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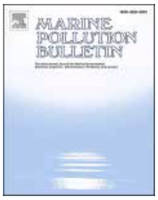

High thermotolerance to extreme marine heatwaves for four New Caledonian sponges

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ABSTRACT

Marine heatwaves (MHWs) are increasingly recognised as a more immediate threat to the persistence of coral reefs than the longer-term impacts of climate change. However, major gaps still exist in our understanding of MHW impacts on many reef organisms. Sponges are functionally important on coral reefs globally. Despite earlier research showing that many sponges have high thermal tolerances, there are currently no data on how New Caledonian reef sponges will respond to MHWs. We conducted a simulated MHW aquarium experiment on four ecologically important New Caledonian sponges from two abiotically contrasting sites. We hypothesised that sponges from the highly fluctuating and thermally extreme Bouraké site would show thermal tolerance, and those from the more stable Nouméa lagoon (NL) would be sensitive to short-term temperature increase. Significant sublethal effects on respiration and photosynthetic efficiency were found in *Cliona orientalis* (both sites) and *Spheciospongia vagabunda* (NL), while *Rhabdastrella globostellata* (Bouraké) and *Cliona jullieni* (NL) exhibited only minor signs of stress up to +4 °C and +6 °C, respectively, above their site-specific monthly mean temperature (26 °C at NL; 28 °C at Bouraké). Above ~33.5 °C, both Bouraké species presented sudden and acute stress (bleaching, necrosis and mortality). All four species showed tolerance up to at least 32 °C, suggesting relatively high thermal thresholds, with specimens of *C. orientalis* displaying similar thermal tolerance to 32 °C independent of their collection site. These findings support the notion that tropical sponges can persist under future warming and MHW scenarios.

1. Introduction

Human activities since the Industrial Revolution have steadily increased atmospheric concentrations of carbon dioxide (CO_2), and 90 % of the consequent reflected solar radiation from the greenhouse effect has been absorbed by the world's oceans (IPCC, 2021). Using simulated models (CMIP6), the Intergovernmental Panel on Climate Change (IPCC) predicts sea surface temperature (SST) anomalies of +1.42 ± 0.32 °C to +3.47 ± 0.78 °C by 2080–99 (means relative to 1870–99 for SSP1–2.6 to SSP5–8.5, ±inter-model SD; IPCC, 2021). However, there is increasing recognition that current extreme thermal anomalies may represent a more pressing environmental threat to global marine ecosystems than longer-term changes to the mean state (Leung et al., 2021).

Marine heatwaves (MHWs) are prolonged periods of elevated SST – defined as exceeding the 90th percentile relative to the local long-term climatology – and can be described by their duration, intensity and spatial extent, sometimes lasting months and covering thousands of kilometres (Hobday et al., 2018). Global annual MHW days have increased by 54 % over the past century (Oliver et al., 2021) and are expected to continue increasing in frequency and duration under current emission scenarios (Holbrook et al., 2022). Higher oceanic temperatures can influence organisms' physiological processes (such as respiration and photosynthesis), increasing metabolic rates and energy demand and affecting ecological function (Vaquer-Sunyer and Duarte, 2011). Prolonged exposure to higher temperatures and extreme MHW events has caused range shifts or relocations of mobile species as well as mass

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mortality and local extinctions (Frölicher et al., 2018). This can lead to irreversible ecological changes and ecosystem-wide biodiversity loss, with consequent effects on human livelihoods and wellbeing (Holbrook et al., 2022). Understanding the impacts of ocean warming and MHWs, regionally and on different taxa, is crucial for the effective conservation and management of marine ecosystems.

Sponges are abundant and often dominant members of benthic marine communities (Morganti et al., 2021) that have many important functional roles, including bioerosion, reef consolidation, creation of microhabitats, contribution to nutrient cycling through efficient water filtration and particle retention, and facilitation of carbon flow through the 'sponge loop' (i.e., a process whereby sponges make nutrients available to higher trophic levels through detritus production; de Goeij et al., 2013; Maggioni et al., 2023a). Some sponges have been proposed as potential 'winners' under future climate change scenarios on coral reefs, with a number of previous studies showing certain resilient species to have higher thermal stress tolerance than other dominant benthic organisms (Bell et al., 2018). However, while tropical sponges have been experimentally exposed to climate change predictions for the end of the century (Fang et al., 2014; Ramsby et al., 2018b), there have been no studies to date examining the impacts of MHWs on tropical sponges from New Caledonia.

The tropical western Pacific is one of the regions most affected by MHWs globally (Frölicher et al., 2018). They occur on average twice *per* year, at an intensity of +1.7 °C and for a duration of 10 days (Holbrook et al., 2022), and the average frequency of Category IV 'extreme' MHWs (>4 x the 90th percentile; Hobday et al., 2018) is projected to increase to more than 50 days year^{-1} by 2050 (IPCC SSP5–8.5; IPCC, 2021; Holbrook et al., 2022). The Pacific archipelago of New Caledonia has one of the largest reef systems in the world, which was given UNESCO World Heritage status in 2008 (Grenz et al., 2013; Payri et al., 2019). Corals at these reefs experienced mass thermally induced bleaching in 2016 (Payri et al., 2018). The large southwest lagoon, adjacent to the capital Nouméa, has relatively stable abiotic conditions (see Fig. S.1-A) and mean SSTs typically ranging from 26 to 27 °C in the austral summer (NOAA, 2024). In contrast, Bouraké, a semi-enclosed mangrove lagoon situated 90 km north of Nouméa, is characterised by extreme diel and tidal abiotic fluctuations relative to neighbouring reefs (see Fig. S.1-B), with organisms exposed to daily variation of 6.5 °C and a maximum of 33.8 °C in the summer months (Camp et al., 2017; Maggioni et al., 2021). Despite these extreme conditions, Bouraké has a diverse and abundant benthic community, thus providing a natural laboratory for understanding how environmental variability might precondition a species to abiotic change. Resident organisms at Bouraké spend 71 % of the time at moderate IPCC-projected end-of-century temperatures (31–32 °C), with regular but brief exposure to extreme temperatures (33–34 °C), which may facilitate acclimatisation (Camp et al., 2017; Maggioni et al., 2021).

Here we examined the physiological response of four ecologically important tropical sponge species from New Caledonia to a simulated MHW. We analysed changes in survivability, respiration and photosynthesis, providing insight into the tolerance to MHWs for these species from this region for the first time. We hypothesised that sponges collected from Bouraké would have high thermal tolerance, as their frequent exposure to high temperatures will have driven acclimation of the sponge holobiont (Ramsby et al., 2018a; Strano et al., 2023), and that sponges collected from the Nouméa lagoon would have low tolerance to temperature stress as a result of their more stable environment. We further hypothesised that a sponge species collected from both sites, *Cliona orientalis*, would show site-specific differences in thermal tolerance. By revealing the different species-specific and site-specific responses of these sponge species to the climate change stressor of temperature, we evaluated whether Bouraké sponges have the ability to acclimate to increase their chances of persistence under projected climate change scenarios.

