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Authors	Bell, James J.;Harman, Luke;McAllen, Rob;Witting, Kea;Wood, Gabriela
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University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

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ORIGINAL PAPER

Short-term metabolic stress response of the temperate cup coral *Caryophyllia smithii* to a simulated marine heatwave

James J. Bell[1] · Luke Harman[2] · Rob McAllen[2] · Kea Witting[1] · Gabriela Wood[1]

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Abstract
Marine heatwaves (MHWs) are increasing in frequency and intensity due to climate change, posing significant threats to marine biodiversity. While tropical coral responses to thermal stress are well studied, less is known about the responses of temperate, azooxanthellate corals to temperature anomalies. The aim of our study was to investigate the physiological response of the temperate scleractinian coral *Caryophyllia smithii* to simulated short-term MHW conditions in Irish coastal waters. Using a controlled laboratory experiment, respiration rates were measured in corals exposed to ambient (12.5 °C) and elevated (19 °C) temperatures over a 14-day period. A linear mixed effects model revealed a significant interaction between treatment and time, with corals under elevated temperature exhibiting a pronounced increase in respiration from Day 7 onward, significantly exceeding control values by Day 13. These results indicate a rapid metabolic stress response, suggesting that short periods of elevated temperature consistent with strong MHWs can disrupt physiological homeostasis in *C. smithii*. Our findings highlight the potential vulnerability of temperate azooxanthellate corals to climate-driven warming and underscore the need to include temperate coral species in climate impact assessments and conservation planning.

Introduction

Marine ecosystems are increasingly exposed to the effects of anthropogenic climate change, with marine heatwaves (MHWs) emerging as one of the most acute and biologically disruptive manifestations of warming seas (Smith et al. 2023; Wernberg et al. 2025). MHWs are defined as discrete, prolonged periods (5 days or longer) of anomalously high sea temperature (>90th percentile temperature for a given time of year; Hobday et al. 2016). These MHWs have increased in both frequency and intensity over the past century and these trends are projected to increase under continued global climate trajectories (Oliver et al. 2018, 2021; IPCC et al. 2021). These episodic, but severe thermal anomalies can exert devastating impacts on marine biodiversity and subsequently ecosystem function (Smith et al. 2023), often leading to mass mortalities and persistent ecological shifts in marine communities (e.g. Garrabou et al. 2022; Bell et al. 2024a, b). While the consequences of MHWs on tropical coral reefs, particularly through coral bleaching, have been well documented (Donovan et al. 2021; Capotondi et al. 2024; Rodrigues et al. 2025), far less is known about their effects on temperate corals, particularly solitary azooxanthellate corals, which dominate many temperate rocky reef habitats. However, those studies that have been conducted on temperate corals have generally found limited tolerance to temperature stress (e.g. Elahi et al. 2016; Gori et al. 2016; Carbonne et al. 2024).

Temperate stony corals are increasingly recognised as important ecological components of shallow and deep rocky reef ecosystems (Costantini et al. 2017; Cerrano et al. 2019; Bell et al. 2024a, b). Though most temperate coral species lack the reef-building capacity of tropical corals (see *Cladocora caespitosa* for a Mediterranean exception), temperate species still contribute to habitat complexity (Sanna and Freiwald 2021). Their calcified skeletons provide settlement surfaces and refuges for a wide range of associated microfauna (Mortensen and Fosså 2006). Many temperate coral species are also long-lived and slow growing, potentially living hundreds of years and growing only several mm each

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✉ James J. Bell
james.bell@vuw.ac.nz

[1] School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand

[2] School of Biological Earth and Environmental Sciences, University College Cork, Cork T12 YN60, Ireland

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year (Miller 1995; Brooke and Young 2009), making them vulnerable to both physical disturbances and environmental change. In recognition of their ecological value, many temperate coral-dominated habitats have been included in national and regional conservation frameworks, including designations as Vulnerable Marine Ecosystems (VMEs) or being protected by legislation (Penney et al. 2009). However, the inclusion of temperate corals in these frameworks has traditionally been driven by concerns over physical damage from activities such as bottom trawling, rather than their sensitivity to climate-related stressors (Portela et al. 2012; Du Preez et al. 2020). As marine heatwaves become more frequent and intense in temperate regions, there is an urgent need to better understand the vulnerability of these overlooked coral communities and to integrate climate resilience into future conservation strategies.

