: 1–2×upper 90th percentile − climatological mean) and Extreme (22°C: 4–5×upper 90th percentile − climatological mean). Historical analysis of MHW events in the study region, over the last decade, showed MHW duration ranged from 5 to 58 days (mean 13 days). We used an experimental duration of 28 days, which represents a realistic but long-duration MHW in the study region.

2.3 | Experimental design

2.3.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Species	Six species from three different groups of marine foundation species
MHW intensity	MHW intensity	Three MHW intensities are tested per species. At each intensity, treatments consist of 5/6 biological replicates

All species were subjected to the same experimental setup and conditions. After collection, kelp ($n=6$), seagrasses ($n=5$) and bivalves ($n=5$) were held in a 1000 L holding tank for 5 days at ambient temperature (14°C) under a photosynthetic flux density of ~100 $\mu mol\, m^{-2}\, s^{-1}$. Following this acclimation period, individuals were placed into independent 2 L aquaria that were sat in 64 L water baths that were used to control experimental temperatures. For kelp, discs (diameter = 3.03 cm, area = 7.07 cm^2) were excised from the central blade. For seagrass, individual shoots held within 10 cm depth of sediment were secured within aquaria. Light was provided through LED lighting tiles (AquaRay) under a photosynthetic flux density of ~120 $\mu mol\, m^{-2}\, s^{-1}$ and a 12:12 light–dark regime. Each 2-L tank was continuously aerated with its own air stone, which also agitated the water to ensure nutrient delivery to tissue surfaces. Water was changed every 3 days with freshly sourced seawater from the adjacent Plymouth Sound to prevent nutrient limitation (seagrass and kelps). Bivalves were fed daily with microalgae feed (Reef Flourish) at a final cell density of 50,000 cells mL^{-1}. Salinity and temperature were checked daily and maintained between 33 and 35 ppt and ±0.5°C.

All individuals were maintained in their experimental 2-L tanks for 5 days before temperatures were raised at a rate of 1°C day^{-1} until the desired intensity was reached. The MHW then progressed for 28 days, before temperatures were then lowered at a rate of 1°C day^{-1} until they returned to control conditions (14°C). At the end of the recovery period, all individuals were subjected to the same CT_{max} trial.

2.4 | Measuring CT_{max}

There is no standardised approach for measuring CT_{max}, as it can be determined using different end points and differing rates of thermal ramping. Indeed, differences in experimental duration can significantly impact estimates (Bates & Morley, 2020; Jørgensen et al., 2019; Ørsted et al., 2022; Peck et al., 2009). Selecting biologically relevant ramping rates that yield CT_{max} values that are representative of a species' functional thermal niche is critical. In the context of MHWs, a ramping rate over the course of days (rather

TABLE 1 Descriptive information of collection of study species.

Common name	Group	Date	Site
Oarweed (*Laminaria digitata*)	Kelp (cool)	June 2021	Firestone Bay 50.361096, 4.159963
Golden kelp (*Laminaria ochroleuca*)	Kelp (warm)	June 2021	Firestone Bay 50.361096, 4.159963
Common eel grass (*Zostera marina*)	Seagrass (warm)	July 2023	Cawsands Bay 50.331311, 4.197916
Dwarf eelgrass (*Zostera noltii*)	Seagrass (cool)	July 2023	Thanckes Lake 50.381224, 4.197824
Blue mussel (*Mytilus edulis*)	Bivalve (cool)	Aug 2022	Sutton Harbour 50.367563, 4.131404
Pacific oyster (*Magallana gigas*)	Bivalve (warm)	Aug 2022	Noss Mayo 50.312244, 4.041249

than minutes or hours) is most appropriate as it is comparable to rates of onset of actual extreme warming events (Holbrook et al., 2020), and therefore, representative of the thermal stress experienced by natural populations.

