

# Photosynthetic response to a winter heatwave in leading and trailing edge populations of the intertidal red alga *Corallina officinalis* (Rhodophyta)

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## Abstract

Marine heatwaves (MHWs) caused by anthropogenic climate change are becoming a key driver of change at the ecosystem level. Thermal conditions experienced by marine organisms across their distribution, particularly towards the equator, are likely to approach their physiological limits, resulting in extensive mortality and subsequent changes at the population level. Populations at the margins of their species' distribution are thought to be more sensitive to climate-induced environmental pressures than central populations, but our understanding of variability in fitness-related physiological traits in trailing versus leading-edge populations is limited. In a laboratory simulation study, we tested whether two leading (Iceland) and two trailing (Spain) peripheral populations of the intertidal macroalga *Corallina officinalis* display different levels of maximum potential quantum efficiency (Fv/Fm) resilience to current and future winter MHWs scenarios. Our study revealed that ongoing and future local winter MHWs will not negatively affect leading-edge populations of *C. officinalis*, which exhibited stable photosynthetic efficiency throughout the study. Trailing edge populations showed a positive though non-significant trend in photosynthetic efficiency throughout winter MHWs exposure. Poleward and equatorward populations did not produce significantly different results, with winter MHWs having no negative affect on Fv/Fm of either population. Additionally, we found no long-term regional or population-level influence of a winter MHWs on this species' photosynthetic efficiency. Thus, we found no statistically significant difference in thermal stress responses between leading and trailing populations. Nonetheless, *C. officinalis* showed a trend towards higher stress responses in southern than northern populations. Because responses rest on a variety of local population traits, they are difficult to predict based solely on thermal pressures.

**Key words:** marginal population, coralline algae, climate change, ecophysiology, photophysiology, macroalgae, Fv/Fm

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## 1 Introduction

Over the last century, more intense, more frequent, and longer-lasting marine heatwaves (MHWs), defined as prolonged periods of anomalously high temperatures, have had increasingly severe effects on the structure of marine communities and ecosystems globally, affecting the sustainability of the goods and

services they provide (IPCC, 2014, 2021, 2022; Oliver et al., 2018, Laufkötter et al., 2020).

Until now, most research on MHWs has focused on extreme summer temperatures that exceed the tolerances of entire species. However, it is important to note that temperatures significantly higher than the average climate can occur at any time of the

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year (Hobday et al., 2016), and both winter and summer MHWs are expected to increase in frequency and duration (Oliver et al., 2018). In addition, it is crucial to recognise that many terrestrial and aquatic groups (such as corals, Berkelmans and Willis, 1999; crustaceans, Layne et al., 1987; fish, Bulger and Tremaine, 1985; insects, Hu and Appel, 2004; molluscs, Chapple et al., 1998; plants, Badger et al., 1982; seaweeds, Lüning, 1984) have demonstrated a reduction in thermal tolerance due to acclimatization to colder temperatures. As a result, not only summer MHWs but also those occurring in winter could have significant effects on the physiology, phenology, and competitive interactions of organisms (Atkinson et al., 2020).

MHWs can take place throughout the entire distributional range of a species, potentially affecting central and both edge populations. According to the “abundant-centre” hypothesis (Brown, 1984), a species is expected to exhibit its highest abundances towards the centre of its distribution, declining toward the range edges, although support, particularly for the genetic predictions of the hypothesis, is sometimes weak (Sagarin and Gaines, 2002; Eckert et al., 2008; Zardi et al., 2015; Ntuli et al., 2020). Leading and trailing edge populations live towards the limits of suitable conditions and the species’ tolerances (Whittaker, 1956; Brussard, 1984; Kolzenburg, 2022), and can be geographically isolated from central and continuous populations (Bridle and Vines, 2007; Bertocci et al., 2011). The predicted decrease in genetic diversity in edge populations appears to be supported for many but not all species (Eckert et al., 2008) as genetic diversity can be influenced by many other factors (e.g. latitude, ecological environmental gradients, population size, phylogeographic history; Yang et al., 2016).