Caryophyllia smithii (the Devonshire cup coral) is a small, solitary scleractinian coral commonly found across the Northeast Atlantic, with a distribution that includes the western and southern coasts of Ireland (Wilson 1975; Bell and Turner 2000). It occupies a wide range of habitats, from shallow subtidal zones to mesophotic and bathyal depths, often colonising vertical walls, overhangs, boulders, and cave systems (Bell and Turner 2000 Coolen et al. 2015). Unlike tropical corals, *C. smithii* lacks symbiotic zooxanthellae and therefore does not experience bleaching. However, as a cold-water adapted, calcifying invertebrate, *C. smithii* may be physiologically sensitive to temperature and pH changes that may disrupt metabolic function (e.g. changes in respiration, metabolic biomarkers, energy reserves and Reactive Oxygen Species), reduce calcification rates, impair gametogenesis, and ultimately lead to death or physiological impairment (see Movilla et al. 2012; Gori et al. 2016; Palladino et al. 2022; Sani et al. 2024; Carbonne et al. 2024 for impacts on other temperate species). For example, for another azooxanthellate species *Desmophyllum dianthus*, Gori et al. (2016) reported that this cold-water coral was highly sensitive to even modest increases in temperature, showing reduced calcification and metabolic performance at just ~ 3 °C above ambient (~ 12 to 15 °C). In addition, Beck et al. (2023) found that elevated summer temperatures (along with reduced food supply) led to reduced coral growth, delayed juvenile maturation and high adult mortality in *Caryophyllia huinayensis*, although these responses varied between life-stages. More recently, Carbonne et al. (2024) found that the temperate zooxanthellate coral *Cladocora caespitosa* bleached and the azooxanthellate coral *Astroides calycularis* died, when exposed to 3.2 °C above the in situ mean temperature from 2012 to 2020. There have also been several relevant studies on deeper-water cold-water corals. For example, a recent study on *Lophelia pertusa* and *Madrepora oculata* found that these species showed 100% mortality at 4 °C above ambient temperature (Chapron et al. 2021). While these earlier studies generally highlight the susceptibility of temperate and cold-water corals to MHWs, not all studies have found strong negative impacts. For example, Kersting et al. (on et al. 2015) reported no mortality in the reef-building temperate coral *Cladocora caespitosa* at temperatures up to 29 °C, which was 4.2 °C warmer than maximum summer temperatures.

In Irish waters, *C. smithii* is one of the most abundant and conspicuous anthozoans on hard substrata where it reaches densities > 100 corals m^2 (Bell 2001). While little is known about the specific functional roles of *C. smithii*, they likely provide small-scale microhabitat for micro-invertebrate species and they may also be important in seafloor carbon cycling (Cathalot et al. 2015). Like many parts of the northeast Atlantic, Ireland experienced its most extreme marine heatwave in 2023 since records began, with the temperature to the west of Ireland reaching > 4 °C warmer than average (McCarthy et al. 2023) and in more coastal waters the maximum temperature (reported off South Wexford at the M5 Buoy, www.met.ie) reached 19.7 °C (2.5–4 °C above normal mean temperature). This 2023 MHW was followed by a further MHW event in 2025, where coastal temperatures again reached 4 °C warmer than average for the time of year. There has been an increased frequency of warm water events in Irish waters in recent years with 2021–2025 occupying 4 of the top 6 years in terms of maximum MHW activity (McCarthy et al. 2023; www.met.ie). Despite these recent extreme events, and the high likelihood that MHW intensity and frequency is expected to increase in the future (IPCC 2021), very little is known about how these events impact on NE Atlantic organisms and ecosystems.

In this study we investigated the physiological responses and mortality of a simulated MHW on *Caryophyllia smithii*. Our assessment not only provides important information on MHW impacts on an abundant subtidal Irish coastal species, but this species also has the potential to act as a model for understanding the effects of increasingly frequent and severe MHWs on other temperate coral species.

