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Not only summer matters: spring warming shapes the gorgonian condition when facing marine heatwaves

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Abstract

Accelerated spring warming is one of the less studied consequences of global change. This study aimed to evaluate the effects of an accelerated increase in seawater temperatures during spring on respiration and zooplankton capture rates, as well as the resulting nutritional condition of one of the main structural species of coastal Mediterranean benthic communities, the red gorgonian *Paramuricea clavata*. Fragments of red gorgonian colonies were maintained in aquaria under historical and accelerated spring temperature rises. While *P. clavata* was able to acclimate and maintain constant respiration rates during historical spring conditions, accelerated warming resulted in significantly higher respiration rates. Conversely, the zooplankton capture capacity was not affected. As a result, gorgonians were significantly depleted in organic matter and overall energy content after accelerated spring warming. These results highlight the crucial role of spring thermal conditions in shaping the health condition of *P. clavata* when facing high summer temperatures, and potential heatwaves.

Keywords: Respiration; feeding; *Paramuricea clavata*; octocorals; accelerated spring warming; climate change; Mediterranean Sea.

Introduction

There is increasing evidence that climate change is driving rapid seawater warming in oceans and seas worldwide (IPCC, 2022). This warming includes a rise in the mean annual sea surface temperature and increases in the frequency and intensity of extreme marine heat events (IPCC, 2019). However, the annual warming trend exhibits seasonal variability with warming concentrating during specific seasons depending on the region (e.g., Chollett *et al.*, 2012; Shaltout, 2019). These changes in sea water temperature can influence the phenology of marine species, determining the timing of life-history events such as migration (e.g., Sims *et al.*, 2001, 2004) and reproduction (e.g., Weishampel *et al.*, 2004; Sawall *et al.*, 2021).

The Mediterranean Sea has been considered a hotspot of climate change because its warming rate (0.38 ºC decade^{-1} between 1982 and 2019; Cramer *et al.*, 2018; Pisano *et al.*, 2020; Garrabou *et al.*, 2022) is significantly higher than the oceans' global average (0.11 ºC decade^{-1}; IPCC, 2019). In this region, the temperature increase mainly concentrates in the spring and summer (Salat & Pascual, 2006). Consequently, high temperatures are reached earlier in the spring than in previous decades (López-García, 2015). To date, however, most of the studies have examined the effect of extreme warming events in the summer (e.g., Marbà & Duarte, 2010; Islam *et al.*, 2021; Garrabou *et al.*, 2022; Darmaraki *et al.*, 2024), overlooking the potential role of accelerated spring warming in shaping the capacity of species to face extreme summer events. The frequency of these extreme events has doubled in recent decades, with marine heatwaves becoming longer and more intense (Darmaraki *et al.*, 2019a; Collins *et al.*, 2019). Many species are affected by these marine heatwaves, which are causing mass mortalities of benthic invertebrates (Garrabou *et al.*, 2009; Rivetti *et al.*, 2014; Marbà *et al.*, 2015). According to Garrabou *et al.* (2022), there have been 676 mass mortality events between 1979 and 2017, affecting 93 species, mostly Cnidaria, Porifera and Bryozoa. In 1999 and 2003, the most impactful mass mortalities in the Mediterranean Sea were recorded, affecting hundreds of kilometres (Cerrano *et al.*, 2000; Perez *et al.*, 2000; Garrabou *et al.*, 2009). Since then, there have been mass mortality events every year, although affecting fewer species at smaller geographical scales (Rivetti *et al.*, 2014; Marbà *et al.*, 2015; Rubio-Portillo *et al.*, 2016; Garrabou *et al.*, 2022). Under the ongoing climate change, the frequency of mass mortality events is expected to further increase in the coming decades (Darmaraki *et al.*, 2019b; Garrabou *et al.*, 2019), with their effects possibly exacerbated by the thermal stress experienced under early warming conditions.