2. Methods

2.1. Sample collection

Sponge species collected are abundant and ecologically important throughout the Indo-Pacific region (Fang et al., 2016; Beepat et al., 2020; Chin et al., 2020). Specimens were collected under permit number 5761-2024/ARR/DDDT, given to IRD by the Province Sud. From Bouraké (21.929° S, 166.004° E), sponge species *Rhabdastrella globostellata* (Carter, 1883; $n = 65$) and *Cliona orientalis* (Thiele, 1900; $n = 76$) were collected on 20th March 2024 at 3–6 m depth, where the water temperature was 27.0 °C; from the Nouméa lagoon, *C. orientalis* ($n = 65$) and *Spheciospongia vagabunda* (Ridley, 1884; $n = 42$) were collected from Îlot Signal (an offshore island; 22.295° S, 166.293° E) and *Cliona jullieni* (Topsent, 1891; $n = 71$) from Baie des Citrons (off the mainland; 22.296° S, 166.437° E) on 19th March 2024 at 3–6 m depth, where the temperatures were 26.0 °C and 25.3 °C, respectively (Fig. S.2 shows sampling locations). Cited temperature data were collected by ReefTEMPS for Nouméa lagoon sites (data are for Îlot Larégnère, ~4 km from Îlot Signal; Varillon et al., 2019) and using a HOBO Pendant MX Water Temperature Data Logger (MX2201, Onset Computer Corporation) for Bouraké (Fig. S.3).

Sponges were left in situ for ~1 month at their respective sampling site, in large, anchored bins covered with nets to prevent predation, to allow osculum and pinacoderm regrowth where cuts were made during collection (Bates and Bell, 2018) and to allow specimens to acclimate to the same depth, temperatures and light exposure. After this, they were transferred, on 22nd and 23rd April 2024, to flow-through experimental aquaria ($n = 23$–34 sponges *per* tank for Bouraké; $n = 29$–30 sponges *per* tank for Nouméa lagoon) at the Reef Lab aquarium facilities (Institut de Recherche pour le Développement) in Nouméa, and acclimated for 6–7 d. For further details on sponge species and collection, see supplementary information.

2.2. Experimental design

This experiment consisted of two independent, simulated MHWs (one *per* collection site, due to the contrasting abiotic conditions; Figs. S.4 and S.5), with three replicate 35 L experimental tanks *per* heatwave and control treatment (12 tanks total) and four 400 L sump tanks (one for each site/treatment combination). Unfiltered seawater was pumped from 3 to 4 m depth to sump tanks, which then continuously flowed to the experimental tanks. Seawater was unfiltered to allow a sufficient supply of particulates and microorganisms for the sponges to feed on (Massaro et al., 2012), although this was not measured in the experiment. Each experimental tank had a lower flume, with a Resun SP3800 submersible pump (220–240 V) at each flume opening set to reverse water flow every 6 h to mimic bidirectional tidal fluctuations and ensure continuous water movement (Möller and Christie, 2019). Light was independently controlled in each tank using Mitras LX7 LED full-spectrum aquarium lights (G-MiLX7206), with irradiance increasing from 0 to 160–190 μmol photons m^{-2} s^{-1} on a 12:12 h light:dark cycle (Table S.3).

Each experimental tank was independently temperature controlled using the Apex Classic system (Neptune Systems), connected to 200 or 300 W aquarium heaters (Aquarium Systems VisiTherm VTX). Control temperatures corresponded to the mean monthly temperature in April/May at each collection site (Fig. S.3; Maggioni et al., 2024); these were maintained at 27.99 ± 0.002 °C and 26.07 ± 0.003 °C (means ±SE, across tanks) for samples from Bouraké and the Nouméa lagoon, respectively. The MHW simulations *per* site were staggered by 1 d to allow time to conduct the physiological measurements at each timepoint. After the acclimation period, the heatwave treatment was increased by 0.38 °C d^{-1} for 12 d to a temperature + 4 °C compared with the control. Peak heatwave temperatures represented the threshold and above of a Category IV 'extreme' MHW (Hobday et al., 2018; Holbrook et al., 2022), based on the long-term climatological mean SST in the study area (Figs. S.4 and S.6; NOAA, 2024). After the +4 °C temperature was reached, the original experimental design was to slowly decrease the temperature back to ambient levels (as a 'recovery' period: see Strano et al., 2022). However, after observations showed only subtle shifts in sponge physiological measurements at this temperature, the temperature was increased a further 2 °C at the same daily rate for 5 d to +6 °C above controls. This level of exposure is representative of a Category IV MHW at the study sites during the austral summer (December to February; Figs. S.4 and S.6). At this point, due to violent civil unrest in the Nouméa area (Doyle, 2024), for security reasons the experiment was prematurely terminated meaning it was not possible to apply recovery period observations as originally planned. Abiotic conditions were measured once daily, including temperature and pH (using a Metrohm 913 pH Meter) and flow rate (the length of time for each tank's outflow to fill a 300 mL vessel). For further details, see supplementary information.

2.3. Physiological measurements

During the 25-day experiment, a series of physiological measurements were performed at different timepoints from T_0 to T_4 (Fig. S.4 and Table S.1). Sponges (three *per* species *per* tank) were haphazardly allocated to the physiological measurements at each timepoint (oxygen evolution and buoyant weight at $T_{0\text{-ox}}$ and $T_{3\text{-ox}}$; pulse-amplitude modulated (PAM) fluorometry at $T_{0\text{-fl}}$–$T_{4\text{-fl}}$) using the designated sponge IDs on paper to limit bias.

2.3.1. Health and survival

Sponge health was monitored daily, with observations recorded on morphological or colour changes, necrosis or mortality. Photographs of individual sponges were taken every 3–4 days. Bleaching (loss of colour via expulsion of symbiotic organisms or their pigments; Ramsby et al., 2018a) was assessed by observing the paling of sponges from dark brown to yellow/white; inward migration of symbionts in the sponge tissue was ruled out via dissection for a subset of bleached sponges. Bleaching observations were further corroborated using PAM fluorometry (see Section 2.3.3). Necrosis (tissue death) was assessed based on the blackening of sponge tissue (with or without the presence of a white bacterial or fungal surface film) and an odour of decay (Achlatis et al., 2017).