In our study, CT_{max} was determined using a 2°C day^{-1} ramping rate that generated a typical thermal performance curve. This was then used to determine key physiological 'end points'. For kelp and seagrass, physiological health was based on the quantum efficiency of photosystem II (F_v/F_m). This represents the relationship between photochemical quenching (F_v) and the total fluorescence when the reaction centres of PSII are closed (F_m) (Butler, 1978). F_v/F_m has been shown to be an effective measurement of macroalgal health (Hereward et al., 2020; King, Wilcockson, et al., 2018), as values below 0.7 indicate stress, potentially due to reduced performance of photosynthetic apparatus (Maxwell & Johnson, 2000). Mortality was determined when F_v/F_m reached 0 indicating tissue was no longer photosynthetically viable. F_v/F_m was measured using Pocket PEA chlorophyll fluorimeter (Hansatech Instruments), after a 15-min period of dark acclimation.

Bivalve respiration typically has a directly proportional linear relationship to temperature, until it reaches a critical temperature where they are no longer able to absorb the amount of oxygen they need, and their respiration decreases. Therefore, it is ideally suited to estimate CT_{max}. Respiration rates were measured as proxy for standard metabolic rates, using microfiber optic oxygen sensors (Firebox 4; PreSens Germany, www.presens.de). Oysters (500 mL) and mussels (250 mL) were placed into airtight containers with planar oxygen-sensitive spots (PreSens). Temperatures were maintained by placing sealed chambers in a water bath. Assays ended after 60 min or when oxygen saturation reached 80%, to prevent individuals experiencing hypoxic conditions. Oxygen consumption was measured every 15 min to ensure active respiration was occurring. Metabolic rate (MR) was calculated using:

$$MR = \frac{(O_2t_0 - O_2t_1)}{T} \times W$$

where O_2t_0 and O_2t_1 represent the oxygen concentration at the start and the end of the experiment (μg mL^{-1}), T is the time of the incubation (min) and W is the wet weight of the individual (g). CT_{max} was assumed when the MR had reached zero and where individuals had open valves and they would not mechanically close when stimulated.

For estimates of CT_{max}, two-way analysis of variance was performed for the foundation species group with Treatment (three levels, No MHW, Moderate MHW and Extreme MHW) and Thermal Affinity (two levels, Cool and Warm) as fixed factors. Where a significant effect was detected ($p < 0.05$), post hoc (Tukey's test) pairwise comparisons were conducted to identify where differences lay. For *Zostera marina* and *Laminaria digitata*, the MHW experiment resulted in the mortality of a few individuals and subsequent CT_{max} trials were conducted on the remaining individuals. For *L. digitata*, two mortalities were observed in the extreme MHW. For *Z. marina*, one mortality was observed in the control and two in the extreme MHW. For *Magallana gigas*, CT_{max} estimates were not reached in the exposure trials and analysis for bivalves consisted solely on *Mytilus edulis* with Treatment as the only factor.

3 | RESULTS

For *L. digitata*, F_v/F_m values in the extreme MHW treatment were lower at the start of the CT_{max} trials (0.62 ± 0.01) than those in the moderate (0.74 ± 0.01) and control (0.73 ± 0.01) treatments (Figure 1a). In the extreme MHW treatment, F_v/F_m values remained comparatively depressed and declined substantially to 0.15 ± 0.10 by 24°C. All tissue in this treatment was non-viable at 26°C (Figure 1b). In the moderate MHW and control treatment, F_v/F_m values followed similar trajectories to each other (Figure 1a). Values remained elevated (>0.7) until 26°C, whereby F_v/F_m values had decreased to 0.46 ± 0.09 in the moderate treatment and 0.41 ± 0.10 in the control. At 28°C, F_v/F_m values were 0.03 ± 0.01 and 0.07 ± 0.06 in the moderate and control treatments, respectively (Figure 1). All tissue was non-viable at 30°C (Figure 1b).