Mass mortalities are of special concern because the Mediterranean Sea is also a biodiversity hotspot since it harbours 7-10% of the worldwide marine biodiversity (Bianchi & Morri, 2000; Coll *et al.*, 2010). A large proportion of this biodiversity (10%) lives in coralligenous assemblages (Ballesteros, 2006). Coralligenous habitats are biogenic calcareous formations primarily composed of calcareous algae and sessile invertebrates, growing under dim light at depths of between 15 and 120 m (Ballesteros, 2006; Martin *et al.*, 2014; Çinar *et al.*, 2020). Among coralligenous species, gorgonians play a paramount structural role (Gili & Coma, 1998), creating the upper arborescent part of the community. Gorgonians can modify the water current flow, light and food availability, as well as sediment resuspension, increasing environmental heterogeneity and enhancing the abundance and diversity of the associated fauna (Gili & Coma, 1998; Ribes *et al.*, 1999a; Cerrano *et al.*, 2010). Furthermore, gorgonians play an important role in benthopelagic coupling, generating a flow of matter and energy between the pelagic and benthic systems, as they capture plankton and particulate organic matter in suspension (Lewis, 1982; Gili & Coma, 1998; Ribes *et al.*, 1999a).

As passive suspension feeders, Mediterranean gorgonians feed mainly in the spring, coinciding with the bloom in primary and secondary pelagic production (Coma *et al.*, 1994; Ribes *et al.*, 1999a, 1999b; Rossi *et al.*, 2006). Zooplankton represents an important food source, providing organic matter of high nutritional value (Coma *et al.*, 1994; Ribes *et al.*, 1999a, 2003; Rossi *et al.*, 2004). In the summer, when the temperature rises, the water column is stratified and plankton abundance is drastically reduced above the thermocline (Coma *et al.*, 2000). Moreover, metabolic rates increase with summer high temperatures, causing higher energy consumption (Previati *et al.*, 2010; Tignat-Perrier *et al.*, 2022). As an energy-saving mechanism, gorgonians decrease their activity in the summer by contracting most of their polyps (Robbins & Shick, 1980; Lasker, 1981; Coma *et al.*, 1994). Consequently, during this period, they mainly rely on the energy reserves stored in the spring (Rossi *et al.*, 2006). Therefore, accelerated spring warming conditions could result in an imbalance between the gorgonians' capacity to acquire food and an increase in energy consumption due to the higher respiration rates at elevated temperatures (Previati *et al.*, 2010). This could finally result in an earlier consumption of spring energy reserves and, consequently, poor nutritional conditions at the beginning of summer, which may ultimately result in a reduced capacity to reproduce and overcome warm summers and potential heatwaves.

Hence, the aim of this study was to experimentally explore whether accelerated spring warming affected the respiration and food capture rates of one of the most abundant and emblematic Mediterranean gorgonians (*Paramuricea clavata*), and to assess the subsequent effects on its nutritional condition.

Materials and Methods

Sample collection, preparation, and experimental setup

In April 2022, 10 fragments of *Paramuricea clavata* were collected at a depth of 15-18 m in Punta Salines (42.06º N, 3.21º E; Montgrí, Illes Medes and Baix Ter Natural Park, Catalonia, Spain) and transported (within 2 h) to the laboratory at the Universitat de Barcelona in an insulated box (30-L volume) maintaining the *in-situ* temperature (12-13 ºC). In the laboratory, each fragment was divided into two portions (5-7 cm branch extension each), which were fixed on glass plates (4 x 4 cm) with epoxy resin (Grotech, Germany) and introduced into two different 80-L tanks filled with Mediterranean seawater. Each tank was equipped with a biological filter (Eheim 2250A, Germany), a submersible pump (Sicce Nano 2000, Italy) to generate a water flow of 3200 L h^{-1}, and a chiller (Teco TK2000, Italy) to maintain the seawater temperature. To acclimate the fragments, the water temperature of the tanks was maintained close to *in-situ* conditions (12.5 ± 0.5 ºC) for two weeks.

After this period, the temperature treatment was started. In one tank (historical spring treatment), the temperature was gradually increased, following the historical temperature cycle recorded at the Medes Islands (20 m depth) from April to June in the period 2002-2017 (excluding 2011 because an accelerated spring warming was recorded then in the study area, with the data obtained from T-Med Net; https://t-mednet.org/). In the other tank (accelerated spring treatment), the temperature was gradually increased by following the historical temperature cycle + 2 ºC (Fig. 1). Over the two months of the experiment, gorgonian fragments in both treatments were fed three times a week with freshly hatched *Artemia salina* (Crustacea, Sarsostraca) nauplii.