Leading and trailing edge populations are expected to experience conditions close to the limits of a species’ tolerances, experiencing temporal variability that will result in these limits being exceeded in some years (Sexton et al., 2009). Investigating and comparing populations at the edges of a species distribution provides an understanding of the factors that shape species ranges and how spatial variation in fitness translates to population-level differences in abundance (Sexton et al., 2009; Araújo et al., 2014; Guo, 2014). Consequently, leading and trailing edge boundaries can act as testing grounds for the investigation of the conditions under which populations can adapt, or fail to adapt, to new and temporary changes in environmental conditions (Sexton et al., 2009).

Marine macroalgae create diverse and productive systems around the world (Charpy-Roubaud and Sournia, 1990; Fredriksen, 2003; Mineur et al., 2015). Among them, articulated coralline algae (Phylum *Rhodophyta*) exhibit high morphological and functional plasticity (Brody, 2004; Ragazzola et al., 2013) and wide geographical ranges in both the northern and southern hemispheres. Among these turf-forming species, *Corallina officinalis* (Linnaeus 1758; Rhodophyta, Corallinales, Corallinaceae) is an important ecological engineer, common around the North Atlantic and North Pacific (Hind et al., 2014; Magill et al., 2019), where it creates complex three-dimensional habitats that enhance biodiversity (Foster, 2001; Steller et al., 2003; Ragazzola et al., 2013).

Macroalgal species and populations display great variety in their responses to elevated temperature conditions (Lima et al., 2007; Straub et al., 2019). Furthermore, most studies of the effects of MHWs on these habitat-forming organisms have focussed on warm-edge populations, where thermal limits are expected to be exceeded under summer conditions (Bennett et al., 2015; King et al., 2019). At the same time, most centre and cold-

edge populations are largely unaffected (Jones et al., 2010; Smale et al., 2019). Seasonal acclimatisation is common in temperate macroalgae, allowing the maximisation of performance over a wide range of temperatures (Davison, 1987; Dudgeon et al., 1990; Kübler and Davison, 1993; Padilla-Gamino and Carpenter, 2007). We test the hypothesis that such seasonality in physiology results in lower thermal tolerance in winter and thus increased vulnerability to winter MHWs. We examined an aspect of the photo-physiological responses (Fv/Fm or ratio of variable to maximum fluorescence) of leading and trailing edge populations of *C. officinalis* to a simulated winter MHWs. We used ambient and predicted sea surface temperature (SST) scenarios (Representative Concentration Pathway (RCP) 8.5, IPCC, 2014) and included natural thermal tidal fluctuations experienced by the populations at their sites of origin.

## 2 Materials and methods

### 2.1 Specimen collection

We sampled two populations of *C. officinalis* in each of two regions: Spain (January 2020) and Iceland (February 2020) while they were submerged in channels and crevices during or close to the lowest low tide in the respective month. We used published genetic data (Tavares et al., 2018; Kolzenburg et al., 2019) to identify southern (or trailing edge, SP) and northern (or leading edge, NP) populations. Trailing edge populations were from the Northwest coast of Spain: southern population 1: O’Carreiro 42.476 386°N, 8.938 735°W and southern population 2: Tragove 42.524 44°N, 8.827 72°W), which are approximately 10 km apart. Leading edge populations were from the Southwest coast of Iceland: northern population 1: Þorlákshöfn 63.844 167°N, 21.373 833°W, and northern population 2: Stafnes South 63.968 444°N, 22.750 861°W), which are approximately 70 km apart. Specimens were kept in the dark, using temperature-insulated containers to maintain near-ambient temperature, and were transported to the Institute of Marine Sciences of the University of Portsmouth, UK, within a maximum of 2 d after collection, with frequent changes of water after collection until arrival. Only specimens without visible damage, bleaching or epiphytes were used in the experimental phase.

### 2.2 Culturing conditions

Individuals (individual = pebble with approximately 2 g algal wet weight of the collected populations) were carefully secured to pebbles following Kolzenburg et al. (2019), recreating natural growth conditions. Specimens of the two populations from a given region were kept in the same aquarium to ensure identical temperature conditions and were differentiated by colour-coding the pebbles for each population using coloured yarn. Aquaria were set up in a closed water bath system.