For *Laminaria ochroleuca*, there was a stepwise decrease in F_v/F_m values with increasing MHW intensity that persisted throughout the CT_{max} trial (Figure 1a). At the beginning of the trial (14°C) F_v/F_m values were 0.50 ± 0.04, 0.67 ± 0.02 and 0.76 ± 0.01, in the extreme, moderate and control treatments, respectively. Declines in F_v/F_m

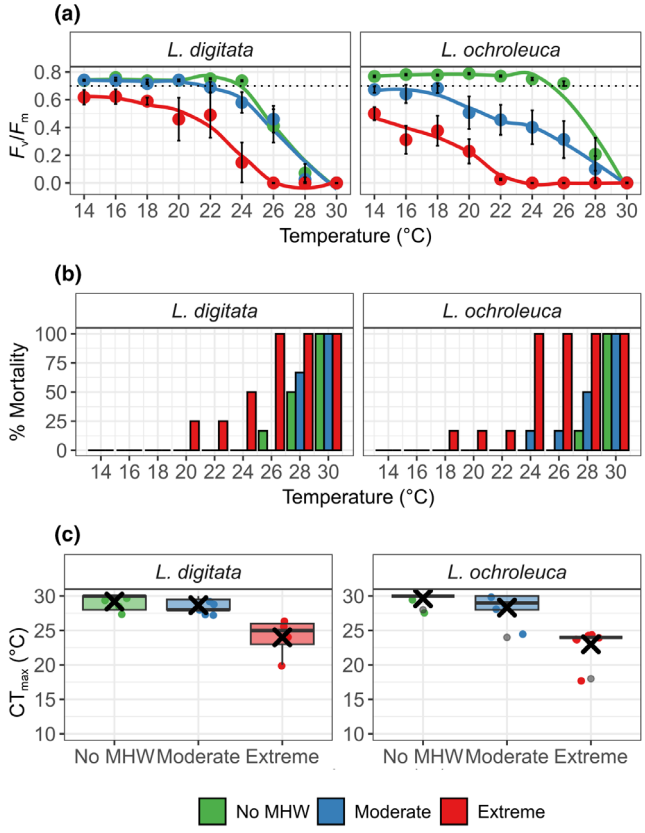


FIGURE 1 CT_{max} stress assays of two kelp species with differing thermal affinities, *Laminaria digitata* (cool) and *L. ochroleuca* (warm) following a 28-day MHW simulation. MHW treatments consisted of 'No MHW' (14°C), 'Moderate' (18°C) and 'Extreme (22°C)'. (a) Mean (±1 SE) F_v/F_m values, (b) proportion of the samples that had reached their 'end point' ($F_v/F_m = 0$) and (c) CT_{max} estimates. Cross indicates mean. MHW, marine heatwave.

TABLE 2 Results of two-way analysis of variance (ANOVA) to test for differences in CT_{max} in marine foundation species following a simulated marine heatwave.

	df	*F*	*p*
Kelp			
Treatment	2	26.7	**<0.0001**
Affinity	1	0.7	0.40
Treatment × Affinity	2	0.06	0.94
Seagrass			
Treatment	2	2.4	0.11
Affinity	1	0.4	0.53
Treatment × Affinity	2	0.3	0.74
Bivalve			
Mytilus edulis	2	1.1	0.37
Magallana gigas	na	na	na

Note: Factors consisted of Treatment (extreme, moderate and no marine heatwave) and thermal affinity (Cool vs. Warm). Bold indicates significance at $p < 0.05$. Analysis was not possible for *M. gigas* as CT_{max} as not reached in exposure trials.

values in the extreme MHW treatment occurred immediately and by 24°C all tissue was non-viable (Figure 1b). For the moderate MHW treatment, declines in F_v/F_m values occurred by 20°C, after which steady reductions were recorded to 0.10 ± 0.09 at 28°C. F_v/F_m values remained elevated (>0.7) in the control treatment until 28°C, where they plummetted to 0.21 ± 0.1. By the 30°C trial, all tissue was non-viable in both the moderate and control treatments (Figure 1b).