Respiration

To evaluate the effects of the treatment (historical and accelerated spring warming conditions) on the metabolism of the colonies (n = 10 per treatment), respiration rates were measured at the beginning of the experiment (April), as well as after 1 and 2 months (May and June). For the analysis, the fragments were individually incubated for 10 h in hermetically sealed plastic chambers (~400 mL in volume) filled with 50 µm pre-filtered Mediterranean seawater at the respective temperature. Temperature was maintained (± 0.15 ºC) in a water bath by a chiller (Teco TK2000, Italy). Constant water movement inside the chambers was created using Teflon-coated magnetic stirrers (Telesystem Multipoint Stirrer, Thermo Fisher

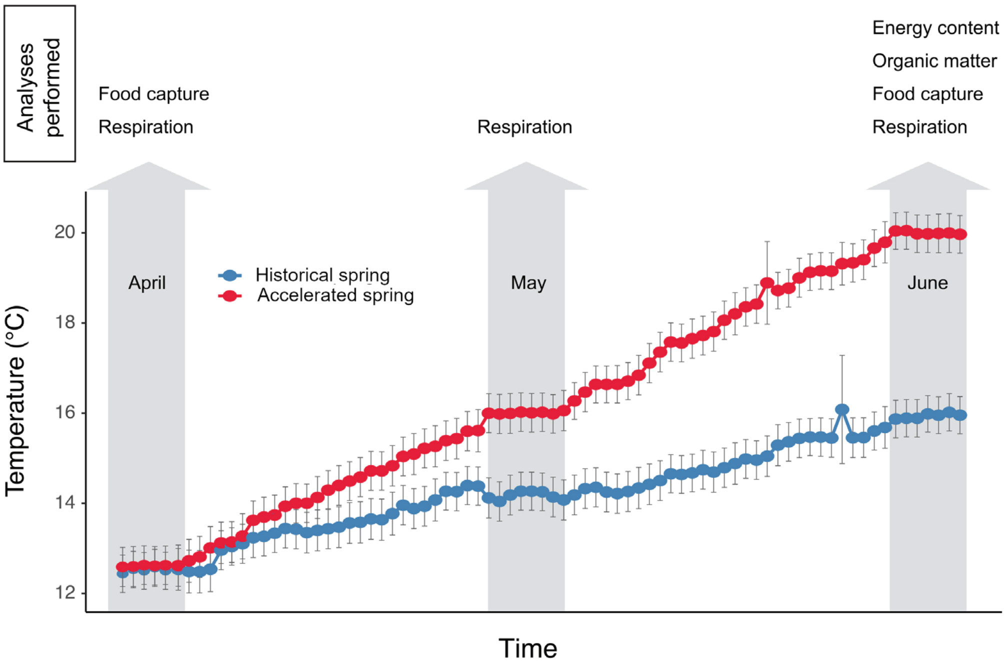

Fig. 1: Temperature increase. The temperature was increased every two days, by 0.1 ºC in the historical spring treatment and 0.2 ºC in the accelerated spring treatment.

Scientific, USA) at 5-6 cm s^{-1}. The dissolved oxygen concentration was measured at the beginning and end of the incubation with an optode (YSI ProODO, USA, accuracy of 0.2 mg L^{-1}). Four chambers per treatment were incubated without gorgonian fragments and used as controls. The gorgonian respiration rate was calculated as the difference between the initial and final oxygen concentrations, corrected by the average oxygen decrease in the control chambers, and normalised by time and gorgonian fragment size (see below). The possible effect of the rate of the temperature increase on gorgonian respiration was analysed by comparing the respiration rate at 16 ºC between the two treatments (since this temperature was reached in May in the accelerated spring treatment and in June in the historical spring treatment). The temperature response was determined by the thermal coefficient Q_{10}, which is commonly used to describe the increase in physiological rates over a 10-ºC change and, therefore, to measure temperature sensitivity (Schmidt-Nielsen, 1997):

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{(T_2-T_1)}}$$

where R_1 is the respiration rate measured at the cooler temperature (12.5 ºC), R_2 the respiration rate measured at 16 ºC, and T_1 and T_2 the respective temperature measurements. Q_{10} was calculated for each fragment (n = 10 per each treatment) and averaged per treatment.