Materials and methods

Sample collection

Individual *Caryophyllia smithii* (Stokes and Broderip 1828) were collected immediately outside Lough Hyne Marine Nature Reserve, Ireland on the open Atlantic coast (51°29'32.7"N, 9°17'31.1"W) at a depth of 17–20 m in June 2025. We only collected corals without the epibiotic barnacle *Megatrema anglicum* to avoid confounding effects of epibiont presence, as these barnacles have the potential

to impact respiration measurements. Corals were removed using a hammer and chisel, taking care not to damage the calyx. Following collection, specimens were maintained for 3 days at 12.5 °C in the University College Cork Renouf Laboratory, reflecting the ambient water temperature at the collection depth. In total, we collected 162 corals. The close proximity of the laboratory to the collection site meant that corals were transported in sealed buckets and were in the lab within 15 min of collection.

Experimental set up

We used a closed aquarium system; therefore, throughout the experiment, daily water changes (75% of each unit's volume) were performed using temperature-adjusted, unfiltered seawater. The unfiltered seawater provided a natural food source for the corals, and no additional food was given. A total of 162 corals were placed in the experimental system at the start of the experiment (control = 81, treatment = 81) and were randomly and evenly distributed among the experimental tanks ($n = 27$ in each tank). However, although we originally planned to measure respiration rates of 11 control and 11 treatment corals at each of six time points (total intended = 132 corals), respiration measurements were ultimately made on fewer individuals (see respiration section below for further details). Measurements were made on a total of 114 *C. smithii* individuals across all sampling time points (control = 57, treatment = 57). Corals were kept in the dark for the duration of the experiment, and red light was used for viewing the corals and when respiration measurements were taken.

Temperature control across the experiment was achieved using an aquarium temperature controller (Apex Classic, Neptune Systems, USA) in combination with temperature probes (YSI Pro30, USA) and heaters for each experimental tank and the water bath. We placed 200 W aquarium heaters (Eheim, Germany), connected to the Apex system, in each of the experimental tanks to directly change temperatures in the MHW simulation treatments. Each unit was also equipped with a bubbler to ensure water circulation.

Simulated marine heatwave experiment

To investigate the biological response of *C. smithii* to a simulated MHW, corals were exposed to temperatures of up to 19 °C, with their respiration rates being compared to those of a control group maintained at 12.5 °C throughout the experiment. The control temperature was consistent with temperature at the time of coral collection. The experimental set-up comprised of six separate experimental tanks (10 L each) with lids, placed within a single larger water bath. This larger water bath was used to maintain a more constant external temperature (see Figure S1). A chiller maintained the temperature in the larger water bath at 12.1 ± 0.32 °C. Both the water bath and experimental units were filled with unfiltered seawater from the lough. Experimental tanks were spatially separated within the larger water bath and randomly assigned to either control or treatment groups ($n = 3$ per group). The three control tanks were maintained at 12.5 °C, while the treatment tanks were increased to the maximum temperature of 19 °C over a 3-day period (Figure S2; Table S1). Unfortunately, there is no specific long-term temperature data for the region where we collected our corals, therefore we based our maximum temperature on data from the long data buoys in the Irish Sea. Specifically, our temperature was consistent with the maximum temperature reported in the recent 2023 and 2025 MHWs in this region (www.met.ie – M5 buoy). This buoy only collects data from 3 to 4 m below the surface, although this depth range does overlap with the depth distribution of our study species in some locations, including the study area (Bell and Turner 2000). Furthermore, earlier temperature data from the specific location where the corals were collected (see Bell 2002), although only from 2001 to 2002 and prior to any MHWs, reached 17 °C during summer months. Therefore, our experimental temperature was only 2 °C above this, making it very likely that corals in our study area will have experienced at least our maximum temperature during recent MHWs. The ramping rate was approximately twice as fast as the recent MHW in the region, although our experiment reached a higher final temperature.

All specimens were monitored daily for signs of mortality after the water was changed, as this activity stimulated the corals to partially or fully extend their tentacles within one hour of the water change. As corals were sacrificed at each sampling time point (see below), the number of individuals examined for evidence of mortality decreased over the course of the experiment.