For CT_{max} estimates, we found a significant main effect of Treatment (Table 2). Post hoc comparisons (Tukey's test) showed the extreme treatment was significantly lower than the moderate and no MHW control, which were similar to one another. For *L. digitata*, CT_{max} estimates in the extreme MHW treatment were 24.0 ± 1.4°C compared with 28.6 ± 0.4°C and 30.3 ± 1.2°C in the moderate and no MHW control respectively (Figure 1c; Table 2). For *L. ochroleuca*, CT_{max} estimates in the extreme MHW treatment were 23.0 ± 1.0°C compared with 28.3.0 ± 0.9°C and 29.6 ± 0.3°C in the moderate and no MHW control respectively (Figure 1c; Table 2).

For *Z. marina*, initial F_v/F_m values (at 14°C) were consistent between treatments ranging from 0.67 ± 0.03 in the moderate MHW treatment to 0.72 ± 0.01 in the control (Figure 2a). During the CT_{max} trial, the extreme and moderate MHW treatments followed similar trajectories to one another (Figure 2a). Both fell gradually to ~0.5 before plummeting rapidly at 38°C. Control values remained elevated (>0.7) until 38°C, where they plummeted to 0.27 ± 0.11. In the extreme MHW treatment all tissue was non-viable by 38°C, whereas in the moderate and control treatments, this occurred at 40°C (Figure 2b).

For *Z. noltii*, initial F_v/F_m values (at 14°C) were consistent between treatments ranging from 0.71 ± 0.04 in the extreme to 0.74 ± 0.02 in the moderate MHW treatment (Figure 2a). Throughout the CT_{max} trial, all treatments remained elevated (>0.7) until 28°C, where extreme and moderate MHW values decreased to 0.57 ± 0.15 and 0.59 ± 0.14, respectively. Values in these treatments remained fairly constant until 38°C, at which point they rapidly declined to 0.15 ± 0.15 in the extreme and 0.18 ± 0.10 in the moderate MHW treatment. F_v/F_m values in the control treatment remained elevated longer and did not decrease until 38°C, where they fell to 0.44 ± 0.10 (Figure 2). All tissues were non-viable at 38°C in the extreme MHW treatment and at 40°C in the moderate MHW and control treatments (Figure 2b).

For CT_{max} estimates, both seagrass species responded in similar ways to the MHW treatments, with mean values lower in the extreme and moderate treatments compared with the no MHW control for both species but this trend was not significant (Table 2). For *Z. marina*, CT_{max} values were 39.0 ± 0.57 in the no MHW control compared with 35.6 ± 1.9 and 32.6 ± 5.3 in the moderate and extreme treatment respectively. For *Z. noltii*, CT_{max} values were 39.6 ± 0.4 in the no MHW control compared with 35.6 ± 2.4 and 36.0 ± 2.0 in the moderate and extreme MHW treatments respectively (Figure 2c; Table 2).

For *M. edulis*, MR (described as $mgO_2 min^{-1} gWW^{-1}$) ranged from 0.70 ± 0.32 in the extreme MHW treatment to 0.74 ± 0.10 in the moderate MHW treatment at the start of the CT_{max} trial (14°C). This increased gradually with increasing temperature in a consistent