Food capture

Incubations to determine the food capture rates were conducted at the beginning (April) and end (June) of the experiment in both treatments. Gorgonian fragments (n = 5 per treatment) were individually incubated in 6-L glass flow chambers (39 cm long x 9 cm wide x 19 cm high), equipped with a motor driven propeller (Telesystem 15.20, with a Telemodul 20 controller, Germany). The chambers were designed to create a unidirectional current around a central platform, where a gorgonian fragment was placed for the incubation (Houlbreque *et al.*, 2004; Gori *et al.*, 2015). Flow speed was measured with an electromagnetic current meter (JFE Advantech AEM1-D, Japan) and all the incubations were run at a flow velocity of 5 cm s^{-1}. The chambers were placed in a water bath connected to a chiller (Teco TK2000, Italy) to maintain the appropriate temperature for each treatment (± 0.15 ºC). For each incubation, chambers were filled with 50 µm pre-filtered Mediterranean seawater and gorgonian fragments were allowed to acclimate until the polyps were fully expanded. Then, living *A. salina* nauplii were added at an initial concentration of approximately 1000 nauplii L^{-1}. In ten replicated 10-ml seawater samples, *A. salina* nauplii were counted at the beginning of the incubation as well as after 1, 3 and 5 hours. The samples were returned to the flow chamber immediately after counting to avoid any concentration reduction. Five control incubations per treatment were run without gorgonian fragments following the same methodology to account for concentration decreases due to nauplii sedimentation or any effect of the propeller. Food capture rates were calculated as the difference between the initial and final nauplii concentrations multiplied by the chamber volume and normalised by time and gorgonian fragment size (nauplii h^{-1} cm^{-1}). The maximum capture rate was determined from the zooplankton consumption during the first hour of the incubation, while the mean capture rate was calculated based on zooplankton consumption over the entire five hours of the incubation.

Size of the gorgonian fragments

Photogrammetry was used to construct three-dimensional models (*structure for motion*) of the gorgonian fragments to calculate the total length of their branches. To do that, each gorgonian fragment was placed on a slowly rotating platform moved by a waterproof servomotor (Steplab, Italy) set in the middle of a well-lit 30-L aquarium. Photos were acquired with a 12-megapixel digital camera (Canon G9, Japan) located at the front of the aquarium. The photogrammetric 3D reconstruction of each gorgonian fragment was performed in Agisoft Metashape (AgiSoft PhotoScan Professional, version 1.2.6, Russia). The length of each gorgonian was used to normalise both the respiration and capture rates (see Bilan *et al.*, 2023; Romo *et al.*, 2025). Given the slow growth rates displayed by this species, photos were only taken at the end of the experiment (June).

Organic matter and energy content

To assess the potential sublethal effects of accelerated spring warming, organic matter and coenenchyme energy content were quantified in all the specimens at the end of the experiment (June).

At this time, all the gorgonian fragments (n = 10 per treatment) were frozen (-80 ºC) and lyophilised (Telstar LyoQuest, Japan; 24 h at -110 ºC and 100 mbar). For organic matter content, approximately 1 cm of each gorgonian fragment was weighed (dry weight, DW) (Mettler Toledo AE200, USA, accuracy of 0.1 mg), after removing the central axis and avoiding the apical part. The coenenchyme was burned in a muffle (J.P. Selecta, Spain; 5 h at 450 ºC) and the ashes were weighed (ash weight, AW). Organic matter was calculated as the ash free dry weight (AFDW = DW – AW) and reported as the % of the DW.

For energy content, approximately 10-25 mg of the lyophilised coenenchyme of each gorgonian fragment was ground into powder and analysed by combustion calorimetry using differential scanning calorimetry (DSC; Mettler Toledo DSC-822e). The DSC temperature was programmed to increase from 30 ºC to 450 ºC (10 ºC min^{-1}) in a synthetic air atmosphere (50 ml min^{-1}). The energy content was reported in calories per mg of organic matter.

Statistical analyses

To assess differences in the respiration and food capture rates between the two experimental conditions over time, we performed a two-way repeated measures ANOVA (Respiration ~ Treatment * Time and Capture ~ Treatment * Time), followed by a post-hoc test. A repeated measures analysis was used because pairs of fragments (one in each treatment) were from the same gorgonian colony. Additionally, respiration rates at 16 ºC (June for historical spring treatments vs. May for accelerated spring treatment) and Q_{10} values were compared between the two treatments with Student's t-test with repeated measures. A one-way ANOVA with the flow chamber as the repeated measures was used to confirm that changes in the nauplii concentration over time (time: 0, 1, 3 and 5 h) were attributable to capture by the gorgonian fragments rather than to settling at the bottom or entanglement within the experimental chambers.