Respiration measurements

Physiological measurements were taken from between 7 and 11 treatment and control corals, which were subsequently sacrificed after each measurement was taken (so measurements were taken from each coral only once), at each of five time points: before the experiment began at T_0 (18th June 2025), T_1 (day 1), T_2 (day 4), T_3 (day 7), T_4 (day 10), T_5 (day 13) (Figure S1). Different corals were sampled at each time point and, as they were sacrificed after respiration measurements, each coral was sampled only once. Corals were randomly selected from the treatment and control

replicate tanks. Sample sizes were $n = 11$ for both control and treatment on Day 0; $n = 8$ for the control and $n = 9$ for the treatment on Day 1; $n = 10$ for both control and treatment on Day 4; $n = 9$ for the control and $n = 10$ for the treatment on Days 7 and 10; and $n = 10$ for the control and $n = 7$ for the treatment on Day 13. Corals were randomly sampled from the experimental tanks at each time point. The differences in sample sizes between time points occurred for two reasons: (1) one of the oxygen sensor spots failed partway through the experiment; and (2) we only measured respiration in corals whose tentacles were fully expanded at the time of measurement, since preliminary observations showed that tentacle expansion had an important positive effect on respiration rates (we measured the oxygen consumption rates - not standardised by AFDW - of five corals with tentacles extended and five with retracted tentacles and found between 5 and 10 times more oxygen used by corals with tentacles expanded). Therefore, it was not always possible to measure respiration rates in all 11 treatment and control corals at each time point.

Respiration was measured by placing corals in clear straight-sided 135 ml glass chambers with white polypropylene caps (#FB02911764, Fisherbrand™, USA). Chambers were filled and sealed underwater to ensure there were no air bubbles. Each chamber was equipped with a PreSens oxygen sensor spot (#SP-PSt3-NAU, PreSens, Germany) attached to its inner surface. A black mesh barrier was placed between a magnetic stirring rod and the coral in each chamber. The entire chamber was placed on a magnetic stirrer at 270 rpm. We began with 12 chambers, with 11 being used for the corals and a blank chamber being added at each measurement point with the same replicate tank water to account for any microbial respiration in the water. Unfortunately, one oxygen sensor spot failed part way through the experiment, reducing sample sizes for some timepoints while we waited for a new dot. All chambers were immersed in a temperature-controlled seawater bath containing a submersible aquarium heater (300 W, Eheim, Germany), a temperature probe (Neptune Systems, USA), and a submersible aquarium pump (300 L h^{-1}, Eheim, Germany) to ensure a homogeneous temperature environment. Corals were acclimated for 30 min in their experimental chambers in the dark and allowed to expand their tentacles before respiration rates were measured. This acclimation period and requirement for tenacles to be expanded was based on initial observations whereby respiration rates did not vary through time once tenacles were expanded but were lower when tentacles were contracted. At each time point, each chamber's oxygen concentration was measured using a PreSens Fibox 4 self-contained fibre-optic oxygen meter. A polymer optical fibre was held against the oxygen sensor spot for at least 5 s to ensure an accurate reading of the oxygen concentration (in mg L^{-1}) in each chamber. Measurements were taken under red light every 20 min for a total of one hour per run. We used this approach as the sensor spot system we had available did not allow for continuous oxygen monitoring. A one-spot calibration was performed on the oxygen probe prior to every respiration measurement day using air-saturated water for 100% oxygen.

Respiration rate (mg O_2 h^{-1}) was corrected by a blank prior to standardising respiration with the ash-free dry weight (AFDW) as suggested by Bell et al. (2020). To obtain the ash-free dry weight (AFDW) of sacrificed individuals at each time point, corals were first dried at 60 °C for 24 h. Corals were then weighed immediately after the drying process was finished and ashed at 500 °C for 5 h using a muffle furnace. Coral respiration rate was then standardised to coral ash-free dry weight (mg O_2 h^{-1} g^{-1}).

Statistical analyses

Mean and median values were calculated using all replicate measurements within each treatment group. Replicates originated from multiple tanks; however, as tank effects were not treated as independent experimental units for descriptive purposes, all available replicate data were pooled to derive treatment-level summary statistics. All statistical analyses were performed in R (version 4.3.3, R Core Team).

