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Environmental variability shapes productivity and thermal responses of a free-living coralline alga

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ABSTRACT

Free-living coralline algae are key foundation species of worldwide distributed coralline algal beds, habitats recognized as biodiversity hotspots and significant sites of carbonate production. Among them, *Phymatolithon lusitanicum* forms extensive beds along the southern coast of Portugal, where frequent upwelling-downwelling alternations create a highly dynamic environment. These oceanographic shifts drive rapid changes in seawater temperature and light, with downwelling associated with higher values and upwelling with lower ones. This variability is likely to influence algal physiological performance and resilience to marine heatwaves (MHWs), which in this region often coincide with intense downwelling. Here, we examined the physiological responses of *P. lusitanicum* to simulated fluctuations in temperature and irradiance, with and without the superimposition of a MHW event, through a mesocosm experiment that realistically simulated natural fluctuations in temperature and light. Physiological responses (photosynthesis, respiration and calcification) were measured during upwelling, downwelling, and transitional periods. *Phymatholithon lusitanicum* showed considerable phenotypic plasticity, with physiological responses closely tracking environmental variability. Metabolic activity increased during downwelling, in terms of both primary and carbonate productivity, whereas upwelling periods led to negative net primary productivity and declines in calcification. Superimposing a MHW on a downwelling period caused no significant adverse effects, indicating high thermal tolerance. These results emphasize the dual role of environmental variability in regulating algal productivity and fostering resilience to extreme warming events, while highlighting the potential for strong negative impacts of cold spells, which represent the extreme end of upwelling regimes and occur as frequently as MHWs in the study region.

1. Introduction

Free-living coralline algae, i.e., rhodoliths (*sensu lato*; Jardim et al., 2025), can form highly biodiverse habitats, the coralline algal beds (including rhodolith and maerl beds, *sensu lato*; Jardim et al., 2025). These systems have an extensive geographic and bathymetric distribution, from tropical to polar areas, and from the intertidal to depths exceeding 200 m (Foster, 2001; Fragkopoulou et al., 2021; Rebelo et al., 2021). Coralline algal beds form aggregations that can cover extensive areas (Foster, 2001; Fragkopoulou et al., 2021) and represent a key coastal shelf habitat, alongside coral reefs, kelp forests and seagrass meadows (Tuya et al., 2023). These beds have long been acknowledged as biodiversity hotspots due to the rich diversity of associated organisms (Tuya et al., 2023; Bulleri et al., 2025; Schubert et al., 2025), resulting from the availability of refuges within the beds that offer shelter and protection from predation and physical disturbances (Kamenos et al., 2003; Steller et al., 2003; Otero-Ferrer et al., 2019). Furthermore, coralline algal beds have been recognized as one of the most important carbonate producers in coastal waters, with values of $CaCO_3$ production comparable to those of coral reefs (Amado-Filho et al., 2012). Through

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high primary productivity and the accumulation of substantial $CaCO_3$ deposits, these environments can sequester and store carbon over both short and long timescales, playing an important role in the oceanic carbon cycle (Nelson, 2009; van der Heijden and Kamenos, 2015; Schubert et al., 2024).

At the organismal level, the physiological performance of coralline algae, particularly photosynthesis and calcification, is strongly influenced by fluctuations in temperature and light (Martin et al., 2006, 2007, 2013a; Sordo et al., 2020; Qui-Minet et al., 2021). These processes typically peak during warm, high-light summer conditions and decline in winter. While such seasonal trends demonstrate sensitivity to long-term variability, short-term physiological responses to rapid environmental changes remain comparatively underexplored. Research to date has largely centered on temperate species inhabiting highly dynamic intertidal habitats, such as rock pools (Guenther and Martone, 2014; Williamson et al., 2014, 2017; McCoy et al., 2016; McCoy and Widdicombe, 2019). In tropical regions, studies on coralline algae have mainly addressed contrasts between stable and variable habitats and the influence of upwelling on growth and carbonate production (Schäfer et al., 2011; Bach et al., 2017; Pulecio-Plaza et al., 2023). For example, Bach et al. (2017) found that *Lithophyllum kotschyanum* from environmentally variable reef flats maintained consistent photosynthetic rates, suggesting adaptation to fluctuating conditions, whereas individuals from stable reef crests were larger and more abundant. Similarly, on the Pacific coast of Panama, coralline algal beds in stable environments supported greater growth and carbonate production than those in upwelling zones, where lower abundance and slightly reduced growth and calcification were observed (Schäfer et al., 2011). In contrast, Pulecio-Plaza et al. (2023) reported enhanced growth and calcification of tropical crustose coralline algae during upwelling relative to non-upwelling periods. These findings underscore the role of environmental variability in shaping algal productivity, as well as its link to enhanced resilience through phenotypic plasticity.

In the context of accelerating climate change, coralline algae face mounting exposure to multiple, interacting stressors, with the intensification of marine heatwaves (MHWs) emerging as a particularly critical threat (Frölicher et al., 2018; Oliver et al., 2019). Elevated temperatures can alter enzymatic activity, metabolism, and energy balance, thereby affecting coralline algal growth and photosynthetic performance (Martin and Hall-Spencer, 2017; Cornwall et al., 2019). While warming generally reduces photosynthesis and calcification across tropical (Vásquez-Elizondo and Enríquez, 2016), subtropical (Schubert et al., 2019), and temperate species (Legrand et al., 2017; Graba-Landry et al., 2018; Qui-Minet et al., 2019; Rendina et al., 2019), individuals from naturally variable environments often display high resilience to MHWs, showing little to no decline in growth or physiological performance (Schubert et al., 2021a; Krieger et al., 2023a; Nannini et al., 2025). These findings reinforce the view that the environmental context in which heatwaves occur critically shapes their biological impacts (Starko et al., 2024).

Environmental variability is a defining feature of marine ecosystems, influencing the physiology, distribution, and resilience of benthic organisms. Species inhabiting dynamic environments are generally more tolerant to fluctuations in environmental parameters (Witman et al., 2023), as such variability favors populations with high phenotypic plasticity (Boyd et al., 2016). In general, organisms inhabiting dynamic and heterogeneous environments have often been found to exhibit higher trait plasticity (Gianoli, 2004; Lázaro-Nogal et al., 2015; Edelaar et al., 2017), which allows them to rapidly adjust to changing conditions. Phenotypic plasticity, the ability of a single genotype to express different phenotypes in response to environmental changes (Fox et al., 2019), enables flexible adjustments in physiology, morphology, and gene expression (Pazzaglia et al., 2021), facilitating acclimatization within a generation and potentially promoting long-term adaptation (Snell-Rood et al., 2018). Exposure to fluctuating conditions, such as recurrent temperature changes, can also induce thermal priming, a process by which organisms develop a form of stress memory that enhances tolerance to future stress events (Jueterbock et al., 2021; Schubert et al., 2021a; Brown et al., 2024; Ferrara et al., 2025). Studies comparing constant and variable environments often report higher stress tolerance and performance in organisms originating from more dynamic habitats (Schaum et al., 2016; Nguyen et al., 2020; O'Dwyer and Murphy, 2021; Schubert et al., 2021a). However, the effects of environmental variability are not universally positive. A recent meta-analysis showed that thermal variability can also exacerbate negative effects on organismal performance, particularly at higher mean temperatures or with larger fluctuation ranges, with outcomes depending on the characteristics of thermal variation, the response metric considered, and organismal traits (Slein et al., 2023). This context dependency highlights the need to better understand how environmental variability shapes organismal responses to climatic extremes. Yet, despite increasing recognition of the ecological importance of environmental variability (Oliver and Palumbi, 2011; Schoepf et al., 2015), relatively few studies have explored how it influences the physiological performance of marine primary producers or their resilience to extreme climatic events such as MHWs.