Finally, Student's t-test with repeated measures was used to compare the organic matter of the gorgonian fragments at the end of the experiment between the two thermal treatments. The energy content data did not meet the assumption for normality; hence, a non-parametric Wilcoxon test was applied for the comparison of this variable between the two treatments.

All the analyses were run using the R software (RStudio Team, 2020) and all data were assessed for normality and sphericity of the variances prior to statistical testing.

Results

Respiration

The respiration rate (Fig. 2) of *P. clavata* showed significant differences between the historical spring treatment and the accelerated spring treatment (ANOVA; F = 25.64; $p < 0.001$), but not for the effect of time (ANOVA; F = 2.69; $p = 0.079$) or for the interaction between treatment and time (ANOVA; F = 2.09; $p = 0.136$).

Oxygen consumption at 16 ºC was significantly higher for the colonies in the accelerated spring treatment (in May) than for those in the historical spring treatment (in June) (t-test; t = 2.77; $p < 0.05$). The average Q_{10} varied from 1.3 for historical spring treatment to 2.5 for accel-

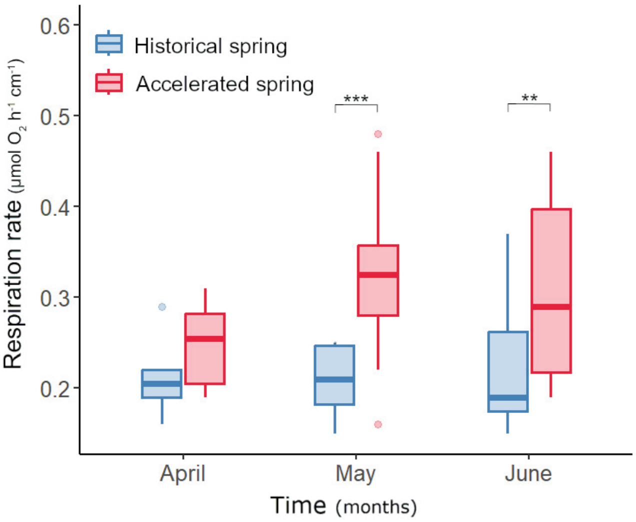

Fig. 2: Respiration. Oxygen consumption rate (μmol h^{-1} cm^{-1}) according to treatment and time (number of colonies = 10). Significant differences are indicated by ** for $p < 0.01$ and *** for $p < 0.001$.

erated spring treatment, showing significant differences (t-test; t = 2.84; $p < 0.05$).

Food capture

The nauplii concentration (Fig. 3) significantly decreased in the presence of gorgonian fragments in both April (historical spring: $p < 0.001$; accelerated spring: $p < 0.01$) and June (historical spring: $p < 0.01$; accelerated spring: $p < 0.01$), while remaining constant in the control incubations (April: $p = 0.488$; June historical spring: $p = 0.222$; June accelerated spring: $p = 0.942$; Table 1).

The maximum capture rate (Fig. 4a) did not show significant differences between the thermal treatments ($p = 0.169$), time ($p = 0.158$) or for their interaction ($p = 0.358$) (Table 2). The mean capture rate (Fig. 4b) also did not show significant differences for any factor (thermal treatment: $p = 0.251$; time: $p = 0.243$) or for their interaction ($p = 0.464$) (Table 2).

Organic matter and energy content

The organic matter content (Fig. 5a) was significantly higher in the historical spring than in the accelerated spring treatment (t-test; t = -3.57; $p < 0.01$). Conversely, there were no significant differences in the energy content per mg of organic matter between the historical and accelerated spring treatments (Wilcoxon test; V = 25; $p = 0.846$) (Fig. 5b).