Changes in respiration rates in response to the MHW treatment were tested using a linear mixed effects model (LMM) fit by restricted maximum likelihood (REML, *lmerTest* package, Kuznetsova et al. 2017). Time and treatment were assigned as fixed effects and cup coral individual and tank (replicate) as random effects. LMM residuals were inspected to assess normality and homoscedasticity assumptions using the *DHARMa* package in R (Hartig 2022). To meet the assumptions, respiration measurements were square root transformed. Pairwise comparisons using estimated marginal means (*emmeans* package in Lenth 2024) and a Benjamini-Hochberg correction were used to control the false discovery rate (FDR) by reducing the likelihood of false positives while investigating combinations of treatments and time frames that could have driven observed effects.

Results

There was no mortality of corals in any of the tanks during the experiment as evidenced by tentacles extension being reported in all corals after each water replacement. The respiration rate of *Caryophyllia smithii* was significantly influenced by both MHW treatment and time, with a strong

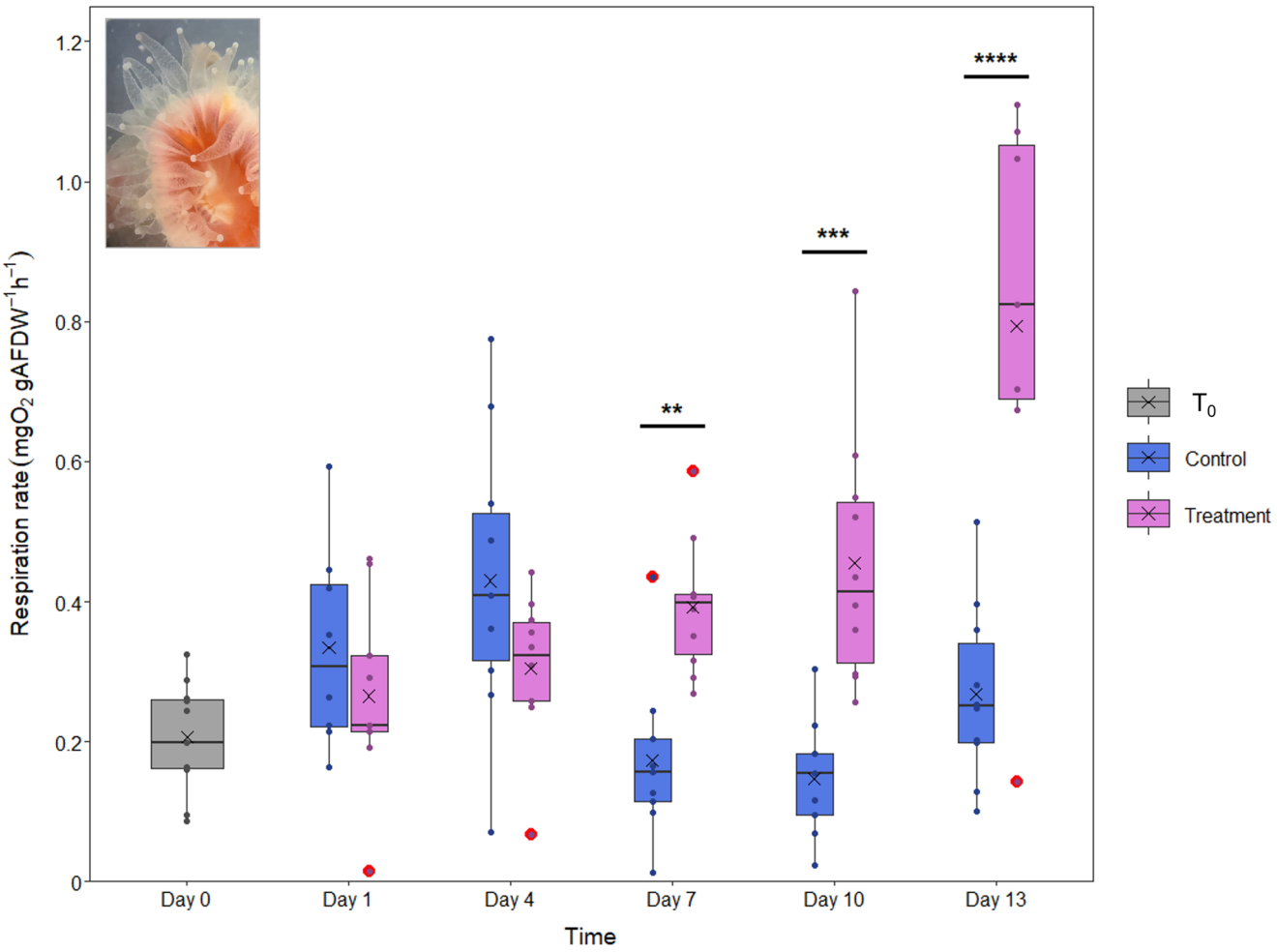


Fig. 1 Respiration rates through time in *Caryophillia smithii*. Horizontal bars in each boxplot represent the median value, while the 'x' symbol indicates the mean respiration rate for each treatment. The lower and upper hinges of the boxplot correspond to the first and third quartiles, respectively. Each point represents an individual's respiration value with red circles indicating outliers. Only significant comparisons are shown with '**' = $p<0.01$; '***' = $p<0.001$, and '****' = $p<0.0001$. Inset photograph depicts one individual *C. smithii* with extended polyps

Table 1 Results of Type III ANOVA with Satterthwaite's method with fixed (a) and random effects (b) tests for *Caryophillia smithii*. Respiration data were square root transformed. P-values are uncorrected, but significance after correction with Benjamini-Hochberg Procedure (SignBH) is reported as: *$p<0.05$; **$p<0.01$; ***$p<0.001$; ns, non-significant