The Algarve coast in southern Portugal is a variable environment, as it experiences seasonal upwelling, as well as warm counter-currents that induce downwelling events (Fiúza, 1983; Criado-Aldeanueva et al., 2006; De Oliveira Júnior et al., 2021). These circulation patterns result in rapid and large changes in seawater temperature at a short time scale (Garel et al., 2016; De Oliveira Júnior et al., 2021), accompanied by strong variation of *in situ* light availability (Schubert et al., 2021a). Hence, marine habitats in this region, including coralline algal beds built by *Phymatolithon lusitanicum* V. Peña (Peña et al., 2015), are exposed to a highly fluctuating environment. This free-living coralline alga is the third most abundant coralline bed-forming species from the Atlantic Iberian Peninsula (Galicia and the Algarve; Peña et al., 2015). Previous studies on *P. lusitanicum* have been so far mainly taxonomic (Peña et al., 2015) and focused on the seasonal variations in physiological rates and their responses to ocean acidification and warming (Sordo et al., 2016, 2018, 2019, 2020). The study from Schubert et al. (2021a) on *P. lusitanicum* was the first to analyse the effects of a MHW event, taking into account the thermal fluctuations due to downwelling periods of the habitat in which this species lives. Their findings indicated that the impacts of MHWs in such environments are seemingly mitigated by the development of thermal stress memory, promoting a high tolerance and resilience. However, the former study focused solely on the influence of temperature fluctuations due to downwelling, without taking into account their alternation with upwelling events and the simultaneous variations in light availability. The importance of the latter on primary production and calcium carbonate deposition is well known in coralline algae (e.g., Martin et al., 2013b; Krieger et al., 2023b; Schubert et al., 2022, 2024).

In this study, the physiological responses of *P. lusitanicum* were assessed under conditions simulating both, the naturally occurring variable temperature and light conditions associated with alternating upwelling and downwelling periods, in the absence and presence of a MHW event, to determine the effects of those environmental fluctuations on (i) algal productivity and (ii) the thermal tolerance and resilience of the rhodoliths.

2. Materials and methods

2.1. Study site and environmental conditions

The studied rhodolith species inhabits a coralline algal bed located 4.7 nautical miles off the coast of Armação de Pêra, in the Algarve, Southern Portugal (37°01′N, 8°19′W; Fig. 1). The estimated area of the bed is 3 km^2, and the depth ranges from 13 to 25 m (Sordo et al., 2018). Previous taxonomic studies have shown that the bed investigated here is almost exclusively dominated by *Phymatolithon lusitanicum* (Carro et al.,

Fig. 1. Location of the coralline algal bed off the coast of Armação de Pêra, south coast of Portugal (red dot; https://mapswire.com/) and the studied rhodolith species, *Phymatolithon lusitanicum* (photo). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2014; Pardo et al., 2014; Peña et al., 2015), a finding that has been repeatedly confirmed in more recent studies conducted at the same site (e.g., Schubert et al., 2022, 2024).

The region is under the influence of strong and persistent coastal upwelling that usually occurs between April and October (Garel et al., 2016). It is generally more pronounced at the west compared to the south coast of Portugal, due to the predominance of northerly winds (Fiúza, 1983; Garel et al., 2016). However, throughout the year, the relaxation of these upwelling-favourable winds results in an unbalanced pressure gradient, which promotes the formation of warm poleward flows, defined as coastal countercurrents (CCCs; Garel et al., 2016; De Oliveira Júnior et al., 2021, 2022). These CCCs typically develop during periods of wind relaxation that interrupt the ongoing upwelling, and are suppressed during strong, sustained upwelling-favourable winds. This alternation between CCCs and active upwelling tends to occur on short timescales, i.e. several days, with relaxation events and resulting CCCs often lasting 1–5 days, but occasionally persisting up to 15 days (Sánchez et al., 2006; Garel et al., 2016). This dynamic interplay between upwelling and CCCs results in sharp and rapid current inversions about once a week, which leads to high variability in both daily and weekly temperature (14–24°C; Garel et al., 2016) and light intensity, as shown by *in situ* data collected at the coralline algal bed (Fig. 2).

An analysis conducted on MHW events, based on sea surface temperature (SST) time series data from 1982 to 2011 provided by the Marine Heatwave Tracker (Schlegel, 2018), indicated that the southern coast of Portugal has been experiencing increasing frequency and severity of MHWs in the past two decades (Fig. 3a). These events are most frequent during spring, summer and autumn, and the majority lasts between 1 and 2 weeks (Fig. 3b and c). The strongest events, with the highest maximum intensities occur mainly during spring and summer (Fig. 3c and d). The data show that over the last 10 years, the majority of MHWs occurred during the spring and summer, with a total of 21 detected events. Of these, 7 were categorized as strong (2-3x the threshold-to-mean difference; Hobday et al., 2016, 2018). Between the spring and summer, the maximum intensity reached so far was 4.3 °C above the climatological threshold and the duration of these events ranged from a minimum of 5 to a maximum of 32 days. The events identified by the Marine Heatwave Tracker align with recorded *in situ* temperature peaks at the coralline algal bed (Fig. 2).

2.2. Sampling and experimental design

Rhodoliths were collected by SCUBA in Armação de Pêra in May 2024, at a depth of 22 m and a seawater temperature of 15 °C. After sampling, the rhodoliths were transported to the nearby Ramalhete marine station and kept in seawater flow-through tanks for preacclimation at a temperature of 15.5 °C and a light intensity of 25 μmol photons m^{-2} s^{-1} (13 h light: 11 h dark; LEDVANCE Flood LED IP65, 50 W, 6500 K, Ledvance, Germany) for 10 days. The preacclimation temperature was chosen as an average between the temperature during