Twice a week, 50% of the aquarium water was replaced with fresh seawater. Water baths ( $n = 6$ ) were temperature controlled by a chiller (TK-2000 chiller, cooling capacity: 870 W, 800 L/h, TECO) to maintain the desired temperatures. The remaining two water baths (total  $n = 8$ ) were passively temperature controlled using a coil system fed by water pumped from the corresponding regulated water bath.

The system was set to a light/dark cycle, representing sunrise and sunset at the time of sampling, controlled by TMC AQUA-BEAM 600 ultima reef white lights with cloud function. Light conditions were (h:min) 8:10/15:50 and 9:20/14:40 for NP and SP, respectively at an *in situ* intensity of 60  $\mu\text{mol}/(\text{m}^2\cdot\text{s})$  and 170  $\mu\text{mol}/(\text{m}^2\cdot\text{s})$  photons for NP and SP, respectively, measured during sampling. Sunset and sunrise were mimicked by a slow

increase and decrease of light intensities over 1 h. A temperature tidal cycle (3.0°C and 1.0°C, for NP and SP, respectively, Fig. 1), following tide times present during field sampling, was reconstructed for all treatments within each 24 h tidal temperature cycle.

Adjustable air diffusers were installed in each aquarium. Salinity (CO310-1 portable salinity probe; accuracy: 0.2%, resolution: 0.1. VWR, Leicestershire, UK) and pH (HQ30d portable multi-parameter meter, PHC301, accuracy:  $\pm 0.02$ ; HACH, Manchester, UK) were measured twice a week on National Bureau of Standards (NBS) scale for all replicates to ensure constant conditions during the experiment. A temperature data logger (HOBO UA-002-64 pendant temperature/light data logger; accuracy: 0.47°C, resolution: 0.1°C; Tempcon, Arundel, UK) was placed in each aquarium for continuous logging.

### 2.3 Marine heatwave calculations

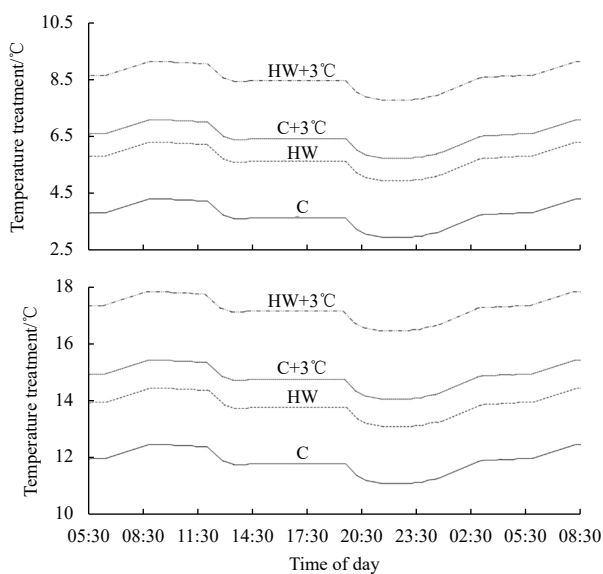
The duration and intensity of an average MHW were calculated for NP and SP following the definition of Hobday et al. (2016), i.e., temperatures exceeding the 90th percentile of the average sea surface temperature (SST) for a minimum of 5 consecutive days in any 30 days over the last 30 years. Records of coastal SST, for the winter months (December to February) in relatively close proximity to each location, were obtained from databases from the following institutions:

(1) location: Reykjavik, Marine and Freshwater Research Institute (<https://sjora.hafro.is/>), Iceland;

(2) location: Villagarcia, Meteogalicia: Ministry of the Environment, Territory and Infrastructures – Xunta de Galicia, Spain, Iq.

For NP and SP data sets, respectively.

Calculations for MHWs resulted in an average duration of 9 d and 11 d MHW, with an SST increase of 2.0°C and 1.8°C above the average for NP and SP, respectively.



**Fig. 1.** Planned daily tidal variations for northern margin populations (top) and southern margin populations (bottom) in the experimental design for the 4 treatments (Control: C, Heatwave: HW, elevated temperature: C+3°C; and heatwave during elevated temperature: HW+3°C). Fluctuations resemble daily average temperature fluctuations and times in historic data. Figure re-drawn and amended after Rendina et al. (2019).