Fixed effects test	Sum Sq	Mean Sq	numDF	denDF	F- value	*p*-value	SignBH
Treatment	0.4087	0.4087	1	4	20.37	**0.0122**	*
Time	0.3758	0.0939	4	79	4.68	**0.0019**	**
Treatment: Time	0.8239	0.2060	4	79	10.26	**<0.0001**	***
Random effects test	npar	logLik	AIC	LRT	df	*p*-value	SignBH
< none>	12	25.89	-27.79				
1| Tank	11	25.88	-29.75	0.0337	1	0.8544	ns

interaction between the two factors (Fig. 1, Table 1a). A linear mixed effects model revealed a significant effect of the MHW treatment ($F_{1,4} = 20.37$, $p=0.0122$; Table 1a), time ($F_{4,79} = 4.68$, $p=0.0019$; Table 1a), and a significant MHW treatment × time interaction ($F_{4,79} = 10.26$, $p<0.0001$; Table 1a), indicating that the effect of the simulated MHW treatment on respiration changed over the course of the experiment. The random effect of tank was not significant ($p=0.85$; Table 1b), suggesting no tank-level variation in respiration response.

At the beginning of the experiment (Day 0), respiration rates were not significantly different across both treatment and control groups (Fig. 1; Table S1a). Respiration rates did increase slightly in both the control (12.5 °C) and MHW

treatment (19 °C) groups on Days 1 and 4, but there was no significant difference between treatments and controls at these time points (Day 1: $p=0.285$; Day 4: $p=0.155$; Table S2b). However, a significant divergence emerged from Day 7 onward, with corals in the MHW treatment exhibiting progressively higher respiration rates than controls (Day 7: $p=0.0011$; Day 10: $p<0.0001$; Day 13: $p<0.0001$; Table S2b).

By Day 13, the treatment group showed the highest respiration rates recorded during the experiment, which was significantly different to all other time points and the control (Fig. 1 and Table S1). We also found higher variability (Fig. 1) compared to the control, suggesting both a strong metabolic response and inter-individual differences in thermal tolerance.