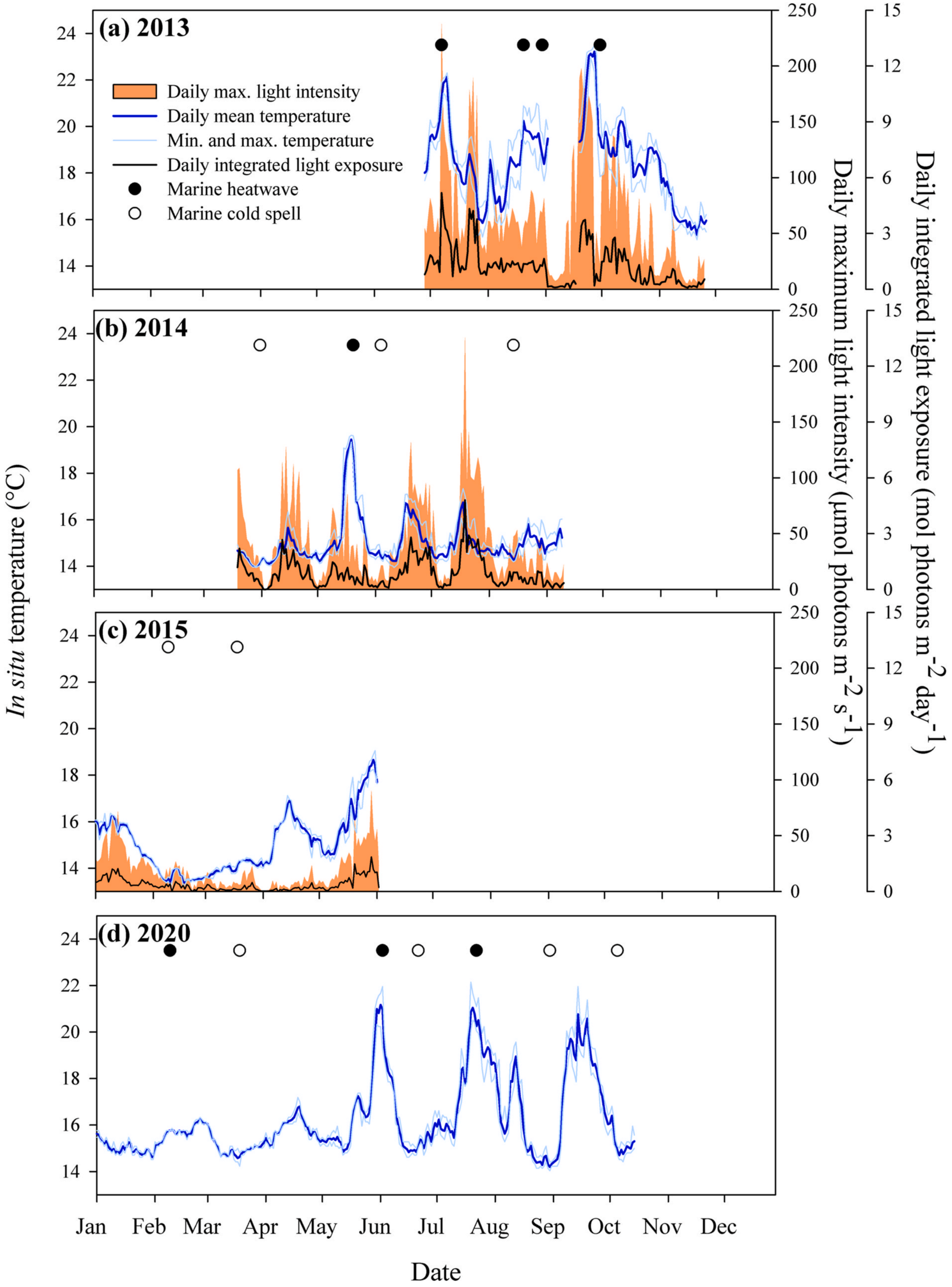

Fig. 2. Environmental variability at the location of the coralline algal bed (22 m depth), off the coast of Armação de Pêra, South Portugal. Graphs (a-d) show available *in situ* temperature and light data, collected by HOBO temperature (Onset, USA) and Odyssey PAR (Dataflow Systems, Ltd., New Zealand) dataloggers. Data show daily mean, maximum and minimum temperature, daily maximum light intensity and daily integrated light exposure, as well as identified marine heatwave and cold spell events during these periods, obtained from the Marine Heatwave Tracker (Schlegel, 2018).

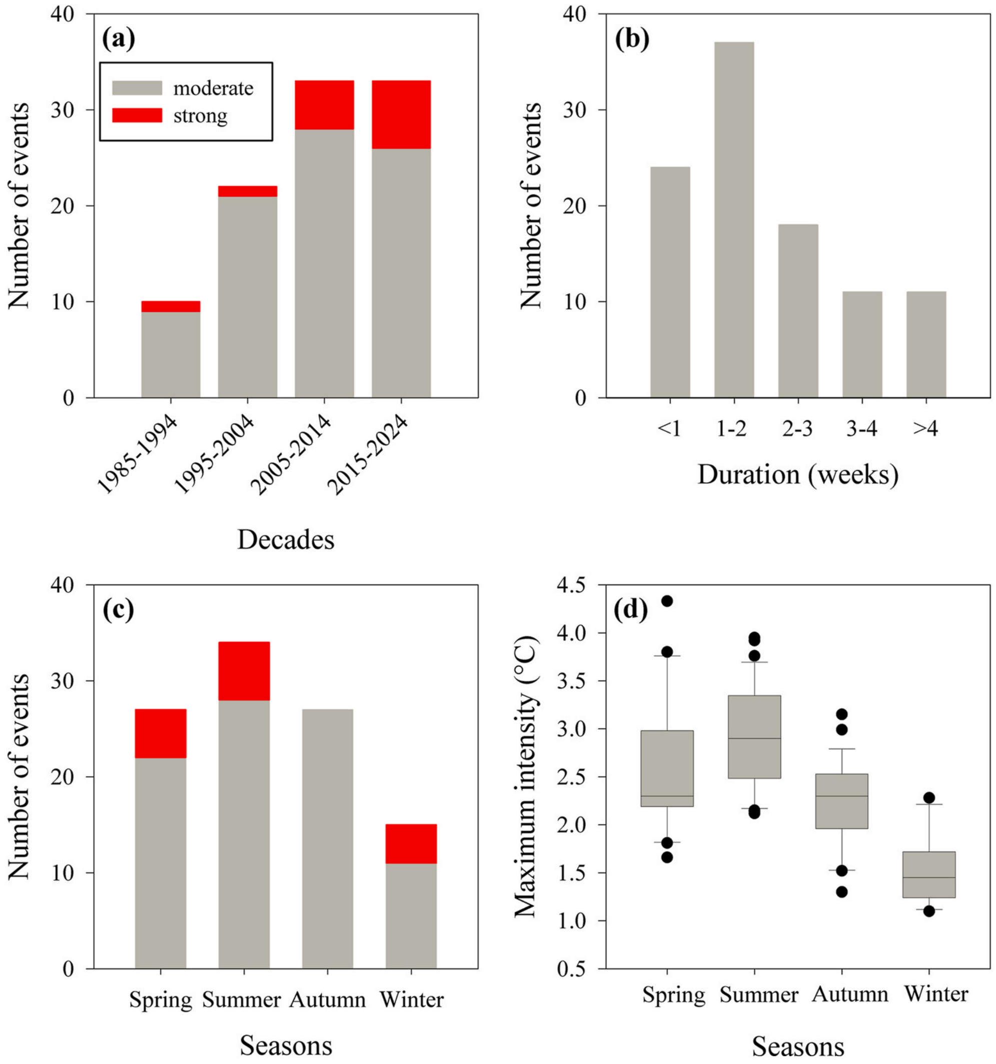

Fig. 3. Marine heatwave analysis for the location of the coralline algal bed off the coast of Armação de Pêra, South Portugal. (a) Number of moderate (1-2x the climatological threshold-to-mean difference) and strong (2-3x) MHW events between 1985 and 2024, by decade, (b) the duration of the events, (c) seasonal variability in the frequency, and (d) intensity of the events. Data were extracted from the Marine Heatwave Tracker (Schlegel, 2018) and are based on a fixed baseline climatology (1982-2011).

collection (15 °C), the mean temperature for the month of April at the study site, according to the seasonal climatology (15.9 °C).

Experimental conditions were established based on a combination of *in situ* environmental data and records from the Marine Heatwave Tracker (Schlegel, 2018), with the aim of simulating natural thermal variability associated with alternating upwelling and downwelling events and a realistic MHW scenario. *In situ* temperature records (Fig. 2) indicated that during seasonal upwelling periods, minimum temperatures reached approximately 14 °C. In contrast, during downwelling phases (excluding MHW events), maximum temperatures ranged between 17 °C and 20 °C. Notably, the lowest of these maxima (~17 °C) typically occurred at the onset of the seasonal transition (April-May). Given that both field sampling and the start of the experiment took place in May, a maximum temperature of 17 °C was selected to represent downwelling conditions. Thus, the extremes for the Control treatment were chosen as 14 °C and 17 °C to simulate upwelling and downwelling, respectively, with temperature increasing/decreasing by 1 °C day^{-1} (Fig. 4). As for the treatment, simulating a MHW event (HW treatment), it mirrored the control conditions, but with the additional simulation of a MHW on top of the second downwelling event. The peak of the MHW event was chosen to be 21 °C (+4 °C above the threshold), based on the maximum intensity recorded for strong events during spring, with an average of 3.7 °C above the climatological mean and a recorded maximum value of 4.3 °C (Fig. 3d).

In parallel with the thermal conditions, light regimes characteristic of upwelling and downwelling events were also simulated to reflect natural variability. Experimental light levels were derived from *in situ* measurements, which indicated that daily maximum light intensity and daily integrated light exposure ranged from values as low as 0 μmol photons m^{-2} s^{-1} and 0 mol m^{-2} day^{-1} under upwelling conditions to as high as 240 μmol photons m^{-2} s^{-1} and 5.2 mol m^{-2} day^{-1} under downwelling conditions (Fig. 2). To avoid imposing extremes, the minimum light intensity used in the experiment was set to 5 μmol photons m^{-2} s^{-1}. The maximum light level was determined based on *in situ* records of peak daily irradiance and daily light exposure, assuming a 13-h light and 11-h dark cycle, corresponding to the local photoperiod conditions during the experimental period. To simulate transitions between upwelling and downwelling phases, light intensity was modulated synchronously with temperature, following three discrete levels: 5 μmol photons m^{-2} s^{-1} (upwelling), 25 μmol photons m^{-2} s^{-1} (intermediate), and 50 μmol photons m^{-2} s^{-1} (downwelling peak) in both experimental treatments (Fig. 4). These corresponded to daily light exposures of 0.23, 1.17, and 2.34 mol photons m^{-2} day^{-1}, for the upwelling, intermediate, and downwelling phases, respectively.