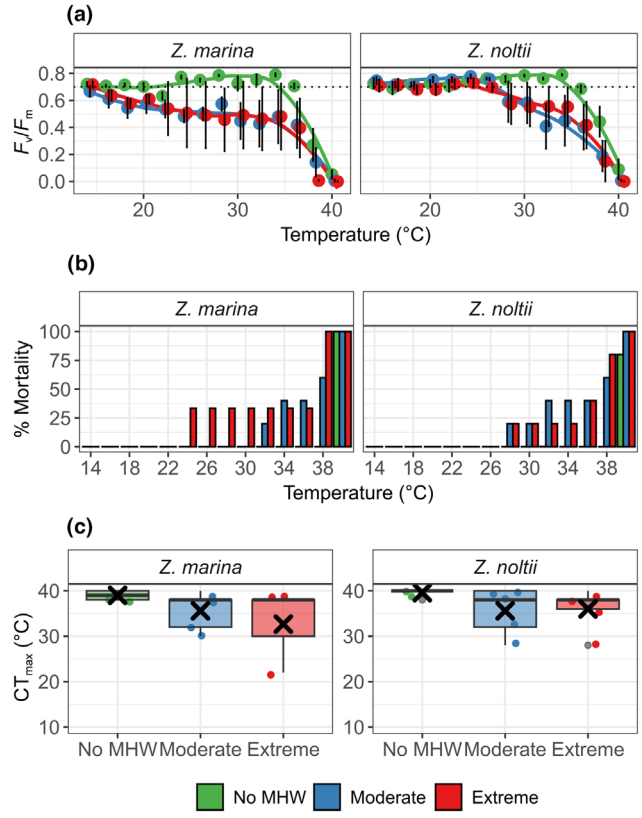


FIGURE 2 CT_{max} stress assays of two kelp species with differing thermal affinities, *Zostera marina* (cool) and *Z. noltii* (warm) following a 28-day MHW simulation. MHW treatments consisted of 'No MHW' (14°C), 'Moderate' (18°C) and 'Extreme (22°C)'. (a) Mean (±1 SE) F_v/F_m values, (b) proportion of the samples that had reached their 'end point' ($F_v/F_m = 0$) and (c) CT_{max} estimates. Cross indicates mean. MHW, marine heatwave.

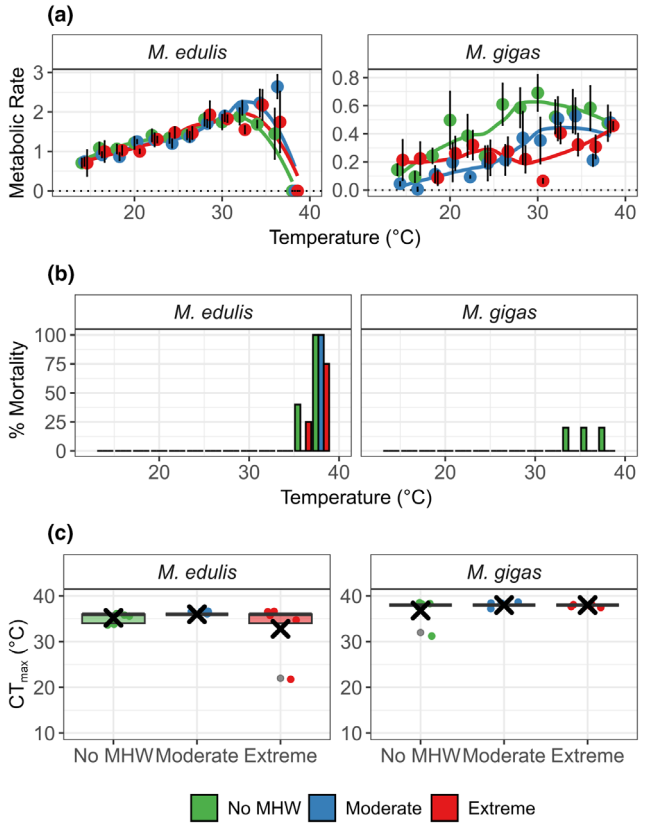


FIGURE 3 CT_{max} stress assays of two bivalve species with differing thermal affinities, *Mytilus edulis* (cool) and *Magallana gigas* (warm) following a 28-day MHW simulation. MHW treatments consisted of 'No MHW' (14°C), 'Moderate' (18°C) and 'Extreme (22°C)'. (a) Mean metabolic rate (±1 SE), (b) proportion of the samples that had reached their 'end point' (mortality) and (c) end point values (CT_{max}), cross indicates mean. MHW, marine heatwave.

manner across treatments (Figure 3a). In the extreme MHW treatment MR peaked at 2.17 ± 0.38 at 34°C, in the moderate treatment at 2.63 ± 0.29 at 36°C and in the control treatment at 1.88 ± 0.20 at 32°C (Figure 3a). In all treatments, all individuals had died by 38°C (Figure 3b). There was no significant difference in CT_{max} estimates between treatments (Figure 3c; Table 2).