2.3.2. Oxygen evolution

Final sponge net photosynthesis (Pn) and dark respiration (R) rates are the increase or decrease, respectively, in oxygen over time, normalised for sponge volume and expressed in $mgO_2\ gAFDW^{-1}\ h^{-1}$. Gross photosynthesis (Pg) was calculated as Pn corrected for R: $Pg = Pn + R$ (Beer et al., 1998). The Pg:R ratio was calculated as an idealised daily budget of 12 h Pg and 24 h R – calculated as $Pg{:}R = (Pg \times 12) / (R \times 24)$ – noting that, as this does not account for diel flux of photosynthesis and respiration rates, it is unlikely to be a true reflection of Pg:R in nature (Pringault et al., 2007). The threshold for phototrophy is defined here as $Pg{:}R > 1$, as *per* Pringault et al. (2007).

R and Pn rates were measured at two timepoints ($T_{0\text{-ox}}$ and $T_{3\text{-ox}}$), on three sponge individuals *per* species *per* tank, 18 at a time. Any bryozoan, algal or other epiphytic growth detected on the $CaCO_3$ base of the *Cliona* spp. and on other sponges was gently brushed off before respiration and photosynthesis measurements (Mobilia et al., 2021). Sponges were then placed in individual 250 mL glass beakers, each fitted with an oxygen sensor spot (PreSens), a submersible magnetic stir bar and a mesh disc to separate the sponge from the bar. Sponges were placed in beakers underwater, at the appropriate treatment temperature, and beakers were hermetically sealed underwater with transparent cellophane and a rubber band after removing all air bubbles so as not to impact the oxygen readings (Jacquemont et al., 2022). Three 100 mL glass blank beakers (without a sponge), sealed in the same way, were used to measure ambient respiration in the seawater (Strano et al., 2022). Beakers ($n = 21$) were placed on two magnetic multipoint stir pads (Thermo Scientific™ Cimarec™ i Telesystem) set to 500 rpm to maintain steady water flow, within two thermally controlled water baths. Water bath temperatures corresponded to the appropriate experimental conditions and were heated using 300 W aquarium heaters and Eheim compactON 600 submersible pumps (220–240 V). Rates of sponge Pn and R were measured by the increase and decrease of seawater oxygen levels over 30 and 40 min, respectively, which corresponded to a 10–20 % change in the oxygen starting values, as tested during pre-experiment trials. Oxygen levels were measured with a fibre optic oxygen meter (PreSens Precision Sensing Fibox 4) after 10 min light acclimation (T_{START}) and again after 30 min light incubation (T_{END}). Incubations were carried out under LED full-spectrum aquarium lights (Mitras LX7, G-MiLX7206) at ~200 μmol photons $m^{-2}\ s^{-1}$. The beakers were then covered in a black plastic sheet, with the aquarium lights turned off, to measure R. Oxygen levels were measured after 10 min dark acclimation (T_{START}), then after 40 min dark incubation (T_{END}). The water bath temperature was monitored throughout the incubations to ensure stability. T_{START} and T_{END} oxygen concentrations for the light and dark incubations were used to calculate the Pn and R rates *per* hour, respectively.

Rates were standardised to beaker volume, corrected for the blanks and normalised to sponge ash-free dry weight (AFDW; i.e., the sponge's tissue weight) by drying sponges for 72 h at 60 °C and then incinerating them for 5 h at 500 °C. As the *Cliona* spp. were attached to a $CaCO_3$ substrate, AFDW of three blank $CaCO_3$ plugs was also determined to correct for organic matter present in plugs and avoid overestimating sponge AFDW. Buoyant weights (BW) of the non-bioeroding sponges included in the oxygen evolution measurements at each timepoint were taken concurrently (following Osinga, 1999), using a seawater-filled 500 mL beaker on an analytical balance (M-pact sartorius AX224, readability to 0.1 mg), correcting for the BW of the ceramic tile. BWs were used to obtain a conversion factor to AFDW (using a regression analysis) to normalise rates throughout the experiment to AFDW without the necessity of sacrificing sponges at the earlier timepoint.

2.3.3. Photosynthetic efficiency

Rapid light curves (RLCs) were performed using an underwater PAM fluorometer (Heinz Walz GmbH DIVING-PAM-II/R Underwater Chlorophyll Fluorometer with Fiberoptics DIVING-F; red actinic light), in fully dark-acclimated conditions (in the morning before aquarium lights were activated and without external light sources), to estimate potential quantum yield of electron flow through Photosystem II (PSII) by measuring the fluorescence emitted by chlorophyll-*a* at increasing levels of photosynthetically active radiation (PAR; Beer et al., 1998). Dark-acclimation ensures that PSII reaction centres are open and the electron transport chain is oxidised (Ralph and Gademann, 2005).

Three sponges *per* species *per* tank were measured at each of five timepoints (more frequently than the oxygen evolution measurements: see Fig. S.4), placed in individual beakers for each measurement to avoid interference from other sponges in the tank. Only the *Cliona* spp., which contain photosynthetic symbionts of the family Symbiodiniaceae (also found in corals) in their surface tissue (Lévi, 1998; Hill et al., 2011; Ramsby et al., 2017), were measured. The PAM's 5.5-mm (active diameter) optical fibre was positioned perpendicular to the upper sponge surface, with a 5-mm spacer to ensure an equal distance between the sensor and the sponge for all measurements. All calculated electron transport rates (ETRs; in μmol electrons $m^{-2}\ s^{-1}$) were relative (ETR factor 0.84), but these are proportional to absolute values of ETR (Bell et al., 2022). The fluorescence parameters derived from the RLCs were ETR (the estimated electron transport rate through PSII reaction centres); F_v/F_m ratio (the photosynthetic efficiency, or the probability of absorbed photons driving electron transport); α_{RLC} (the initial slope of the RLC in the light-limiting region of PAR); ETR_m (the maximum ETR in the RLC); and E_K (the saturation irradiance; Beer et al., 1998; Serôdio et al., 2006). α_{RLC}, ETR_m and E_K values were calculated as *per* the empirical equations in Platt et al. (1980), which allow for a continuous photosynthetic response to light. For further details and PAM settings, see supplementary information.

2.4. *Data analysis*

The data from Bouraké and Nouméa lagoon were analysed independently for differences among timepoints and treatments. Data were analysed and graphs produced in R Studio (V. 2025.09.1 + 401; Posit PBC). Time-to-event analysis for sponge survival or bleaching was performed using the Kaplan-Meier estimate in the R package *survival* (Therneau, 2021), and *p*-values were calculated using a log-rank test.