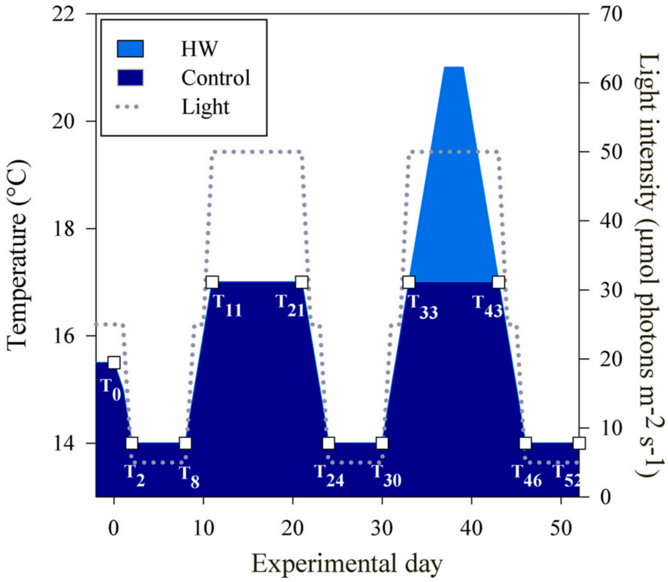

Fig. 4. Experimental design and treatment conditions. Rhodoliths of *Phymatolithon lusitanicum* were exposed to alternating upwelling and downwelling conditions in the Control (C) group (14–17 °C) and to the same sequence with an additional simulated marine heatwave (HW) during the second downwelling period (T_{max} = 21 °C, +1 °C day^{-1}) in the HW group. Light intensity fluctuations were identical across treatments. White squares indicate the time points (T_0 - T_{52}) at which physiological measurements were taken.

To achieve the target light intensities, light conditions within the experimental tanks were initially set to 50 μmol photons m^{-2} s^{-1} using a calibrated quantum sensor (LI-250A, LI-COR, USA). Neutral-density shading films were then applied in calibrated combinations above the tanks to achieve the desired reductions to 25 and 5 μmol photons m^{-2} s^{-1}.

The experimental setup consisted of ten 25-L tanks (n = 5 for each treatment), which were connected to a seawater flow-through system. Prior to entering the tanks, the water was filtered through sand filters, followed by two in-line cartridge filters (10–20 μm and 5 μm) and two UV filters (16 and 8 W), then pumped into a 2000-L head tank, where the temperature was lowered to 13 °C by a cooling pump (i-Komfort, Kripsol), before entering the indoor experimental tanks. Each individual tank was equipped with water and air inflow tubes, and with a sensor and a heater connected to the Aquatronica centralized system (ACQ115, Aquatronica S.r.l., Italy), which was used to control and record the temperatures during the experiment, in the tanks randomly assigned to a treatment.

2.3. *Photosynthetic and calcification rates*

Physiological measurements (photosynthetic, respiratory and calcification rates, as described in Schubert et al., 2021a) were taken at the beginning, peak onset, peak end, and conclusion of each upwelling and downwelling event, which resulted in 11 measurements over time (Fig. 4). At each time point, the same rhodoliths (n = 1 per tank, n = 5 per treatment) were incubated in custom-made closed chambers (V = 70 mL) with filtered seawater (0.45 μm) at their respective treatment temperature and light conditions. Water inside the chambers was kept homogenised by a magnetic stirrer. The temperature was maintained by an immersion circulation bath (Julabo F10-C), which kept the water inside the chambers at the desired temperature, by continuous circulation through the outer water jacket of the chambers. The samples were first incubated at their corresponding treatment temperature and light intensity for 1 h to determine photosynthetic and light calcification rates. Subsequently, another 1-h incubation was carried out, in darkness, to determine respiratory and dark calcification rates.

To determine net photosynthesis (NP) and respiration (R) rates, oxygen levels were measured at the beginning and at the end of each incubation, using a Microx 4 oximeter (PreSens, Germany). The water in the chambers was collected before and after every incubation, stored in borosilicate tubes of 25 ml each in duplicates and poisoned with $HgCl_2$. The water samples were later used for total alkalinity (TA) analyses to determine light (LG) and dark calcification rates (DG). This analysis was performed based on the alkalinity anomaly principle, according to which for each mol of $CaCO_3$ that precipitates, TA decreases by two mol (Smith and Kinsey, 1978). The TA measurements were conducted, using the modified Gran titration method (Hansson and Jagner, 1973). The titration was carried out with HCl 0.1 M, using the Titroline 7000 automated titration system (SI Analytics, Mainz, Germany) connected to an autosampler (TW alpha plus, SI Analytics, Mainz, Germany). Data was analysed with the Titrisoft 3.2 software (SI Analytics, Mainz, Germany). For quality control, a certified reference material of known total alkalinity was used to calibrate the method (supplied by the Marine Physical Laboratory, Scripps Institution of Oceanography, USA).

Daily primary productivity (Pprod) was calculated as the product of net photosynthesis (NP) and the daily light period (13 h), minus the product of respiration (R) and the daily dark period (11 h). Similarly, daily calcification productivity (Gprod) was estimated by multiplying light calcification rates (LG) by 13 h and adding the product of dark calcification (DG) and 11 h.

At the beginning and the end of the experimental period, photosynthesis- and calcification-irradiance curves were performed (n = 5 per curve), to assess potential differences in the light response of the rhodoliths upon exposure to the two experimental treatments. For this, rhodoliths were incubated first in the dark and subsequently under eight increasing light intensities and finally again in darkness, with a duration of 1 h for each incubation. Oxygen measurements and water sampling for TA analysis was performed as described above, to determine net photosynthesis (NP), light (R_L) and dark respiration (R_D), and light (LG) and dark calcification (DG). For each curve, a series of parameters were then calculated. Gross photosynthesis (GP) was determined by substracting respiration rates (average of R_D and R_L) to the measured net photosynthesis (NP). Maximum photosynthetic rates (NP_{max} and GP_{max}) were calculated as an average of the maximum values above saturating irradiance. Photosynthetic efficiency (αP) was estimated by linear least-squares regression from the initial slope of the light response curve. The compensation irradiance (E_c) was estimated as the ratio R_D/α, and the saturation irradiance (E_k) from the ratio NP_{max}/α. For the calcification-irradiance curves, maximum light calcification rates (LG_{max}) and the initial light utilization efficiency (αG) were determined as described above for photosynthesis. Saturation irradiance (E_k) was estimated as the ratio of $LG_{max}/\alpha G$ and the compensation irradiance (E_c) as DG/α.

At the end of the experiment, all the rhodoliths were dried in the oven at 60 °C for 48 h to determine the dry weight, which together with the volume of the incubation water and the incubation time was used to normalize the physiological measurements.

2.4. *Statistical analysis*

To test for potential differences between the two experimental groups (i.e., main effects), they were first analysed together and compared. Subsequently, each treatment was analysed separately, for each physiological parameter, to assess physiological rates over time in response to fluctuating environmental conditions. Specifically, to test for differences in physiological responses between the two experimental conditions, while accounting for repeated measurements (i.e., non-independence) over time, a linear mixed-effects model was fitted to each physiological parameter, with “treatment” as a fixed effect, and “day” and “tank” as random effects. When significant treatment effects were detected ($p < 0.05$), pairwise comparisons were conducted by fitting a linear model at each time point to identify when the differences occurred. Additionally, a one-way ANOVA was performed, for each treatment separately, to test for differences in the mean values of physiological parameters through time points. Prior to the analysis, normality of the data was assessed with the Shapiro-Wilk test. In case of not normally distributed data, logarithmic transformations were applied (i.e., R and LG for the control group; Pprod for the HW treatment). The ANOVA was used for normally distributed data (DG, log_R, log_LG, Pprod and Gprod for the control group and DG, R, LG and log_Pprod for the HW treatment), and was followed by Tukey's HSD test. In the case of data that did not follow normality (NP and GP for both treatments and Gprod for the HW group), the Kruskal-Wallis test was used, followed by the Dunn's test with Bonferroni correction.