For *M. gigas*, MR ranged from 0.21 ± 0.14 in the extreme MHW treatment to 0.04 ± 0.01 in moderate treatment at the start of the trial (14°C). MRs increased gradually with increasing temperature and by the end of the trial (38°C) ranged from 0.45 ± 0.02 in the extreme to 0.48 ± 0.07 in the moderate MHW treatment (Figure 3a). We recorded minimal mortality by the end of the trial, indicating that CT_{max} had not been reached (Figure 3b).

4 | DISCUSSION

Whilst CT_{max} is increasingly seen as a trait suitable for predicting the impact of MHWs, the impact of MHWs themselves in shifting CT_{max} has largely been overlooked. Given thermal history has long been known to mediate wider measures of thermal tolerance, this leaves uncertainty within frameworks built to understand where and when MHWs will be most impactful. Here, we addressed this in a range of foundation species in a dynamic system in the WEC. We found no positive effects of pre-exposure to MHWs on subsequent estimates of CT_{max} but observed clear negative impacts on some groups of foundation species.

Simulated MHWs had detrimental effects on the physiology of both the warm (*L. ochroleuca*) and cool (*L. digitata*) kelps, which manifested into dramatic reductions in CT_{max}. For *L. digitata*, this was not surprising as 22°C (extreme MHW treatment) is known to cause widespread damage to tissue structure (Simonson et al., 2015), meaning cellular damage was likely not repaired by the time of the CT_{max} trial. For *L. ochroleuca*, the even starker reduction in CT_{max} was surprising given the greater thermal safety margins assumed with leading-edge populations and previous studies indicating it can tolerate exposure to temperatures of 24°C for 2 weeks (Franco et al., 2018). Indeed, Leathers et al. (2023) showed *L. ochroleuca* can resist exposure to a similar extreme MHW treatment for 2 weeks but widespread tissue deterioration occurred after 4 weeks. Compared with other Laminarian kelps in the NE Atlantic, *L. ochroleuca* produces and stores far

fewer sugars in summer (Schiener et al., 2015), and once they are depleted, the mechanisms required to mediate thermal stress may be less efficient, effective or completely unavailable. Therefore, it is more likely that reductions in CT_{max} were a product of depletion of internal reserves over time, rather than acute cellular damage. Regardless of the underlying mechanism, a dramatic shift in CT_{max} of kelp populations has implications for assessing population vulnerability. For *L. digitata*, a CT_{max} of ~24°C indicates there is still a thermal safety margin for subsequent MHW resistance as such temperatures are not anticipated in the study region over the coming decades. Therefore, other limits such as reproductive failure (Bartsch et al., 2013) imposed by prevailing temperature isotherms are more likely to mediate a range contraction in the short term. However, for *L. ochroleuca*, a reduced CT_{max} of 18°C is more concerning as summer temperatures regularly reach this in the study area. Therefore, the continued proliferation of this species in the study area and anticipated northward expansion, mediated by the release of its reproductive cold limit (Franco et al., 2018; Izquierdo et al., 2002), may be curtailed to some degree by cumulative MHWs events.

Marine heatwave treatments had clear negative impacts on the physiology of both seagrasses. This is surprising as both species regularly experience temperatures >22°C elsewhere in their ranges and both have shown resistance to far higher temperature treatments. For example, *Z. marina* has shown acclimatory capacity to simulated MHW exposures of 27–29°C (Jueterbock et al., 2020; Yan et al., 2023), whilst *Z. noltii* can survive acute temperature shocks of 37°C (Massa et al., 2009). Acclimation (phenotypic plasticity) and/or local adaptation can result in different tolerance limits between populations (King, McKeown, et al., 2018) and has been observed between a number of *Zostera* populations (Gu et al., 2012; Jueterbock et al., 2016). Therefore, impacts on physiology may be a product of the differing thermal capacity of our populations compared with those found elsewhere. Despite an impact on physiology, this did not translate into significant reductions in CT_{max} estimates. However, it should be noted that for *Z. marina*, we observed considerable variability, as increasing MHW intensity caused a marked reduction in CT_{max} for some individuals whilst others remained comparable with control values. Such inter/intra individual variation in response to thermal stress may be related to spatial heterogeneity in/across leaves, which has been frequently observed in terrestrial plants (Li et al., 2015; Sperdouli & Moustakas, 2012; Xu et al., 2011) and recently in seagrass (Ruocco et al., 2019).