Linear mixed effects models using the *nlme* package (Pinheiro et al., 2025), run with Restricted Maximum Likelihood, were used to determine the effects among species of treatment and timepoint on each of R, Pg and Pg:R, as well as on all PAM fluorometry parameters (see Tables S.11 and S.15). Fixed and random effects were constant across dependent variables for consistency and relevance to the experimental design. For oxygen evolution data, each model retained fixed effects Species, Timepoint and Treatment, with all interaction terms, and the random effects of Species nested within Tank. For the PAM fluorometry data, in which there were repeated measures, the random effect of Sponge (nested within Species and Tank) was also included, to group observations from the same sponge specimens across timepoints. For relative ETR (the RLCs) the models included an additional fixed effect of PAR, which was fitted as a quadratic term. As there was only one species for Bouraké in the PAM measurements, the fixed and random effects of Species were removed from the models. The final models were interpreted using both a two-way ANOVA table (Type III) and Benjamini-Hochberg-corrected pairwise comparisons of the estimated marginal means (EMMs), calculated using the *emmeans* package (Lenth, 2021). Both adjusted and unadjusted *p*-values are reported, with adjusted *p*-values <0.05 considered statistically significant. Data are presented as raw data boxplots or raw data means (±standard error (SE)) using the *ggplot2* package.

The *nlme* package accommodates unequal variances and clustered datasets. To approximately meet the normality assumption, for both sites R and Pg data were log+1 transformed, α_{RLC} was square transformed, ETR_m square-root transformed and E_K log transformed. Pg:R data for Nouméa lagoon were log transformed, and the model for Nouméa lagoon R included a term allowing variance to differ among species due to a violation of the constant variance assumption. Pairwise comparisons were carried out on the scale of the model. Some models showed a possible violation of the normality assumption, even after data transformations, so the LME model results were supported by running non-parametric permutations tests (results contained in data spreadsheets). For each relative ETR model, all ETR values at 0 PAR (which all equalled 0) were omitted from the analysis to avoid skewing the data distribution. One outlier was removed from the Pg:R analysis (COB/$T_{0\text{-}ox}$/HW), as it was found to be influential and invalidated the model, but its removal did not impact the key findings, with the exception of one minor instance (see Section 3.2.1); no other outliers were removed from any dataset. R and Pg measurements from the same sponge were left in as they did not impact the key findings. One datapoint was removed from the R dataset (SV/$T_{3\text{-}ox}$/HW) as a repeated measure. Some α_{RLC}, ETR_m and E_K values were missing from the PAM fluorometry reports for each species, leading to slightly smaller sample sizes for these datasets.

3. Results

3.1. *Health and survival: time-to-event analysis*

Sponge survival differed between sites, with Bouraké species exhibiting either mortality or bleaching at the peak temperature of 34 °C, and Nouméa lagoon species showing no apparent effect on their health and survival at the peak temperature of 32 °C.

At Bouraké, *R. globostellata* showed significant mortality in the HW treatment compared with the control treatment (Table S.10). Median lethal time was 23 days, with survival probability down to 5 % by Day 25, and high necrosis and a very low chance of survival at 34 °C (Figs. 1-B and S.7). In contrast, no mortality was observed for *C. orientalis*, but there was significant bleaching (Figs. 1-A and S.8) in the HW treatment compared with the control treatment (Table S.10). By Day 21, 38 % of samples were bleached, which increased to 75 % by Day 22, consistent with a very high probability of bleaching from ~33.5–34 °C.

There was no mortality, necrosis or bleaching observed in any of the sponges collected from the Nouméa lagoon, which were incubated to a maximum temperature of 32 °C.

3.2. *Oxygen evolution*

Sublethal temperature effects on oxygen evolution varied among species regardless of site, with *C. orientalis* from both sites and *S. vagabunda* displaying significant shifts with higher temperature, and the remaining species showing no significant responses.

3.2.1. *Bouraké*

For the Bouraké species, there was a significant three-way interactive effect of species * timepoint * treatment on mean Pg ($p = 0.006$) and R ($p < 0.001$), but not on Pg:R ($p = 0.28$).

C. orientalis showed a response to higher temperature at $T_{3\text{-}ox}$ (32 °C), with increased mean Pg and R and decreased Pg:R compared with measurements at $T_{0\text{-}ox}$ (28 °C). Pg decreased over time in the control (C) treatment and increased in the heatwave (HW) treatment (Fig. 2-A-i), while R increased over time in the HW treatment and remaining stable in the C treatment (Fig. 2-A-ii). Pg:R significantly decreased over time in both treatments, noting that the removal of an outlier in the Pg:R dataset for the species resulted in the significant result in the control, so should be treated with caution (Fig. 2-A-iii).

In contrast, *R. globostellata* exhibited no response on mean Pg, R or Pg:R at 32 °C (Fig. 2-A-iv to -vi). See Tables S.4, S.12 and S.13 for full statistical results.

3.2.2. *Nouméa lagoon*

For the Nouméa lagoon species, there was no significant three-way interactive effect of species * timepoint * treatment, but there was a significant effect of the timepoint * treatment interaction on mean R ($p = 0.03$).

C. jullieni showed no response to higher temperature at $T_{3\text{-}ox}$ (30 °C) on mean Pg, R or Pg:R compared with measurements at $T_{0\text{-}ox}$ (26 °C) (Fig. 2-B-i to -iii)).

In contrast, *C. orientalis* (Nouméa lagoon) showed a response at $T_{3\text{-}ox}$, with elevated mean R. R increased over time in the HW treatment in contrast with no change in the C treatment (Fig. 2-B-v). The Pg:R ratio dropped to <1 at $T_{3\text{-}ox}$ in the HW treatment, though this change was not statistically significant (Fig. 2-B-vi).

S. vagabunda exhibited increased mean R with higher temperature. R in the HW treatment increased over time, compared with a decrease in the control (Fig. 2-B-vii). See Tables S.5, S.16 and S.17 for full statistical results.

3.3. *Photosynthetic efficiency*

Temperature effects on photosynthetic efficiency were variable among species and sites, with *C. orientalis* from Bouraké showing significant decreases with higher temperature, and both *Cliona* spp. from Noumea lagoon displaying only minor responses. There was a slight lab-induced light acclimation effect detected at the earlier timepoints, with ETR initially increasing over time for all species and treatments.