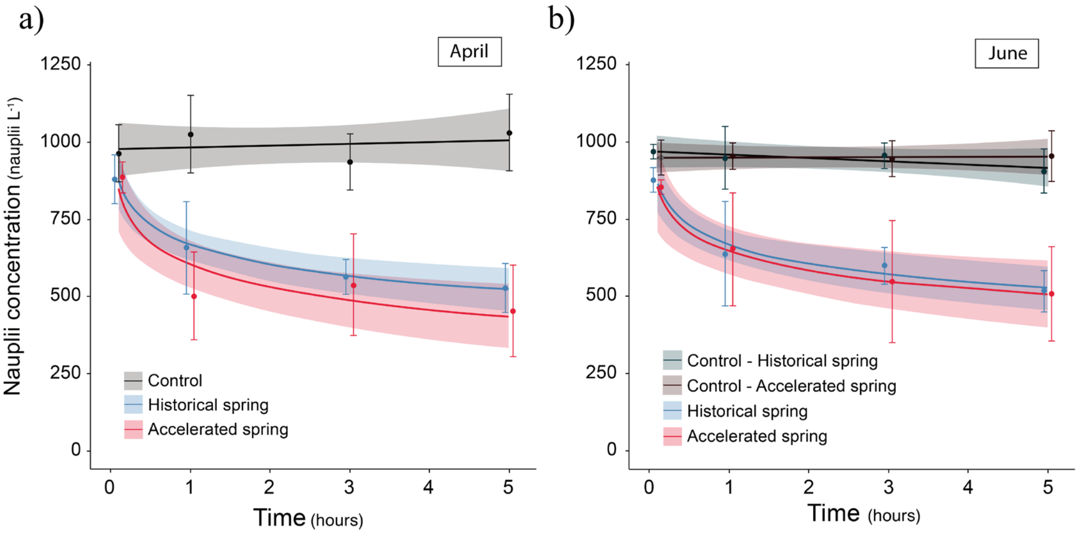

Fig. 3: Nauplii concentration. Concentration of *Artemia salina* (nauplii L^{-1}) in the (a) April and (b) June incubations (mean ± SD) (number of colonies = 5). Function y ~ log(x) adjusted to data with gorgonians and y ~ x to data without gorgonians.

Table 1. Nauplii concentration. One-way repeated-measures ANOVA to explore changes with time in nauplii concentration in the incubations. *numDF* degrees of freedom of the numerator, *denDF* degrees of freedom of the denominator, *SS* sum of squares, *MS* mean square, *F* F value, *p* probability. Significance was set at $p < 0.05$.

	Month	numDF	denDF	F	p-value
(a) With gorgonians					
Historical spring	April	1	14	19.88	<0.001
Accelerated spring	April	1	14	10.69	<0.01
Historical spring	June	1	14	17.11	<0.01
Accelerated spring	June	1	14	17.02	<0.01
(b) Control					
Historical spring	April	1	14	0.51	0.488
Historical spring	June	1	14	1.64	0.222
Accelerated spring	June	1	14	0.01	0.942

Table 2. Capture rate. Two-ways repeated-measures ANOVA to probe the effect of the temperature on the gorgonian's capture capacity. *numDF* degrees of freedom of the numerator, *denDF* degrees of freedom of the denominator, *SS* sum of squares, *MS* mean square, *F* F value, *p* probability. Significance was set at $p < 0.05$.

	numDF	denDF	F	p-value
(a) Maximum capture rate				
Treatment	1	12	2.14	0.169
Time	1	12	2.27	0.158
Treatment x Time	1	12	0.91	0.358
(b) Mean capture rate				
Treatment	1	12	1.45	0.251
Time	1	12	1.51	0.243
Treatment x Time	1	12	0.57	0.464

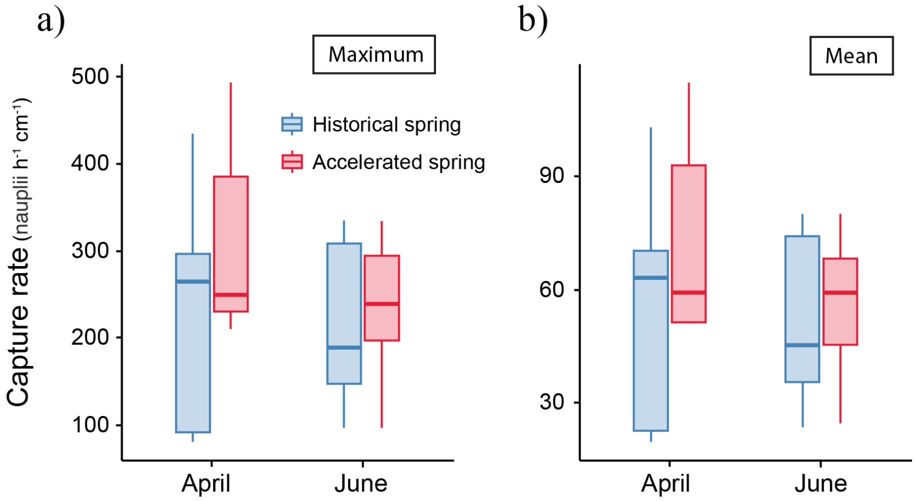

Fig. 4: Food capture. The zooplankton (a) maximum and (b) mean capture rate (nauplii h^{-1} cm^{-1}) (number of colonies = 5).