To assess effects of the experimental conditions on the light-curve parameters, three comparisons were carried out: between the initial and final control curves, between the initial and final HW curves, and between the final control and final HW curves. Prior to the analysis,

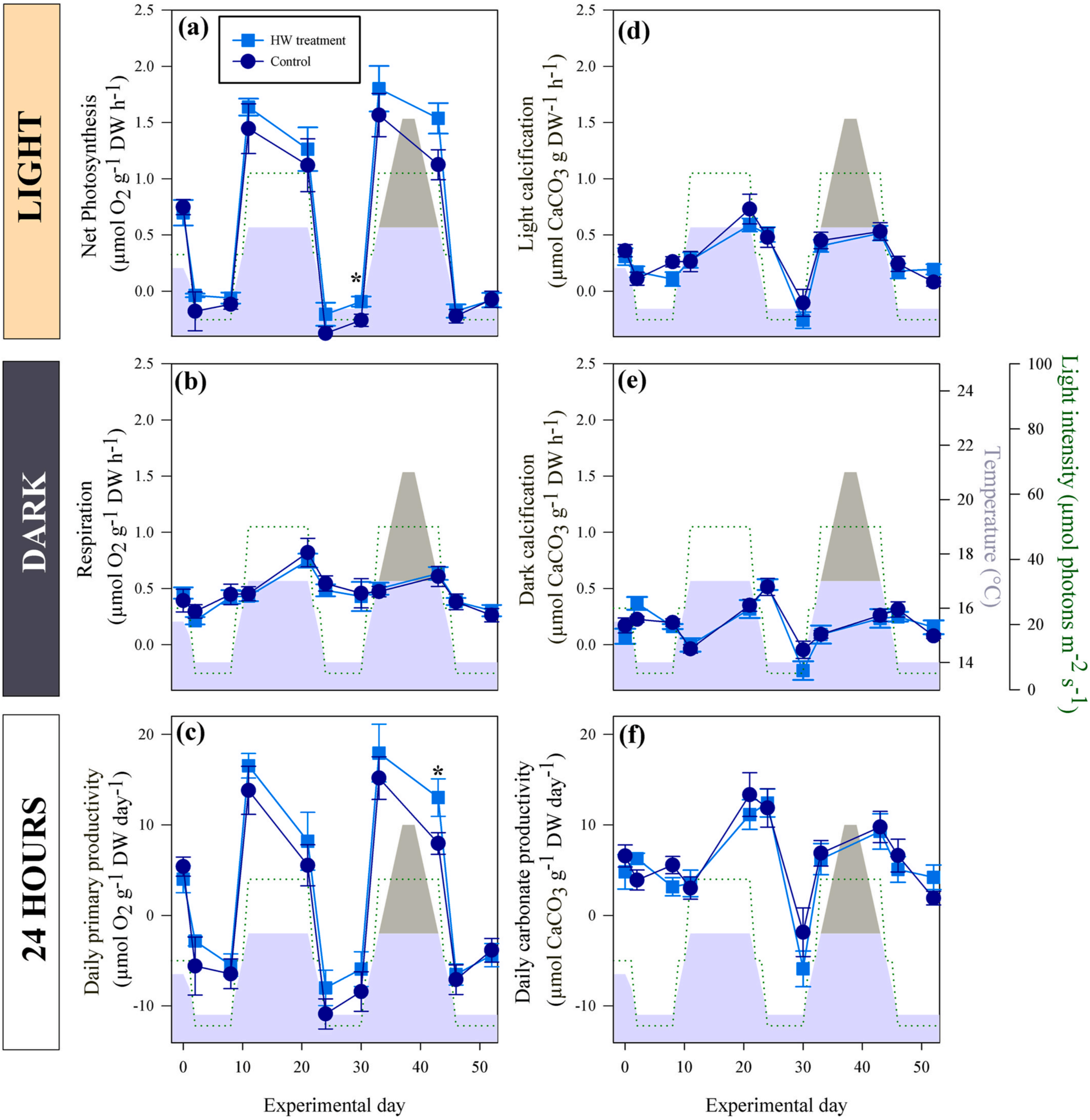

Fig. 5. Physiological responses of *Phymatolithon lusitanicum* under alternating upwelling and downwelling conditions. Panels (a) and (b) show photosynthetic and respiratory rates, respectively, and panel (c) shows the resulting daily net primary productivity. Panels (d) and (e) show light and dark calcification rates, while panel (f) represents the resulting daily integrated carbonate productivity. Experimental temperature (grey shading, dark grey highlightening the MHW) and light intensity (dotted green line) are indicated in each panel. Values represent mean ± SE (n = 5 per time point and treatment). Significant differences (ANOVA, $p < 0.05$, Tukey post hoc) between groups (Control vs. HW treatment) are indicated by asterisks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

normality was assessed with the Shapiro-Wilk test. For normally distributed data (NP_{max}, GP_{max}, DR, α, E_k and E_c for both photosynthesis and calcification, LG_{max}), a one-way ANOVA was performed to compare the parameters between initial and final curves. If deviations from normality were detected, logarithmic transformations were applied (i.e., E_c for the initial vs. final control and initial vs. final HW analyses; E_k for the final control vs. final HW analysis). The Kruskal-Wallis test was applied to non-normally distributed data (DG). When directly comparing the final control with the final HW curves, all parameters followed a normal distribution and were thus analysed with a one-way ANOVA.

All analyses were performed in R (R version 4.2.2, R Core Team, 2024), using the “tidyverse” (Wickham et al., 2019), FSA (Ogle et al., 2025), “lmerTest” (Kuznetsova et al., 2017), and “performance” (Lüdecke et al., 2021) packages. The program used to create the graphs was SigmaPlot11.

3. Results

The comparison between the Control group and the HW treatment, which included a MHW simulated on top of the second downwelling period, revealed limited physiological differences between the two groups (Fig. 5). Pairwise comparisons across measurement days (Table 1) indicated minor differences between Control and the HW treatment: net photosynthesis was slightly higher in the HW treatment at the onset of the second downwelling period (T_{30}), and daily primary productivity was slightly elevated in the HW treatment, immediately following the MHW event (T_{43}). Although gross photosynthesis showed a significant main effect, no significant differences were detected between treatments at any individual time point (Table 1). Furthermore, in the HW treatment, physiological responses measured during the final upwelling phase, immediately following the HW event (T_{46}–T_{52}), did not significantly differ relative to those observed during the first upwelling period (T_2–T_8, Table S1). This suggests that, despite a transient increase in primary productivity at a single timepoint immediately after the MHW, the algae's overall physiological performance did not differ between the Treatment and Control groups following the event.

Table 1

Results of linear mixed-effects models (LMM) testing for differences in physiological responses of *Phymatolithon lusitanicum* between experimental conditions (Control vs. HW) across measurement days. Significant effects ($p < 0.05$) are shown in bold; when detected, pairwise comparisons between days were performed. GP_{max} and LG_{max} = maximum gross photosynthesis and light calcification, Gprod and Pprod = daily integrated carbonate and primary productivity.