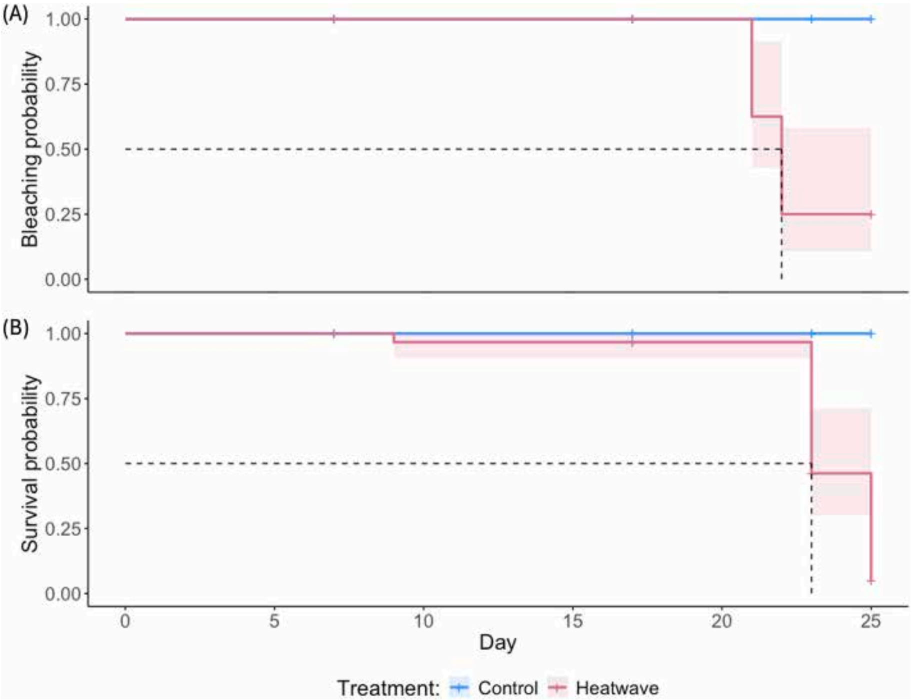

Fig. 1. Kaplan-Meier survival analyses illustrating time-to-event for (A) bleaching of *Cliona orientalis* (Bouraké) and (B) survival of *Rhabdastrella globostellata per* treatment over time. Figures show estimated probability of survival/bleaching (shading = 0.95 CIs), with the median line indicating the time at which 50 % of the sample has experienced the event. Temperatures (°C; HW treatment daily mean ± SE): Day 9 = 29.00 ± 0.01; Day 20 = 33.39 ± 0.01; Day 22 = 34.00 ± 0.01.

3.3.1. *Bouraké*

C. orientalis (Bouraké) showed a strong response in the measured chlorophyll fluorescence parameters at $T_{4\text{-fl}}$ (34 °C), with a significant decrease in mean F_v/F_m, α_{RLC}, ETR_m, E_K and relative ETR compared with the control treatment and earlier timepoints. There were significant timepoint * treatment interactions for all parameters (all $p < 0.001$). F_v/F_m decreased over time in the HW treatment compared with no change in the C treatment (Fig. S.9-A), and was 71.8 % of the control at 34 °C. α_{RLC}, ETR_m and E_K all significantly decreased over time in the HW treatment compared with significant increases in the C treatment. Lower relative ETRs in the HW treatment than in the C treatment were found across all levels of PAR at $T_{4\text{-fl}}$, as well as at $T_{3\text{-fl}}$ at PAR 561 and above (Fig. 3-A). See Tables S.6, S.7 and S.12–14 for full statistical results.

3.3.2. *Nouméa lagoon*

For the Nouméa lagoon species, there was a significant three-way interactive effect of species * timepoint * treatment on F_v/F_m ($p < 0.001$), and significant timepoint * treatment interactions for α_{RLC} ($p < 0.001$), E_K ($p < 0.001$) and relative ETR ($p = 0.007$).

C. jullieni exhibited some response to higher temperatures in the chlorophyll fluorometry results, with largely higher mean values in the HW treatment than the C treatment, but some temperature-induced response at $T_{4\text{-fl}}$ (32 °C). F_v/F_m significantly decreased over time, compared with no change in the C treatment (Fig. S.9-B), while α_{RLC} increased in the C treatment and decreased in the HW treatment. ETR_m and E_K increased over time in both treatments. Relative ETR increased over time in both treatments, with the HW treatment showing a drop at $T_{4\text{-fl}}$ relative to the control (Fig. 3-B).

C. orientalis (Nouméa lagoon) showed similarly mixed results, with F_v/F_m (Fig. S.9-C) and α_{RLC} decreasing in the HW treatment relative to the control, and ETR_m and E_K increasing. Relative ETR increased in both treatments from $T_{0\text{-fl}}$ to $T_{3\text{-fl}}$ across most levels of PAR, with values in the HW treatment then showing a significant downward trend between $T_{3\text{-fl}}$ and $T_{4\text{-fl}}$ at PAR 561 and above (Fig. 3-C). See Tables S.8, S.9 and S.16–18 for full statistical results.

4. Discussion

Extreme MHW events can have broad ecological effects on marine ecosystems, with the high temperatures impacting organisms' physiology, biology, behaviour and survival (Leung et al., 2021). This study assesses the physiological effects of simulated MHWs on tropical sponges, focusing on four ecologically important sponge species from two contrasting sites in New Caledonia. Species from Bouraké were expected to show high tolerance to increased temperatures due to the extreme abiotic fluctuations experienced daily by organisms at this site (Camp et al., 2017; Maggioni et al., 2023a). We instead found *C. orientalis*, collected from both Bouraké and Nouméa lagoon, to have comparable thermal stress responses up to 32 °C, independent of collection site. The four sponges' physiological stress responses were variable and species-specific but, while there were sublethal effects in all species ranging in severity, there were no signs of tissue necrosis and bleaching until temperatures reached 33.5–34 °C, or ~6 °C above the monthly mean temperature at Bouraké. The acute and sudden effects of the peak temperature on both Bouraké species indicate strict thermal thresholds. However, compared with previous studies, these thresholds are relatively high, suggesting these four sponge species may be able to survive future projected ocean warming and extreme MHW events (IPCC, 2021).

4.1. *Species-specific variability in sublethal effects but shared tolerance to 32 °C*

The four species displayed variable sublethal effects in oxygen evolution and photosynthetic efficiency at higher temperatures but, despite this study's hypotheses positing high and low thermal tolerance of sponges from Bouraké and Nouméa lagoon, respectively, no species displayed bleaching or low survivability up to at least 32 °C (+4–6 °C above the site-specific monthly mean). Previous studies from other tropical regions have reported sponge bleaching and/or mortality at >29 °C (Fang et al., 2018), at 31.5 °C (Botté et al., 2023), or at 32 °C (Ramsby et al., 2018a), so a thermal threshold of above 32 °C can be