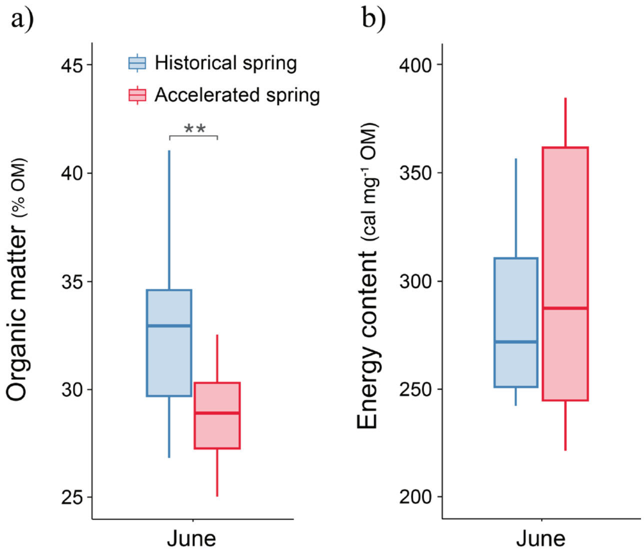

Fig. 5: Organic matter and energy content. (a) Organic matter (% OM) and (b) energy content (cal mg^{-1} OM) of the gorgonian fragments (number of colonies = 10). Significant differences are indicated by ** for $p < 0.01$.

Discussion

Our results highlight the importance of the rate of rising spring temperatures in shaping the physiological condition of *Paramuricea clavata* when facing unusually high summer temperatures and potential marine heatwaves. This is evidenced by the lower organic matter content observed in the gorgonians exposed to accelerated spring warming compared to those experiencing historical spring conditions. Additionally, Q_{10} values clearly demonstrated that the respiration rate at a given temperature depended not only on the temperature difference, but also on the rate of the temperature increase. At 16 ºC, *P. clavata* fragments exhibited a higher respiration rate in the accelerated spring setting than in the historical spring one, indicating their capacity to acclimate when the temperature increases progressively.

However, to date, most of the studies on the response of the red gorgonian *P. clavata* to heatwaves have overlooked the potential sublethal effects caused by accelerated spring warming conditions, mostly focusing on their resistance and potential recovery (e.g., Gómez-Gras *et al.*, 2021; Rovira *et al.*, 2024; Capdevila *et al.*, 2025). The lack of studies on accelerated spring warming could be related to the fact that, during these events, the species remains within its natural thermal range and, thus, is considered well-adapted to spring fluctuations (Torrents *et al.*, 2008; Ledoux *et al.*, 2015; Pivotto *et al.*, 2015; Pratlong *et al.*, 2015). Above thermal tolerance limits, several gorgonian species, including *P. clavata*, reduce polyp activity as an energy-saving strategy (Robbins & Shick, 1980; Lasker, 1981; Coma *et al.*, 1994). This behaviour mitigates mismatches between decreased food availability and elevated metabolic rates due to high summer temperatures. However, our results show that accelerated spring warming leads to an imbalance in gorgonian metabolism, driven by a rapid increase in respiration rates.

Most of the research has mainly focused on the respiratory response of hexacorals and octocorals to different temperatures, without considering the possible effects of the rate of the temperature changes (e.g., Al-Sofyani & Floos, 2013; Naumann *et al.*, 2014; Haryanti & Hidaka, 2015; Paradis *et al.*, 2019; Lange *et al.*, 2023). Respiratory thermal acclimation (*sensu* Angilletta, 2009) is typically assessed by comparing respiration rates at different temperatures or by examining the temperature dependence of the respiration rate (i.e., Q_{10}). When the Q_{10} value is approximately 1, respiration is considered thermally independent, indicating complete reversible acclimation. These results are generally interpreted as a product of homeostasis, resulting from seasonal adjustments in enzyme concentration and type (Hochachka & Somero, 2002) as well as changes in the cellular membrane structures (Angilletta, 2009 and the references therein), and are thought to provide a metabolic advantage to organisms inhabiting environments with fluctuating temperatures (Griffiths, 1979; Gaudy & Thibault-Botha, 2007). Indeed, the capacity for reversal thermal acclimation (*sensu* Angilletta, 2009) in many corals has been linked to their local thermal regime (Torrents *et al.*, 2008; Ledoux *et al.*, 2015; Pivotto *et al.*, 2015; Pratlong *et al.*, 2015), genetic drift (Ledoux *et al.*, 2015; Pivotto *et al.*, 2015; Pratlong *et al.*, 2015; Crisci *et al.*, 2017), and microbiome plasticity (Tignat-Perrier *et al.*, 2022).