### 2.4 Experimental design

Initial acclimation to laboratory conditions under temperatures measured at the respective sampling sites lasted 14 d, before exposure to temperature increase and simulated heatwaves after Day 14 of the experiment (Figs 2, S1 and S2). Two individuals for each of the two populations from the same region were placed in separate 4 L aquaria and three aquaria were randomly assigned to one of four treatments. After exposure, they were cultured for a further 23 d and 25 d, depending on the average duration of the MHW for NP and SP, respectively (Figs 2, S1 and S2).

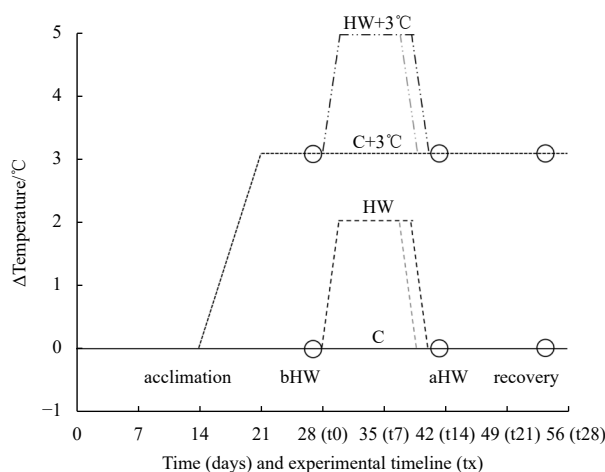
Treatments were designed to simulate present temperature conditions (Control, C); heatwaves under present conditions (heatwave, HW); average future conditions (raised temperature, C+3°C), and heatwaves under future temperature conditions (future heatwave, HW+3°C). Control conditions were set to *in situ* temperatures measured during sampling (4.3°C and 12.1°C for NP and SP, respectively) and future temperature conditions were simulated by raising the present temperature by 3°C, according to IPCC (2014) forecasts.

The acclimation to elevated temperature for treatment C+3°C was conducted over 7 d with a slow increase of  $\sim 1^\circ\text{C}$  over 2 d.

Four phases defined the measurement periods in the experiment (Fig. 2): (1) before heatwave (bHW; Days 21–28 with measurements starting at Days 28 (=t0) and performed every other day), (2) during the heatwave (dHW; Days 29–37 (t1–t9) and Days 29–39 (t1–t11), for NP and SP, respectively), (3) after heatwave (aHW; Days 38 (t10) and Days 40 (t12), for NP and SP, respectively), (4) a 14-d recovery period following the heatwave treatment (Recovery; Days 38–51 (t10–t23) and Days 40–53 (t12–t25) for NP and SP, respectively).

### 2.5 Photophysiological measurements

Photosynthetic variables were measured before and every other day throughout the heatwave and recovery period. A Junior Pulse-amplitude modulated (PAM) Chlorophyll Fluorometer (Walz, Germany) was used to determine the maximum potential quantum efficiency of Photosystem II (Fv/Fm). This entailed a



**Fig. 2.** Planned temperature variations in northern margin populations (grey) and southern margin populations (black) in 4 treatments (Control: C, heatwave: HW, elevated temperature: C+3°C and heatwave during elevated temperature: HW+3°C). The key time points during the experiment: before the heatwave (bHW), after the heatwave (aHW) and after the recovery (recovery) phases are indicated as open circles and with abbreviations. Figure re-drawn and amended after Rendina et al. (2019).

saturation pulse intensity of 8, approximating 420  $\mu\text{mol}/(\text{m}^2\cdot\text{s})$  photons, a saturation pulse length of 0.8 s and an amplification factor (gain) of 1 in combination with the software WinControl-3 (Walz, Germany), each morning before “sunrise” in the aquaria to ensure dark acclimation.

## 2.6 Data analysis

Analyses of covariance (ANCOVA) were used to evaluate the effects of temperature increase and heatwaves on individuals from different populations from northern and southern regions, taking into account a potential tank effect, as a result of both populations from each region being placed in the same aquaria (Underwood, 1997).