There was no discernible impact of MHW treatments on the physiology or subsequent CT_{max} estimates of either bivalve studied. For *M. gigas*, this was not surprising given its broad thermal niche and ability to tolerate acute temperature shocks. Indeed, *M. gigas* has shown previous resistance to short-term shocks (~ hours) of over 40°C (Rajagopal, Van der Velde, Jansen, et al., 2005). However, populations of *M. gigas* have been shown to be susceptible to mass mortality events in summer when temperatures exceed >19°C in the presence of pathogens, post-spawning stress or poor water quality (King et al., 2021, 2022; Malham et al., 2009; Mortensen et al., 2016). This suggests that whilst elevated temperature in isolation may be tolerable, concurrent stressors can interact to reduce thermal tolerance and erode population resilience. *M. edulis* showed an unexpected capacity to tolerate temperatures up to 38°C, which far exceeds the temperature thought to constrain the southern limit of this species (Fly et al., 2015). However, *M. edulis* has shown capacity to tolerate short-term exposures (hours) up to 41°C (Jones et al., 2010; Rajagopal, Van der Velde, Van der Gaag, & Jenner, 2005) and, as such, it is likely the range of this species is not dictated by lethal exposures associated with MHWs. Instead, either short-term shocks associated with exposure to atmospheric heatwaves during low tide emersion or a longer-term boundary for scope for growth, may be more important factors to consider over the coming decades.

An increasing frequency and intensity of MHWs will subject populations of marine foundation species to elevated thermal stress in the coming years and decades. This has the potential to drive both positive and negative legacies that may impact resistance to subsequent MHWs. Whilst responses varied between groups of foundation species, we found no evidence of a 'thermal priming effect', which has been documented in a number of seagrasses (Nguyen et al., 2020; Pazzaglia et al., 2022) and corals (Brown et al., 2023), and has been proposed as an intervention measure for seaweeds (Jueterbock et al., 2021). This may be due to the intensity of the priming stimulus either being too weak (seagrasses and bivalves) or too strong (kelp) to trigger an acclimatory response and does not necessarily mean this mechanism will not become evident as MHWs intensify. We did find clear negative impacts on both kelp species, with the most severe effects occurring in a population that would be considered resistant to near-term warming, based on thermal safety margins. Such reductions in CT_{max} driven by thermal history could have major implications for the resistance of these populations to future MHW events and continued MHW intensification. It should be noted, however, that the longer-term persistence of these responses was not examined and that CT_{max} may return to baseline levels following a period of recovery under benign conditions.

In conclusion, our results demonstrate that pre-exposure to realistic MHW simulations can significantly reduce the capacity of some marine foundation species to tolerate subsequent acute thermal challenges. Clearly, CT_{max} is a labile rather than fixed trait and thermal history, in this case exposure to MHWs themselves, can erode the resilience of an individual or population to subsequent stress. Given the increasing use of thermal traits (including CT_{max}) in predictive frameworks for MHW impacts this has broader implications beyond the current study species and system. Moving forward, there is a pressing need for further experimentation and field validation to determine the real-world implications of shifts in CT_{max} and to fully explore interactions with other potential stressors. For example, as intertidal organisms, our species are also subjected to rapid and sharp periods of thermal stress during low tide emersion, and as such, atmospheric heatwaves may also be a fundamental consideration for assessing CT_{max} in these species. In doing so, increasing confidence can be built into population vulnerability assessments that are currently affected by uncertainties.

AUTHOR CONTRIBUTIONS

NGK and DAS conceived the designed study. TL conducted all data collection. NGK and KES analysed the data. NGK led the manuscript preparation, and all authors contributed equally to subsequent edits. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Figshare repository https://doi.org/10.6084/m9.figshare.26206613 (King et al., 2024).

STATEMENT OF INCLUSION

Our study includes scientists based in the country where the study was carried out and authors are from a range of career stages.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Study species biogeographic context.

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