Physiological variable	Main effect		Pairwise comparison		
	t-value	p-value	Time point	t-value	p-value
Net photosynthesis	2.850	**0.005**	T0	−0.372	0.719
			T2	0.822	0.435
			T8	0.845	0.423
			T11	0.821	0.435
			T21	0.470	0.651
			T24	1.443	0.187
			T30	2.363	**0.046**
			T33	0.839	0.426
			T43	2.169	0.062
			T46	0.549	0.598
			T52	−0.074	0.943
Gross photosynthesis	2.308	**0.023**	T0	0.089	0.931
			T2	0.483	0.642
			T8	0.380	0.714
			T11	0.606	0.561
			T21	0.183	0.860
			T24	1.311	0.226
			T30	0.859	0.415
			T33	0.862	0.414
			T43	1.692	0.129
			T46	0.847	0.421
			T52	0.297	0.774
Respiration	−0.382	0.703	-	-	-
Light calcification	−1.711	0.090	-	-	-
Dark calcification	−0.767	0.445	-	-	-
Gprod	−1.215	0.227			
Pprod	2.648	**0.010**	T0	−0.852	0.419
			T2	0.951	0.369
			T8	0.528	0.612
			T11	1.019	0.338
			T21	0.759	0.470
			T24	1.253	0.246
			T30	0.951	0.369
			T33	0.776	0.460
			T43	2.369	**0.045**
			T46	0.313	0.762
			T52	−0.330	0.750

In contrast, over the 52-day experiment, pronounced and significant temporal fluctuations in physiological rates closely followed the imposed upwelling and downwelling cycles (Fig. 5), revealing that natural light and thermal variability exerted a much stronger influence on algal metabolism than the short-term MHW event (Table S1). In the Control, starting from stable intermediate temperature and light conditions during pre-acclimation, and simulating naturally occurring rapidly alternating upwelling and downwelling conditions, net photosynthesis declined significantly under low temperature and light (i.e., upwelling), reaching negative values that indicated that respiration exceeded gross photosynthesis (Fig. 5a–Table S1). On the other hand, during the subsequent downwelling, net photosynthesis increased significantly. Respiration showed a similar but slightly delayed trend, increasing during downwelling and peaking toward its end, while declining during upwelling (Fig. 5b). Integrated over the day, these dynamics resulted in negative daily productivity during upwelling and highest productivity at the onset of downwelling, followed by a decline (Fig. 5c).

Calcification rates (light, dark) also responded strongly and significantly to the alternating upwelling and downwelling periods and the associated variations in temperature and light (Fig. 5d and e, Table S1). Yet, these processes showed patterns distinct from photosynthesis and more closely aligned with respiration. Downwelling conditions promoted increases in calcification rates, though the response lagged behind rising temperature and light, particularly for dark calcification, such that peak values occurred at the end of the downwelling period and into the transition to upwelling, when temperature and light were already declining (Fig. 5d and e). In contrast, upwelling strongly suppressed calcification, leading to negative rates indicative of net carbonate dissolution at the end of those periods. As a result, daily net carbonate productivity peaked at the end of downwelling and during the subsequent transition to upwelling, with the lowest values found during upwelling conditions and transition to subsequent downwelling (Fig. 5f).

To capture the overall impact of alternating upwelling and downwelling conditions on *P. lusitanicum* performance, we calculated the mean daily primary and carbonate productivity, for each period. Specifically, for net primary productivity, which responded immediately to changes in temperature and light (Fig. 5c), mean values were calculated from measurements performed at the onset and the end of each upwelling and downwelling period. Net primary productivity was strongly suppressed during upwelling (ANOVA, $F = 32.21$, $p < 0.0001$), reaching highly negative values, whereas downwelling periods showed significantly enhanced productivity, though without significant differences from the stable intermediate conditions, i.e. initial values (Fig. 6a). For carbonate production, which responded with a delay to changes in temperature and light, the strongest effects occurred at the end of each period and during transitions (Fig. 5f) and thus, to assess the effect of the alternating conditions, measurements from the end of one period and the onset of the next were averaged. Mean carbonate productivity also responded significantly to alternating upwelling and downwelling periods (ANOVA, $F = 7.93$, $p = 0.0005$). Values were slightly lower, though not significantly, during the upwelling-to-downwelling

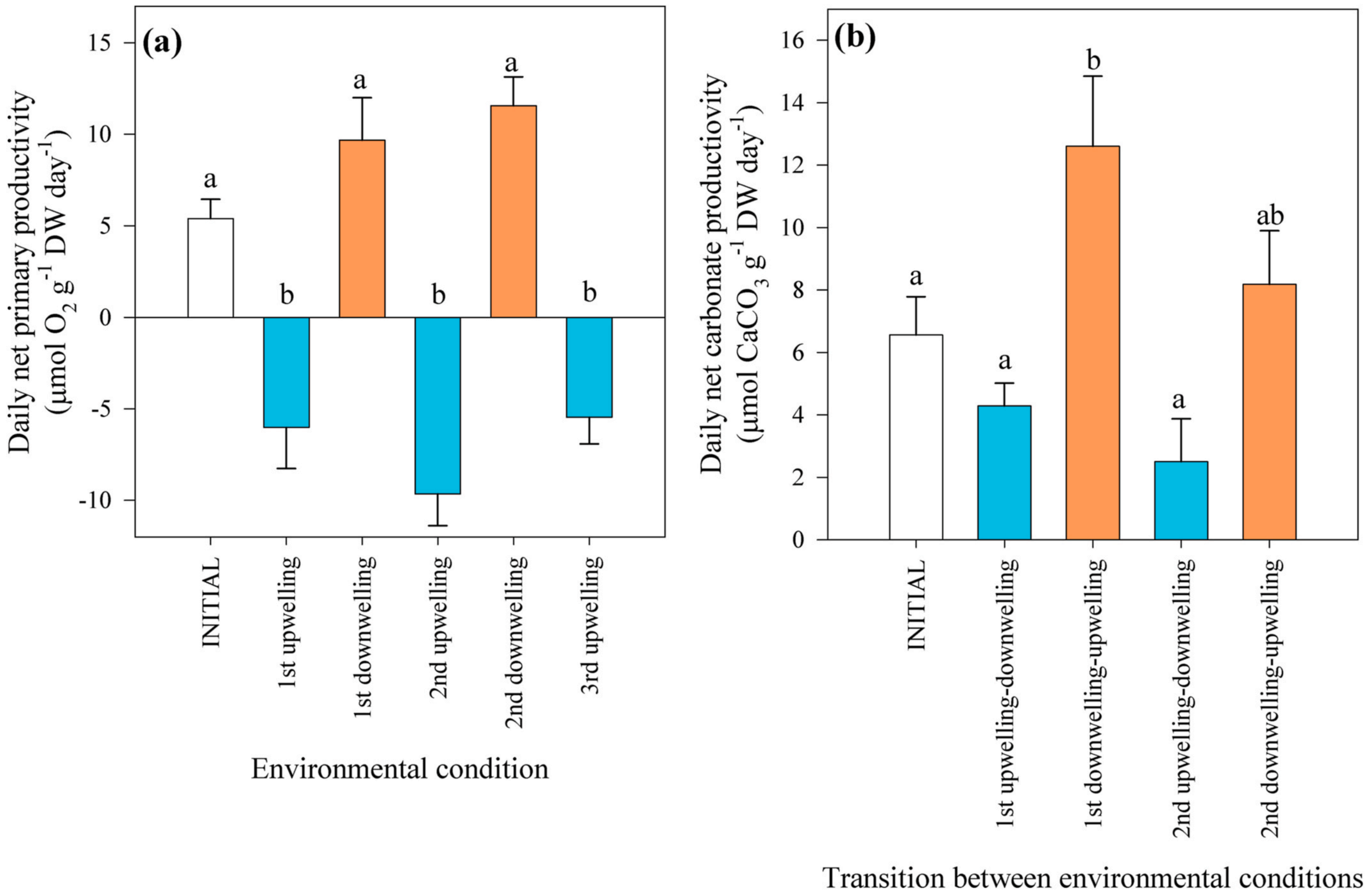

Fig. 6. Summary of the mean effects of stable, upwelling, and downwelling periods on daily net productivity of *Phymatolithon lusitanicum* (based on Fig. 5c–f). Bars in panel (a) represent the average of daily mean primary productivity from the onset to the end of each upwelling and downwelling period in the Control, color-coded as: white = stable initial conditions (15.5 °C, 25 µmol photons m^{-2} s^{-1}), turquoise = upwelling conditions (14 °C, 5 µmol quanta m^{-2} s^{-1}), and orange = downwelling conditions (17 °C, 50 µmol photons m^{-2} s^{-1}). Bars in panel (b) represent the average of daily mean carbonate productivity during the transitional periods between consecutive conditions - from the end of one condition to the onset of the next - reflecting the delayed response of calcification to changing temperature and light (see Fig. 5f). Values represent mean ± SE. Significant differences between conditions (ANOVA, $p < 0.05$, Tukey post hoc) are indicated by different lowercase letters. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

transition (reflecting the delayed effect to upwelling) and significantly higher due to downwelling (downwelling-to-upwelling transition; Fig. 6b).