The analyses included the factors region (fixed, with two levels, northern and southern populations), population (random, with two levels, nested in region), temperature increase (fixed, with two levels, Control and C+3°C, orthogonal to all other factors), and heatwave (fixed, with two levels, HW and HW+3°C, orthogonal to all other factors), while tank (random, 24 levels) was included as a covariate. Analyses of the Fv/Fm were run for measurements taken before (t0), early (t2) or later (8 d after the beginning of experimental treatments, at t8) during the heatwave, early after the end of the heatwave (5 d after the end of experimental treatments, at t14 and t16 for NP and SP, respectively), and at the end of the recovery phase (t22 and t24 for NP and SP, respectively). The analysis at the end of the recovery phase was run separately for each region, including the factors population, temperature increase, heatwave, and the covariate tank. Normality of residuals was tested with Shapiro-Wilk test, homogeneity of variances are verified with Levene’s test, and the homogeneity of regression slopes are checked before running the analyses (Underwood, 1997). Estimated marginal means were calculated for post-hoc multiple comparisons of the means with Bonferroni multiple testing correction, when appropriate. The analyses were run in R, using the package rstatix (Kassambara, 2021).

Linear mixed-effect models (LME) were used to evaluate if populations fully recovered after the heatwave, as the method accounts for the correlation among repeated measures of the same individual before and after the experimental treatment (Bolker et al., 2009). The model included the fixed factors region (fixed, with two levels, NP and SP), temperature increase (fixed, with two levels, Control and C+3°C, orthogonal to all other factors), heatwave (fixed, with two levels, HW and HW+3°C, orthogonal to all other factors), time (fixed, with two levels, before the heatwave and at the end of the recovery phase, orthogonal to all other factors), and 1 tank|replicate as random effect. This analysis did not include population as a factor, to avoid the non-independence between levels, as individuals of the two populations from each region were placed in the same tank. The significance of the fixed factors was assessed using the Wald test (Zuur et al., 2007; Crawley, 2012). Model assumptions were assessed by visually inspecting plots of residuals vs. fitted values. The model was fitted using the function lmer in the R package lme4 (Bates et al., 2015). For detailed results of the statistical analyses, see Tables S1 and S2 in the supplementary information.

## 3 Results

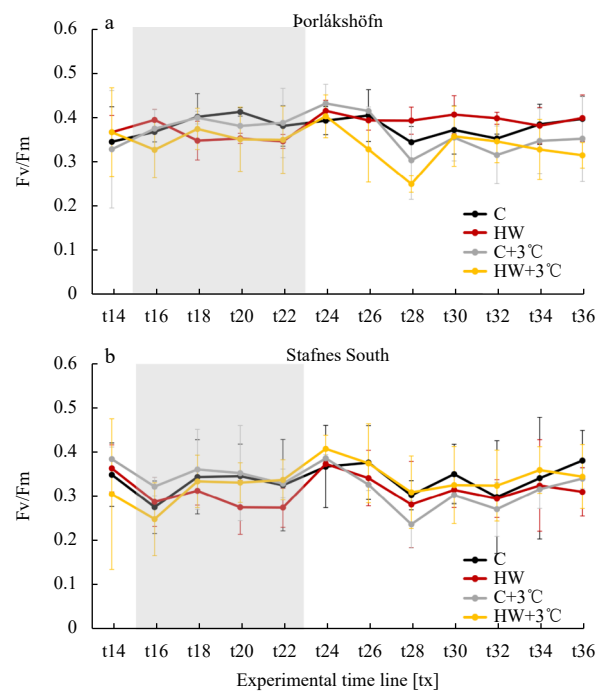
After acclimation and before exposure to elevated temperature and/or MHW conditions, no significant differences among replicates assigned to different experimental treatments were detected (Table S1, t0).