Within the control group, respiration decreased significantly between Day 4 and Day 10 ($p=0.0001$; Table S1b), with no other time-point comparisons reaching statistical significance after multiple testing correction. In the treatment group, respiration increased significantly between several time points, indicating a cumulative thermal stress response. Notable increases were observed from Day 1 to Day 10 ($p=0.0094$), Day 1 to Day 13 ($p<0.0001$), and Day 4 to Day 13 ($p<0.0001$) (Table S1b). The most substantial increase occurred between Day 7 and Day 13 ($p=0.0009$; Table S1b), consistent with the visual trend in the boxplot (Fig. 1).

Discussion

Our study provides new empirical evidence of the physiological sensitivity of the temperate scleractinian coral *Caryophyllia smithii* to MHW conditions, highlighting the potential vulnerability of this important temperate species to climate-driven thermal extremes. Our controlled laboratory experiment demonstrated significant changes in respiration rate under elevated temperature (19 °C), which occurred rapidly. While respiration in control conditions (12.5 °C) declined after a peak on Day 4, corals in the MHW treatment exhibited a substantial increase in respiration from Day 7 onwards, culminating in significantly elevated rates by Day 13. These findings suggest that *C. smithii* exhibits a rapid response to thermal stress. This response may represent an increased metabolic demand by corals under thermal stress, which could result in reduced energy availability for growth or reproduction when natural populations are exposed to prolonged heatwaves. Our results are consistent with the limited number of previous studies on temperate corals (Gori et al. 2016; Palladino et al. 2022; Sani et al. 2024; Carbonne et al. 2024) showing negative impacts of temperature.

Physiological responses to elevated temperature

Respiration rate is a key physiological proxy for metabolic performance and energy balance in marine invertebrates (Brey 2010), particularly in sessile species such as corals where behavioural thermoregulation is not possible. However, while respiration reflects changes in metabolic rate, it does not on its own distinguish between stress, acclimation, or general temperature-driven metabolic changes. In this study, *C. smithii* respiration responded rapidly to thermal exposure. Despite the initial similarity in respiration between control and treatment groups on Days 1 and 4 there was a rapid response by Day 7, whereby treatment corals began to diverge markedly, with significantly higher respiration than controls, a trend that continued and intensified through Day 13. This pattern likely reflects a compensatory metabolic response to prolonged heat stress (Brey 2010). Elevated respiration under sustained thermal exposure can indicate increased energy demands associated with cellular stress responses, protein turnover, and tissue repair mechanisms (Portner 2002). In the absence of photosymbionts, *C. smithii* must rely on heterotrophic feeding and stored energy reserves to meet these demands. Prolonged thermal exposure may thus deplete energy stores, potentially impacting the ability to deal with near-term future temperature stress (Anthony et al. 2009; Yu et al. 2025). Interestingly, while there is no current evidence that *C. smithii* can change feeding rates in response to stress, Aichelman et al. (2016) reported that increased heterotrophy mitigates thermal stress impacts in another temperate coral, *Oculina arbuscula*. In our experiment, we did not provide corals with supplemental food and therefore it is possible that the higher energetic demands on corals in the treatment tanks depleted their food reserves more quickly than in the controls, potentially affecting respiration rates. We believe this is unlikely as the water was replenished daily. Furthermore, if food limitation were occurring in the treatment tanks, we would expect to see reduced respiration rates as the corals began to die or reduce their metabolism, which is not what we observed.

The high variation (compared to earlier days and controls) observed in respiration rates within the treatment group by Day 13 may reflect individual-level differences in stress tolerance or resource exhaustion (that could not be compensated for by feeding), suggesting that some corals were approaching or exceeding their physiological limits. By contrast, the progressive decline in respiration among control corals could indicate a natural senescence of metabolic activity under stable thermal conditions, or a response to reduced activity if food had become more limited in the laboratory (Edmunds 2011). This highlights the importance of including temporal dynamics in stress experiments, as

single time-point assessments may miss crucial transitions in physiological state and that very short-term temperature stress response may not capture coral responses. We also found that the variability in respiration rates increased markedly on Day 4, but only in the control corals. This variability may have resulted from some corals not having their tentacles fully extended, or from some individuals retracting their tentacles during respiration measurements.