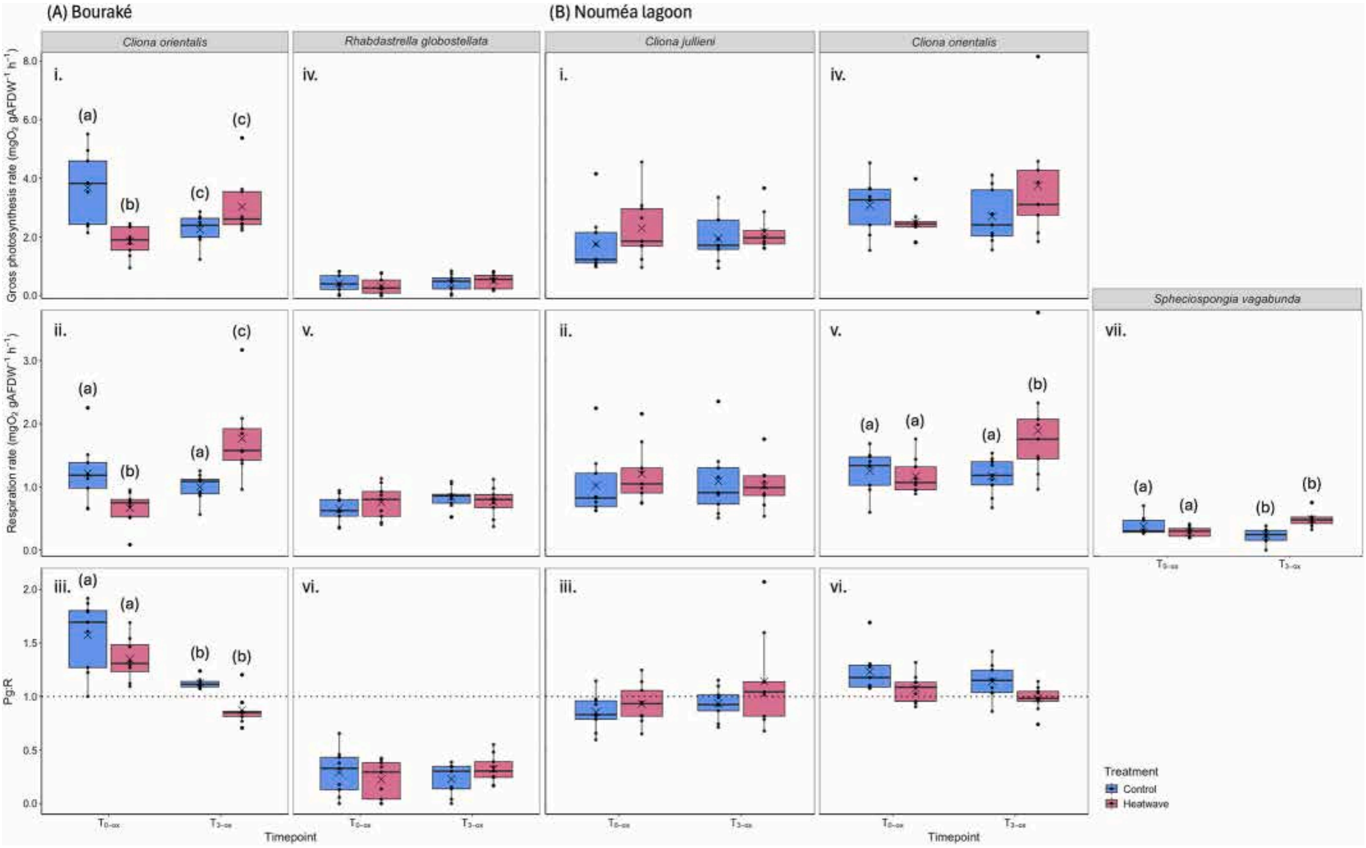

Fig. 2. Oxygen evolution boxplots over time for Bouraké species *Cliona orientalis* (A-i–iii) and *Rhabdastrella globostellata* (A-iv–vi), and Nouméa lagoon species *Cliona jullieni* (B-i–iii), *C. orientalis* (B-iv–vi) and *Spheciospongia vagabunda* (B-vii) (for A-iii and B-vii $n = 35$; all other plots $n = 36$). Plots (from top row to bottom row) are for gross photosynthesis rate (Pg), dark respiration rate (R) and the ratio of Pg to R; note that axis scales differ for each variable but are the same across species. The threshold for phototrophy in Pg:R (=1.0) is represented by a horizontal dotted line. For each boxplot, the horizontal bar represents the median, 'x' represents the mean, and the lower and upper hinge represent the first and third quartile, respectively. Lower-case letters (a, b and c) show significant changes between timepoints and treatments, at $\alpha = 0.05$.

considered relatively high.

Temperature is a strong driver of elevated respiration rates in sponges, indicating higher metabolic activity, energy usage and physiological stress (Strano et al., 2022; Bosch-Belmar et al., 2024), which was observed here in *C. orientalis* from both sites and *S. vagabunda*. According to the Metabolic Theory of Ecology (Brown et al., 2004) respiration is predicted to increase at twice the rate of photosynthesis for every degree increase in temperature, potentially leading to system heterotrophy (Harris et al., 2006; Vaquer-Sunyer and Duarte, 2011). This was observed in both *C. orientalis* populations, with Pg:R ratios trending downwards and falling below 1, indicating that oxygen produced through photosynthesis was no longer compensating for the stress-induced increases in energy requirements, thus leading to productivity losses (Pringault et al., 2007). This is consistent with earlier research on corals at Bouraké that exhibited reduced Pg:R ratios, with respiration rates 11–74 % higher than at reference sites (Camp et al., 2020), due to the highly fluctuating and relatively extreme temperatures (Camp et al., 2017; Maggioni et al., 2024).

The reduction in chlorophyll fluorescence parameters at 34 °C in *C. orientalis* (Bouraké) may indicate initial photosystem damage (Rasmusson et al., 2020), and loss of photosynthetic product in this species has been linked to lower rates of bioerosion, a critical ecological function in oligotrophic ecosystems like coral reefs (Achlatis et al., 2019). *C. jullieni* may have been displaying photoinhibition at the peak temperature, a process whereby photosynthetic activity of PSII is reduced above a certain threshold of light intensity (Murata et al., 2007). Thermal stress may lower this threshold in Symbiodiniaceae (Bhagooli and Hidaka, 2004), as well as suppress protein synthesis, inhibiting the repair of damaged PSII reaction centres (Takahashi et al., 2004; Murata et al., 2007). *C. jullieni* showed no signs of bleaching or mortality, despite the apparent damage to its photosynthetic apparatus, potentially due to the efficiency of its symbionts' repair machinery, as well as the host's photoprotective capacity and defensive mechanisms, such as antioxidant enzyme synthesis, host tissue thickness and heat-shock protein production (Bhagooli and Hidaka, 2004; Takahashi et al., 2004).

Differential physiological responses to thermal stress among sponge species may be due to their capability at a molecular level to protect against heat-induced cellular damage through increased expression of genes involved in oxidative response, signal transduction and immunity pathways (Guzman and Conaco, 2016). Commonly, the rapid upregulation of heat-shock protein HSP70 can facilitate the regulation and refolding of denatured proteins (Webster et al., 2013; Guzman and Conaco, 2016; González-Aravena et al., 2019). Downregulation of critical molecular functions, such as apoptosis, protein synthesis, detoxification and cytoskeleton rearrangement, has been linked with greater thermal sensitivity (Webster et al., 2013). Bennett et al. (2018) further attributed a greater concentration of storage lipids, phospholipids and sterols to higher thermal tolerance in tropical sponges, improving cell membrane integrity and cell homeostasis.