Differences among populations were clear from the beginning of the exposure (t2; Þorlákshöfn (NP2) and Stafnes South

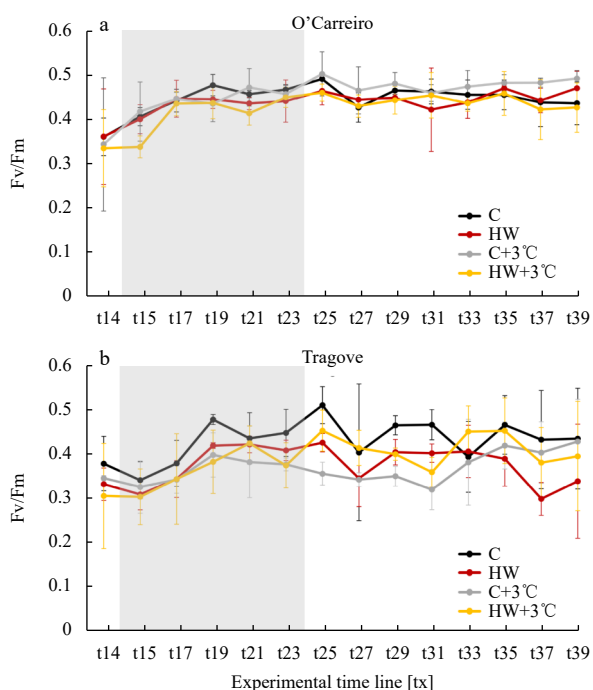
(NP1):  $P = 0.0016$ , Stafnes South vs O’Carreiro (SP2)  $P < 0.001$ , O’Carreiro vs Tragove (SP1)  $P = 0.0049$ ; Tables S1 and S2, Fig. S3). Soon after the exposure to experimental treatments (t2), the interaction temperature  $\times$  heatwave was close to significant (ANCOVA,  $P = 0.058$ ). Edge populations showed different response times after the start of a winter MHW. Southern, trailing-edge populations responded quickly to exposure to a winter MHW, with a clearer upward trend from the beginning of the MHW, while northern, leading-edge populations showed no obvious effect (Figs 3 and 4).

After prolonged exposure to the winter MHW and temperature increase (t8), the effects of temperature increase, region and population became evident, with no significant interactions among these factors (Table S1). The ranking of the populations was similar to that observed since the beginning of experimental treatments, two populations showed consistent significant differences (NP1 vs SP2,  $P < 0.001$  on t2 and t8; Table S2, Fig. S3). MHW exposure had no significant effects on any population at t8. The difference between current and increased temperature was not obvious from the graphs, but as this result was derived from a covariance analysis, any such an effect could have been masked by a tank effect that was apparent only at t8 (ANCOVA,  $P = 0.019$ ). Another trend during MHW exposure found in NP1 and, to a lesser degree, SP1 was a generally more depressed response to HW and HW+3°C treatments than to C and C+3°C treatments.

Both leading and trailing edge populations showed an initial trend of reduction in Fv/Fm rates immediately at the start of the recovery phase. Farther into the recovery period (t16), significant differences were detected among populations exposed to different experimental treatments (ANCOVA,  $P = 0.016$ , Fig. S4). Although post-hoc comparisons did not differentiate populations



**Fig. 3.** Successive Fv/Fm measurements (mean  $\pm$  SE) before (t14), throughout the heatwave (grey highlighted) and recovery phases in northern margin Population 1 (top) and Population 2 (bottom). Black, red, grey and yellow lines represent Control (C), heatwave (HW), elevated temperature (C+3°C) and Heatwave in elevated temperature (HW+3°C) treatments, respectively.



**Fig. 4.** Successive Fv/Fm measurements (mean  $\pm$  SE) before (t14), throughout the heatwave (grey highlighted) and recovery phases in southern margin Population 1 (top) and Population 2 (bottom). Black, red, grey and yellow lines represent Control (C), heatwave (HW), elevated temperature (C+3°C) and heatwave in elevated temperature (HW+3°C) treatments, respectively.

among levels of temperature increase  $\times$  heatwave (Table S3), the pattern was consistent through time during the recovery phase (t12–t16, analyses not shown).