The exposure of rhodoliths to Control and HW treatment conditions did not cause major changes in overall physiological performance in terms of parameters derived from initial and final light–response curves (Fig. S1). Still, some parameters changed significantly due to the simulated alternating upwelling and downwelling conditions. In both experimental groups, dark respiration increased from the initial stable intermediate temperature and light conditions to final values after exposure to alternating upwelling and downwelling, while dark calcification shifted from low net calcification to net carbonate dissolution (Table S2). In addition, the E_k decreased significantly from initial to final values in the HW treatment. Despite some differences between parameters derived from initial and final light–response curves, no differences were found in the final parameters of the two experimental groups indicating that the simulated MHW did not produce additional changes beyond those observed in the Control (Fig. S1, Table S2).

4. Discussion

Our study showed that *P. lusitanicum* exhibited clear physiological shifts under the simulated upwelling and downwelling regimes, reflecting its acclimation to the natural environmental variability of its habitat. Overall, physiological performance and daily productivity increased during downwelling and declined during upwelling. These rapid adjustments to changing conditions had a stronger influence than the simulated MHW, indicating a high physiological plasticity that underpins this temperate free-living coralline alga's resilience to anomalous warm events, while also exposing its sensitivity to colder and low-light conditions during upwelling.

Current research on the impact of fluctuating environmental conditions on coralline algal physiology remains scarce and mostly limited to temperate intertidal zones and tropical regions. However, several investigations have examined how changing light and temperature conditions can impact the physiology of coralline algal communities, in particular those associated with seasonal variations. While these occur over a much longer timeframe than the fast changes in the studied region, they consistently confirm that both temperature and irradiance can significantly affect coralline algal physiological performance. Notably, higher primary production and calcification rates are generally observed during summer (i.e., periods of elevated irradiance and temperature), while lower values are recorded during winter (i.e., periods of low temperatures and light intensities) in the studied species (Sordo et al., 2020), as well as in other temperate coralline algae (Martin et al., 2006, 2013b; Qui-Minet et al., 2021) and coralline algal communities (Martin et al., 2007). Similar trends have also been reported in studies analysing changes on a shorter timescale, which are either focused on intertidal species naturally subjected to strong daily fluctuations in environmental parameters (Egilsdottir et al., 2016), or simply conducted by analysing the physiological responses to changes in an experimental setup (Baek et al., 2022).

Temperature is known to significantly affect growth and photosynthesis in seaweeds (Eggert, 2012). Consistent with our findings, small increases in temperature that do not exceed the range normally experienced in the natural environment often increase growth, as well as photosynthesis and calcification in coralline algae (this study; Martin et al., 2006; Steller et al., 2007; Schubert et al., 2021a). Similarly, irradiance also plays a central role in regulating photosynthesis and calcification. The dependence of these processes on light underscores the importance of accounting for natural variations in light availability in studies of coralline algal physiological performance. As light intensity increases, photosynthetic activity generally rises, as typically seen in photosynthesis-irradiance curves (Geider and Osborne, 1992). Furthermore, studies have also consistently shown that calcification rates in coralline algae are significantly higher under light than in darkness (e.g., Gao et al., 1993; Egilsdottir et al., 2016; Schubert et al., 2022), with a strong correlation between light intensity and calcification (Borowitzka and Larkum, 1987; Martin et al., 2006, 2013b; Schubert et al., 2022). This relationship can be partly attributed to the close link between photosynthesis and calcification in coralline algae (Schubert et al., 2022; McCoy et al., 2023), as photosynthesis not only drives energy production for ion transport but also raises the pH in the surrounding medium, facilitating the precipitation of calcium carbonate (Borowitzka and Larkum, 1987; Schubert et al., 2021b; Krieger et al., 2023b).

Our study demonstrates that the natural alternation between upwelling and downwelling in the study region exerts strong, but opposing, effects on rhodolith productivity. While both primary and carbonate productivity were influenced by environmental fluctuations, primary productivity exhibited stronger declines during upwelling, leading to negative values. In contrast, carbonate productivity showed a more stable response across conditions, with smaller decreases during upwelling and modest increases during downwelling that offset each other, resulting in average values similar to those under initial stable conditions (Fig. 6a and b). This difference may be attributed to the lower light saturation threshold for calcification compared to photosynthesis in *P. lusitanicum*, as revealed by the results of the light-response curves. Because calcification can occur efficiently under lower irradiance levels, the reduced light availability during upwelling likely had a lesser effect on carbonate productivity, compared to the algae's primary productivity. Moreover, the rapid physiological responses of *P. lusitanicum* to changes in light intensity and temperature indicated a high degree of phenotypic plasticity and an ability to quickly respond to fluctuating conditions. This plasticity is further supported by the limited differences observed between the initial and final values of the light-curve parameters, suggesting that the physiological adjustments to the simulated upwelling/downwelling likely did not involve major transcriptional changes, and highlighting an inherent capacity to cope with environmental variability. These findings align with those of Schubert et al. (2021a), who also found notable physiological trait flexibility in *P. lusitanicum* under variable temperature regimes. High phenotypic plasticity is a common trait among organisms inhabiting dynamic and heterogeneous environments (Gianoli, 2004; Lázaro-Nogal et al., 2015; Edelaar et al., 2017), as it enables rapid adjustment to environmental variability. In coralline algae, trait plasticity has been observed in populations from naturally fluctuating habitats compared to those from more stable ones (Bach et al., 2017). Overall, these findings underscore the strong influence of regional environmental variability on coralline algal physiology, and highlight the adaptive plasticity of *P. lusitanicum* to fluctuating conditions.

Because environmental factors play a central role in shaping algal physiological performance, extreme temperature events, such as MHWs, will likely impose significant physiological impacts. In this context, our study builds on previous work examining the resilience of *P. lusitanicum* to MHWs (Schubert et al., 2021a). While that study focused on temperature fluctuations associated with naturally occurring downwelling, our research expands on this by incorporating also the naturally occurring high-frequency alternations between upwelling and downwelling, along with simultaneous changes in light intensity. Overall, our results support the previous findings, as no detrimental physiological effects were observed following the MHW, confirming the species' high resilience to high-temperature stress.

Research on the specific impacts of MHWs on coralline algal physiology is currently limited, but evidence shows a high variability of responses to increasing temperatures (Martin and Hall-Spencer, 2017; Cornwall et al., 2019). It is known that increases in temperature beyond the upper critical limit can have adverse effects on the physiology of seaweeds (Eggert, 2012). A meta-analysis of studies related to ocean warming by Cornwall et al. (2019) found coralline algal calcification to be affected by increasing temperatures; however, these negative effects were only observed when temperatures exceeded 5.2 °C above ambient conditions. Several studies focusing on the effects of MHWs on coralline algae have demonstrated variable responses across species, but an overall high tolerance and resilience of this group to extreme temperature conditions (Rendina et al., 2019; Koerich et al., 2021; Ragazzola et al., 2021; Schubert et al., 2021a; Krieger et al., 2023b, 2023c; Nannini et al., 2025).

The ability of organisms to withstand elevated temperatures often depends on the ecological context of their habitats, with those from more variable environments, such as *P. lusitanicum*, typically exhibiting enhanced phenotypic plasticity and thermal resilience (Schubert et al., 2021a; Witman et al., 2023; Nannini et al., 2025). Recent papers by Schubert et al. (2021a) on the species studied here, from the southern coast of Portugal, and by Nannini et al. (2025) on three rhodolith species from the same region, showed consistently high resilience to MHW events. The region is characterised by strong daily fluctuations in temperature, which likely play a central role in promoting acclimatization through trait plasticity and thermal tolerance mechanisms.