Another potential factor in species-specific thermal tolerance is the composition of their abundant and diverse microbial communities (Taylor et al., 2007; Strano et al., 2023). There is considerable current research focused on the effect of microbial abundance on sponge stress tolerance. High microbial abundance (HMA) sponges house denser, more diverse and more specific microbial communities than low

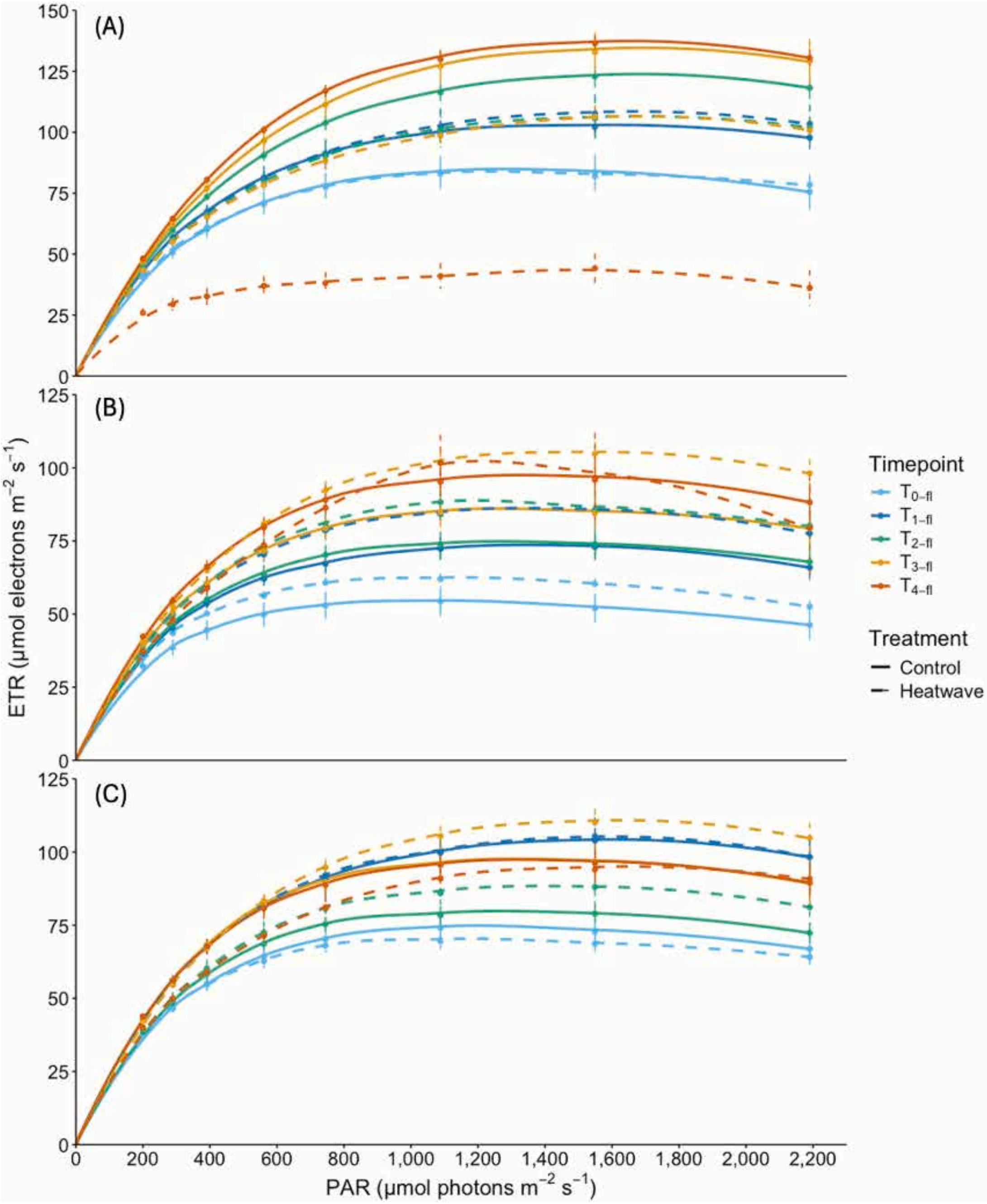

Fig. 3. Rapid light curves for (A) *Cliona orientalis* (Bouraké), (B) *Cliona jullieni* and (C) *C. orientalis* (Nouméa lagoon) (all species $n = 90$) at each timepoint for each treatment, showing raw mean electron transport rate (ETR; ± SE) as a function of photosynthetically active radiation (PAR). Note that each graph is on a different scale.

microbial abundance (LMA) sponges, which has implications for functional flexibility (Gloeckner et al., 2014). *R. globostellata*, presumed to be an HMA sponge (predicted based on microbiome composition in Moitinho-Silva et al., 2017; see also Maggioni et al., 2023b for microbiome characterisation of Bouraké samples), may therefore use energy acquired through microbial symbiosis to compensate for environmental stress (Morganti et al., 2017). Trophic strategies do not, however, explain all the results in this study: *C. jullieni* from the Nouméa lagoon, a likely LMA sponge (predicted from Moitinho-Silva et al., 2017, based on other Indo-Pacific clionaid species), showed Pg:R ratios <1 across most treatments and timepoints suggesting net heterotrophic nutrition (Pringault et al., 2007) and thus greater exposure and susceptibility to external environmental change through higher pumping rates (Weisz et al., 2008; Posadas et al., 2022), but also revealed thermal tolerance up to 30–32 °C (4–6 °C above its site-specific monthly mean). This may be due to Nouméa lagoon specimens of *C. jullieni* harbouring the Symbiodiniaceae genus *Symbiodinium* (Hill et al., 2011), which is known to resist bleaching due to a high photoprotection capability (Krämer et al., 2012). *C. orientalis* from other Indo-Pacific regions is known to harbour *Gerakladium*, though genotyping of the Symbiodiniaceae ITS2 rDNA region would be needed to determine symbiont identity in New Caledonian specimens. While generic symbiont differences may influence sponge host tolerance, high intra- and inter-generic, and some intra-specific, diversity in thermal tolerance has been exhibited by Symbiodiniaceae (Krämer et al., 2012; Díaz-Almeyda et al., 2017). Future ITS2 gene sequencing approaches for the *Cliona* spp. in this study may elucidate the species-level genetic foundations of observed differential physiological responses.