Additionally, values for HW+3°C generally lay below those for HW after the MHW exposure for NP1 and SP1 (though not NP2 or SP2), with the difference being stronger for NP1 than SP1. During the recovery phase after MHW exposure, Fv/Fm values for NP1 were generally depressed under C+3°C and HW+3°C treatments compared to the non-temperature-elevated treatments. However, NP2 did not show such clear trends in its response (Fig. 3). There was a reduction from the beginning to the end of the recovery for all but the C treatment. All treatments showed non-significantly higher Fv/Fm values at t10, the beginning of the recovery phase; rates then dropped through the following 4 d, after which they seem to recover. Similar to leading-edge populations during recovery, the second trailing edge population, SP2, did not reflect the trend of the other southern population SP1; its response to temperature treatments was clear, not significantly lower than the C during the MHW exposure phase. Overall, the responses of SP2 to all treatments were more variable during the recovery phase than those of SP1. Ultimately, no obvious or statistically significant post-MHW effect could be determined for either SP1 or SP2.

No significant difference was found between t0 at the start of the experiment and t22 or t24 for NP and SP, respectively, at the end of the 14-d recovery phase (Figs 3 and 4, Tables S4 and S5). This verifies the full recovery of all populations after exposure to a winter MHW.

#### 4 Discussion

We found no negative effect of a winter MHW on *C. officinalis*

with, unexpectedly, no difference between leading and trailing edge populations, rejecting our hypothesis of increased vulnerability of these populations to MHWs during winter as compared to during summer (Rendina et al., 2019). A remarkable capacity for recovery was observed for both leading and trailing populations, with no stark reduction or increase of Fv/Fm values from before MHW exposure compared to the end of the recovery phase.

The average length of winter MHWs was 2 d and 4 d longer, for northern and southern populations respectively than that of a summer MHW (7 d) experienced by central populations (Rendina et al., 2019). Resilience of leading and trailing edge populations to the exposure to winter MHWs, not only under present but also under future predicted thermal SST conditions, indicates that these populations may already be well adapted to high winter temperature fluctuations in their locations of origin (Kim et al., 2018; Kolzenburg et al., 2022). As part of the daily cycle, these organisms are also exposed to abiotic stresses such as desiccation, direct sunlight, and fluctuations in oxygen availability (Hampe and Petit, 2005; Egilsdottir et al., 2013; Williamson et al., 2014). In addition, microclimatic variability in the intertidal is vast, with local influences on the physiology, structure and distribution of intertidal organisms (Helmuth et al., 2002).

Rendina et al. (2019) found significant negative effects of predicted future temperatures combined with a summer MHW on the physiology (photosynthesis, respiration and light and dark calcification) of central populations of *C. officinalis*. Our data support those findings, but suggest that populations from both regions, in contrast, may be resilient to future winter temperature conditions and future winter MHWs (as well as the combination of both), despite their exposure to narrower annual sea surface temperature variation than central populations (Kolzenburg et al., 2022). Southern populations showed a positive trend in Fv/Fm ratios under all conditions. This trend was not significant, however, and so does not conclusively indicate local adaptation or enhanced response potential to temperature rise in trailing edge populations. Further studies are required to test whether this could be indicative of a critical capacity to adapt to forecasted rises in SST coupled with increases in the frequency and intensity of winter as well as summer MHWs.

Photosynthetic efficiency, measured as Fv/Fm, was reduced during exposure to future temperatures, either ambient or a future winter MHW, in all four tested populations, demonstrating high thermal sensitivity of photosynthetic performance, a process known to be generally temperature-dependent (Crafts-Brandner and Salvucci, 2002), under winter conditions. At first these findings may suggest low resilience and little local adaptation to extreme temperature events with little capacity to tolerate exposure to winter MHWs under a predicted SST increase of 3°C (IPCC, 2014). Full recovery of all populations under all conditions following an extended recovery period, however, suggests instead a high capacity for resilience in the face of thermal stress.

While we present photophysiological measurements of the efficiency and thermal plasticity of the first stage of photosynthesis and respiration, the electron transport efficiency of Photosystem II, measured as Fv/Fm, however, understanding the full physiological resilience of these leading and trailing edge populations to future MHWs requires additional information on photosynthesis and respiration as well as light and dark calcification rates.