The link between environmental variability and resilience is particularly relevant for *P. lusitanicum*, as our findings, together with previous research, suggest that its observed thermal resilience may be rooted in the natural long-term exposure to environmental variability, which supports mechanisms like enhanced phenotypic plasticity and thermal priming. In this context, exposure to moderate temperature increases may act as a priming stimulus, capable of inducing a 'stress memory' via epigenetic modifications, promoting the transgenerational transfer of advantageous traits, such as increased stress tolerance (Wang et al., 2016). Although being extensively studied in terrestrial plants, research on thermal priming is currently scarce for coralline algae. A recent study by Nannini et al. (2025) provided further evidence of potential priming in this group. In this study, where free-living coralline algae were exposed to two consecutive MHWs, the recorded physiological impacts for two of the studied species were stronger during the first event compared to the second. This suggests that the initial exposure to high temperatures might have "primed" the algae, enabling them to better withstand subsequent heat stress. This pattern is consistent with findings for other marine organisms, such as macrophytes and corals. For instance, a two-heatwave study on seagrasses demonstrated that preheated individuals exhibited greater tolerance to repeated thermal stress, while non-primed plants experienced significant reductions in photosynthetic capacity, leaf growth, and chlorophyll *a* content (Nguyen et al., 2020). Additional research has shown that the priming of gametophytes can result in an increased thermotolerance (Gauci et al., 2024) and increased growth (Quigley, 2018) in the resulting sporophytes. Similarly, in corals, exposure to sublethal temperature fluctuations has been associated with increased thermal tolerance (Brown et al., 2024) and improved long-term recovery compared to individuals from more thermally stable environments (Ferrara et al., 2025).

While a lot of attention has been given to understanding effects of warming events, potential impacts of cold stress remain largely unexplored. Recent findings suggest that cold stress may have a more detrimental impact on coralline algae than elevated temperatures. For instance, Cornwall et al. (2019) reviewed the thermal thresholds of coralline algae and found that while calcification is generally only impaired when temperatures rise more than 5.2 °C above ambient conditions, a reduction of just 2 °C below ambient temperatures can already produce negative effects. This is consistent with our findings, highlighting that MHWs are unlikely to have a major impact on the overall physiology and no long-lasting impacts in *P. lusitanicum*. In contrast, upwelling conditions significantly impaired algal performance. In the study region, marine cold spells (MCSs) represent the extreme manifestation of these conditions and occur as frequently as MHWs (Fig. 2 and S2a). MCSs are defined as discrete periods when sea surface temperature falls below the 10th percentile of a seasonally varying climatology for at least five consecutive days (Schlegel et al., 2021) and have been recorded locally with temperature decreases of up to 4.5 °C (Fig. S2d). Notably, in our experiments, a temperature drop of only 1.5 °C already caused marked physiological declines, suggesting that MCSs may exert even stronger negative effects on *P. lusitanicum*, particularly given the reduced light conditions typically associated with these events. To explore this idea, we compared previously published growth rates measured over three years with the frequency of extreme events (MHWs and MCSs) occurring during the same periods (Fig. 7). Growth rates closely reflected the type of event and the responses observed here: they were highest during periods dominated by MHWs, lowest when only MCSs occurred, and intermediate when both events were similarly frequent, consistent with the experimental responses observed in this study. While variations in other environmental factors associated with upwelling and downwelling conditions (e.g., nutrient availability, sedimentation), not included in our experimental design, may also influence algal productivity, the close agreement between our experimental results and *in situ* growth patterns nevertheless highlights light and temperature as key drivers.

5. Conclusion and future research

Phymatolithon lusitanicum is a free-living coralline alga with a broad latitudinal distribution, ranging from cold-to warm-temperate regions, including Scotland, Ireland, the Iberian Peninsula, and the Western Mediterranean Sea (Peña et al., 2015; Bunker et al., 2018). This wide distribution suggests substantial environmental tolerance, particularly along the west and south coasts of the Iberian Peninsula, which experience strong, highly dynamic upwelling and downwelling regimes (Fiúza, 1983; Criado-Aldeanueva et al., 2006; De Oliveira Júnior et al., 2021), with MCSs and MHWs representing the respective extremes of these regimes (see Fig. 2). These fluctuating conditions appear to promote the species' high physiological plasticity and resilience to MHWs (this study; Schubert et al., 2021a). However, our results also indicate that cold water and low light, characteristic of upwelling, strongly reduce the species' productivity and growth. Consequently, for coralline algal beds along the southern coast of Portugal formed by *P. lusitanicum*, cold anomalies may pose a greater threat than short-term warming events, as they locally combine reduced temperatures and low-light conditions that constrain algal productivity.

Despite their potential impact, physiological effects of MCSs remain largely unexamined. Further research is needed to evaluate how these cold-water anomalies may affect the performance of coralline algae, particularly in regions where such events are recurrent. In this context, while thermal priming has been increasingly investigated in relation to heat stress, the concept of cold priming - where prior exposure to sublethal cold temperatures enhances resilience to subsequent cold events - remains largely unexplored in marine systems. Evidence from terrestrial plants suggests that cold priming can trigger physiological adjustments that improve tolerance to low temperatures (Li et al., 2014). However, no studies to date have assessed this phenomenon in marine macroalgae. Given the potential vulnerability of temperate coralline algae to temperature drops found in this study, and consistent with the meta-analysis by Cornwall et al. (2019), it is important to investigate the potential impacts of MCSs and whether cold priming could contribute to their resilience in these variable coastal environments. In addition, in regions characterized by strong upwelling-downwelling dynamics, such as the study area, MCSs often coincide with broader environmental changes, including shifts in light availability, nutrient supply, and sedimentation, whose combined effects on coralline algal physiology also remain poorly understood and should be accounted for in future research.

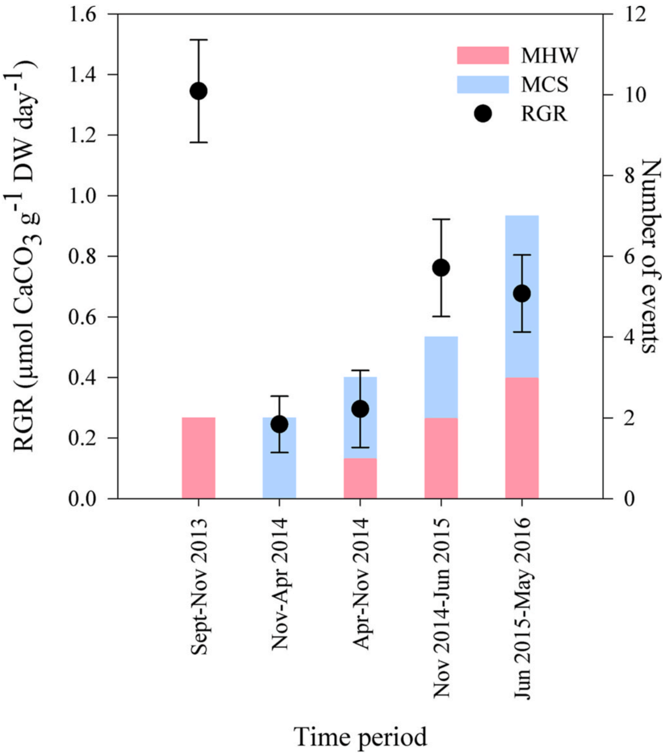

Fig. 7. Relationship between growth rates of the free-living coralline alga *Phymatolithon lusitanicum* and the occurrence of marine cold spells (MCSs) and marine heatwaves (MHWs). Previously reported relative growth rates (RGR) of *P. lusitanicum* from the same location studied here (southern Portugal) (Sordo et al., 2020) are shown alongside the number of MCS and MHW events during those periods. Event counts were obtained from the Marine Heatwave Tracker (Schlegel, 2018).

CRediT authorship contribution statement

Martina Cerpelloni: Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. **Matteo Nannini:** Investigation, Writing – review & editing. **Tainá L. Gaspar:** Investigation, Writing – review & editing. **Fernando Tuya:** Formal analysis, Writing – review & editing. **Carolina V. Mourato:** Investigation, Writing – review & editing. **João Silva:** Conceptualization, Resources, Supervision, Writing – original draft, Writing – review & editing. **Nadine Schubert:** Conceptualization, Formal analysis, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108039.

Data availability

The authors declare that all data supporting the findings of this study are available within the paper and its supplementary information files.

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