4.2. Site-independent stress response of *C. orientalis*

The stress responses of *C. orientalis* appeared to be independent of the collection site. Specimens from both sites displayed similar sublethal effects, which suggests limited local acclimation. The increase in photosynthetic efficiency and capability at temperatures as high as 32–33 °C points towards resiliency and a high thermal threshold relative to conspecifics, with studies of *C. orientalis* in other Indo-Pacific regions showing it to lose photosynthetic integrity from 32 °C (Ramsby et al., 2018a). Such inter-regional differences between populations of *C. orientalis* may have a genetic basis, and ITS2 genotyping of associated Symbiodiniaceae could reveal population-specific tolerance levels.

Geographically separated conspecific sponge populations can be highly genetically differentiated (Xavier et al., 2010; Oury et al., 2020), with clionaid species characterised by low and philopatric dispersal (Marlow et al., 2019). However, geology and oceanic current regimes strongly influence population connectivity, which is not necessarily limited by geographic distance (Nichols and Barnes, 2005; Chaves-Fonnegra et al., 2015). The connectivity of geographically separated coral populations in the southwestern region of Grande Terre's lagoon has been reported, aided by northeast-to-southwest currents (Oury et al., 2020). Given their similar physiological responses in this study, it could be suggested that the Bouraké and Nouméa lagoon populations of *C. orientalis* are genetically connected, with favourable and strong oceanic current patterns facilitating larval dispersal across the 90-km stretch of the lagoon (Chaves-Fonnegra et al., 2015; Marlow et al., 2019). Moreover, other *Cliona* spp. are reported to have generally low genetic diversity and rates of evolution (León-Pech et al., 2015; Quek et al., 2022), which may explain the lack of acclimation shown in this study by the Bouraké population compared with the Nouméa lagoon.

4.3. Lethal effects above a strict thermal threshold

Acute bleaching and mortality occurred in both Bouraké species when exposed to temperatures above ~33.5–34 °C, suggesting relatively high but strict thermal thresholds for these New Caledonian species. While Nouméa lagoon species were not experimentally exposed to 34 °C, it can be extrapolated from the lack of physiological response at 32 °C that they may share an upper thermal threshold with species from Bouraké that is independent of population-specific environmental acclimation. This question could be further explored in subsequent studies.

The bleaching and reduction in holobiont photosynthetic potential of *C. orientalis* (Bouraké) at the peak temperature indicates a loss of symbionts, which has been reported previously in this species under thermal stress (Ramsby et al., 2018b). In coral Symbiodiniaceae, environmental stress can generate reactive oxygen species, which damage cell components and break down PSII reaction centres, potentially leading to the removal of symbionts by the host (Krämer et al., 2012). While no mortality was observed in *C. orientalis* in this experiment, the loss of photoautotrophic energy through bleaching has been linked to mortality for Great Barrier Reef (GBR) populations at persistent higher temperatures (Fang et al., 2014), as the species may lack the nutritional flexibility for heterotrophic compensation (Weisz et al., 2010; Fang et al., 2018). Ramsby et al. (2018a) found no signs of recovery of GBR *C. orientalis* that bleached at 32 °C, after one month at a reduced temperature of 30 °C. Bleaching recovery has occurred in other clionaid species (Marlow et al., 2018), though recovery potential may depend on the magnitude of sponge energy (lipid) stores, as well as the duration and frequency of MHWs. Recovery may also depend on population-specific acclimation, as previous exposure to higher temperatures or thermally resilient Symbiodiniaceae in corals has been reported to aid bleaching recovery (Camp et al., 2017; Ramsby et al., 2018a), which may confer an advantage to organisms inhabiting environments such as Bouraké (Alessi et al., 2024).

The suddenness of *R. globostellata*'s necrosis and mortality at the peak temperature, despite showing no change in the measured stress response parameters at lower temperatures, could be due to failure of host cell repair and protection mechanisms, leading to extensive cell damage, gene transcription inhibition and loss of vital biological function (Webster et al., 2013). It could also be attributed to irreversible and destabilising microbial community shifts occurring at sublethal temperatures (Ramsby et al., 2018b), with the down-regulation of genes mediating the host–symbiont association, the loss of critical symbiotic microbes and their functions (e.g., detoxification by ammonia-oxidising archaea; Zhang et al., 2014), and an influx of opportunistic and pathogenic bacteria (Bell et al., 2018; Strano et al., 2022, 2023). *R. globostellata* from Bouraké houses 53.2 % Chloroflexi (Maggioni et al., 2023b), one of the most functionally diverse sponge-associated bacterial phyla (Moitinho-Silva et al., 2017), perhaps providing the holobiont with the flexibility and acclimation ability required to withstand extreme environmental conditions. However, this mechanism may fail at temperatures near 33 °C, as Bouraké attains this threshold temperature only for very short timeframes during low tides in the summer (i.e., 1–2 h; Maggioni et al., 2023a), while the exposure during this MHW simulation lasted 2–3 d. The species and its microbiome may not be acclimated to prolonged exposure to these extreme temperatures. The potential irreversible microbial breakdown at sublethal temperatures implies that current ocean warming and MHW events may have undetected impacts on sponge microbial communities, leading to sponge microbiome dysbiosis and mortality in future climate change scenarios (Bell et al., 2018). Characterisation of the microbiome of *R. globostellata* to confirm thermal thresholds for microbial breakdown, as well as recovery potential, is warranted.

5. Conclusion

Our study elucidated the physiological response to thermal stress of four New Caledonian sponges exposed to simulated MHWs. The four species in this study showed differential and species-specific sublethal effects of thermal stress but illustrated (or suggested) similarly high thermal optima (>33 °C), above which bleaching and mortality were observed. *C. orientalis* specimens of the two sites behaved similarly with respect to high-temperature exposure, in contrast to our hypothesis. These sponges may be capable of survival under ocean warming projected for 2100 and through extreme MHW events predicted in the near future (IPCC, 2021), and could eventually dominate reef ecosystems in the New Caledonia region if corals cannot withstand the environmental shifts. This study has shed light on the 'critical thermal limits' (Bosch-Belmar et al., 2024) of these tropical sponge species, which can be used as indicators of the resilience under future environmental change of this UNESCO World Heritage reef ecosystem.

CRediT authorship contribution statement

Barbara J. Graham: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Simon K. Davy:** Writing – review & editing, Supervision, Data curation. **Lisa Woods:** Formal analysis, Writing – review & editing. **Torsten Thomas:** Writing – review & editing, Supervision, Methodology. **Riccardo Rodolfo-Metalpa:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **James J. Bell:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: James Bell reports financial support was provided by Fonds Pacifique. Riccardo Rodolfo-Metalpa reports financial support was provided by Fonds Pacifique. If there are other authors, they 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.marpolbul.2025.119138.

Data availability

Raw data and R scripts can be made available upon request.

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