To date, the only study offering insight into the photophysiology of articulated intertidal coralline alga species across their distribution in the NE Atlantic is one by Williamson et al. (2018). Similarly, studies on the initial phase of the photosynthet-

ic light reaction (Fv/Fm) of macroalgae and the effects of extreme temperatures have only recently emerged.

The considerable variety displayed in responses to elevated temperature conditions among and within populations indicated the need to incorporate the full geographical distribution of species, including central and more peripheral populations in studies of species' vulnerability to MHWs. A comparative study of southern (trailing) and northern (leading) edge populations of *Fucus vesiculosus* and *Zostera marina* by Mota et al. (2018) showed higher thermal resistance and recovery in southern populations of *F. vesiculosus* but the opposite for northern and southern populations of *Z. marina*. Although we found no significant difference in the response of leading and trailing margins, the positive trend in Fv/Fm ratios in trailing edge but not leading edge populations suggests similar intraspecific differentiation between southern and northern populations of *C. officinalis* in their responses to MHW conditions.

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## Supplementary information:

**Fig. S1.** Temperature development (mean  $\pm$  SD) during the experiment for northern marginal populations. The grey background represents heatwave exposure time. Black, red, grey and yellow lines represent Control (C), Heatwave (HW), elevated Temperature (C+3°C) and Heatwave in elevated temperature (HW+3°C) treatments, respectively.

**Fig. S2.** Temperature development (mean  $\pm$  SD) during the experiment for southern marginal populations. The grey background represents heatwave exposure time. Black, red, grey and yellow lines represent Control (C), Heatwave (HW), elevated Temperature (C+3°C) and Heatwave in elevated temperature (HW+3°C) treatments, respectively.

**Fig. S3.** Physiological response (Fv/Fm; mean  $\pm$  SE) of individuals from distinct populations (1, 2) and regions (3) early (t2) or late (t8) during the heatwave. Panel 4 shows the effect of temperature increase on the physiological response of individuals late during the heatwave. Letters above the bars indicate homogenous groups among populations according to post-hoc pairwise comparisons of the estimated marginal means with Bonferroni multiple testing correction.

**Fig. S4.** Physiological response (Fv/Fm; mean  $\pm$  SE) of individuals from distinct populations exposed to temperature increase and heatwaves early after the end of the heatwave (5 days after the end of experimental treatments, at t14 and t16 respectively for Northern and Southern populations). C = Control, C+3 = elevated temperature, HW = heatwave, HW+3 = heatwave in elevated temperature.

**Table S1.** Summary of ANCOVA analyses on the effect of temperature increase (Te) and heatwave (Hw) on the physiological response (Fv/Fm) of individuals from two distinct populations (Po) in each region (Re) before (t0), early (t2) or later (8 days after the beginning of experimental treatments, at t8) during the heatwave, and early after the end of the heatwave (5 days after the end of experimental treatments, at t14 and t16 respectively for Northern and Southern populations). Significances are highlighted in bold.

**Table S2.** Post-hoc pairwise comparisons of the estimated marginal means with Bonferroni multiple testing correction ( $\pm$  SE), to assess differences in the physiological response (Fv/Fm) of individuals from distinct populations early (t2) or later (8 days after the beginning of experimental treatments, at t8) during the heatwave. Significances are highlighted in bold.

**Table S3.** Post-hoc pairwise comparisons of the estimated marginal means with Bonferroni multiple testing correction ( $\pm$  SE), to assess differences in the physiological response (Fv/Fm) of individuals among combinations of Temperature increase (Te) and Heatwave (Hw) within each population early after the end of the heatwave (5 days after the end of experimental treatments, at t14 and t16 respectively for Northern and Southern populations). C = control, C+3 = raised temperature, HW = heatwave, HW+3 = heatwave under future temperature conditions. Significances are highlighted in bold.

**Table S4.** ANCOVA on the variation of the effect of temperature (Te) and heatwave (Hw) on the physiological response (Fv/Fm) of individuals from distinct regions (Re) after exposure to temperature increase (Te) and heatwave (Hw), by comparing its variation across time (end of the recovery phase versus before the heatwave). Significances are highlighted in bold.

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