While most coral climate research has focused on tropical, symbiotic species (Hoegh-Guldberg et al. 2017, 2023), our results confirm that azooxanthellate corals like *C. smithii* are also vulnerable to thermal stress. Unlike zooxanthellate species that exhibit bleaching when symbiosis breaks down under heat, *C. smithii* does not bleach but may still suffer metabolic dysregulation. Brooke et al. (2013) found that the deep-sea temperate coral, *Desmophyllum pertusum* (previously *Lophelia pertusa*) likely has a narrow thermal tolerance window, as deviations of 4–6 °C from its typical ambient temperature can lead to mortality. Our findings only partly align with this view, as we found that *C. smithii* did not die at 6.5 °C warmer than ambient, although its respiration rate did increase. It is important to note that our experiment was a short duration and while it might seem we used a high temperature, the maximum 19 °C treatment we used is consistent with summer maxima recorded in shallow Irish coastal waters during the recent 2023 MHW events (www.met.ie), suggesting that such thermal stress is increasingly representative of future summer conditions. Furthermore, our treatment temperature was only a 1.5 to 2 degrees warmers than those previously reported at our collection site (Bell 2002), so is ecologically relevant.

We did not report any mortality in response to the MHW treatment, although given the strong respiration response it seems likely that mortality would have occurred if the experiment had been longer. Although earlier temperate coral studies have not specifically measured respiration as a stress response, our results are largely consistent with previous work reporting negative impacts of temperature stress (e.g. Gori et al. 2016; Carbonne et al. 2024). Collectively, these studies highlight that temperate corals are likely to have high susceptibility to long and extreme MHWs. Importantly, the distribution of *C smithii* extends down the coast of mainland Europe (Rees 1962), where average summer temperatures will be warmer than on the Irish coast and much further north around the United Kingdom coast, where summer temperature will be much cooler. This could indicate that different populations in different locations may be locally adapted to different temperature maxima (Baumann et al. 2021) meaning that thermally-tolerant corals could expand their range poleward in a warming ocean (e.g. Yamano et al. 2011). Alternatively, the maximum thermal threshold for *C. smithii* may already be close to our experimental temperature, which currently allows the corals to persist in the warmer, more southerly waters. Any further increase in temperature could therefore result in a contraction of the species' range. Further, longer term studies, at a range of temperature extremes would be useful to fully determine the likelihood of mortality under future MHW conditions.

In natural populations, sustained elevation of respiration without a corresponding increase in energy intake can result in negative energy budgets, leading to reductions in growth, calcification, reproduction, and ultimately survivorship (Grottoli et al. 2014). For *C. smithii*, whose small size and solitary morphology already impose energy constraints, such imbalances could be critical. High respiration rates sustained over multiple weeks could compromise gametogenesis or resorption of reproductive tissue, as seen in other anthozoans under thermal stress (Shick et al. 1996). Furthermore, if increased respiration reflects a chronic stress state, it may signal a tipping point beyond which coral health rapidly declines. The sharp rise in both the mean and variability of respiration by Day 13 in our treatment group could represent such a threshold. Given that *C. smithii* often forms dense aggregations in shaded overhangs and vertical reef walls, the decline of even small populations could have other, as yet unquantified, ecological impacts.

Conclusion

This study provides clear evidence that *Caryophyllia smithii*, a dominant temperate coral in Irish waters, is physiologically sensitive to marine heatwave conditions. We observed an increase in respiration rate under short-term high temperature exposure that could have subsequent effects on growth, reproduction, and survival. Our results demonstrate that future MHWs that are only slightly longer or more intense than recent events are likely to have detrimental impacts on *Caryophyllia smithii* and potentially other cold-water coral species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-026-04888-5.

Authors' Contributions Conceptualization: James Bell, Rob McAllen, Gabriela Wood; Formal analysis and investigation: Kea Witting, Gabriela Wood, James Bell; Writing - original draft preparation: James Bell, Rob McAllen and Gabriela Wood; Writing - review and editing: all authors; Resources: Luke Harman, Rob McAllen.

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Data availability Data is avaialable on reasonable request from the authors.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethics Approval No research ethical approval was needed for this study as the experimental work was conducted with an unregulated invertebrate species. Samples were collected from outside the boundaries of Lough Hyne Marine Nature Reserve and therefore no permit was needed.

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