In our experiment, the lack of significant changes in the respiration rate and the low temperature sensitivity of *P. clavata* respiration (Q_{10} = 1.3) under historical spring conditions support its capacity for reversible thermal acclimation to seasonal changes in seawater temperatures (Angilleta, 2009). This null or minimal temperature dependence in the respiration rates of *P. clavata* has been previously observed with a rough Q_{10} estimate of 1.1 (Coma *et al.*, 2002). However, our results also showed that during accelerated spring warming, *P. clavata* was unable to effectively regulate its respiration, as indicated by the significantly higher respiration rate and sensitivity coefficient (Q_{10} = 2.5) measured at 16 ºC under accelerated spring warming (0.31 ± 0.10 µmol cm^{-1} h^{-1}, in May) compared to historical spring warming (0.22 ± 0.07 µmol cm^{-1} h^{-1}, in June). This limited reversible thermal acclimation to rapid seawater warming could have important ecological consequences for the energy budget of corals (Newell & Branch, 1980), increasing their vulnerability to summer heatwaves driven by the ongoing global change (Garrabou *et al.*, 2022). Therefore, our study highlights the importance of considering spring conditions when assessing gorgonian resistance, as accelerated spring warming may be crucial for understanding their overall resilience.

On the other hand, *P. clavata* exposed to the same thermal changes (from 12.5 to 16 ºC) but with different rates of the temperature increase (0.1 ºC every two days in the historical spring treatment *versus* 0.2 ºC every two days in the accelerated spring treatment) showed significantly different Q_{10} values. This highlights the importance of also considering the rate of temperature change when studying the thermal sensitivity of species respiration. Previati *et al.* (2010) found that *P. clavata* respiration was temperature-sensitive, with a Q_{10} of 1.9, when comparing the respiration rate at 14 ºC and 20 ºC with a temperature increase rate of 2-3 ºC every 10 days. However, this high Q_{10} value could be a consequence of the rapid warming, as we observed in this study for the species exposed to the accelerated spring warming. This indicates that the rate of temperature increase should be taken into account when assessing the thermal sensitivity of species, which is a current topic of discussion in terrestrial ecology (Mundim *et al.*, 2020; Wu *et al.*, 2021; Heine, 2023; Li *et al.*, 2025).

The sublethal effects caused by increased respiration rates may be exacerbated if the feeding rates are reduced under thermal stress, as has been observed in the tropical coral *Stylophora pistillata* (Ferrier-Pagès *et al.*, 2010). Indeed, *P. clavata* contracts its polyps at temperatures above 22 ºC, reducing its feeding rates (Previati *et al.*, 2010; Tignat-Perrier *et al.*, 2022). Our experiment, which never exceeded 22 ºC, showed that the capacity of *P. clavata* to capture zooplankton was not affected by the spring warming rate. This aligns with previous observations that the ingestion rates of *P. clavata* are unaffected by temperature, but correlate with food availability (Ribes *et al.*, 1999a). However, feeding rates could be reduced if high spring temperatures eventually lead to an advanced, prolonged and stronger water column stratification (Coma *et al.*, 2009), which reduces food availability for passive suspension feeders (Coma & Ribes, 2003; Coma *et al.*, 2009). Moreover, increased respiration during accelerated spring warming increases the corals' energy demand, which is not compensated by enhanced feeding, ultimately resulting in a reduction of organic matter content. Therefore, although the gorgonian tissue maintains a constant energy content, the overall loss of organic matter leads to less energy being available to the colony at the end of accelerated spring warming.

Energy resources are finite and need to be partitioned into different biological processes such as respiration, growth, defence, recovery and reproduction (Giesel, 1976; Lawrence, 1985; Lawrence & McClintock, 1994). Therefore, the physiological consequences of accelerated spring warming may lead to a trade-off in energy investment among the biological processes in gorgonians. It is well established that reproduction requires high energy investment and is linked to seasonal cycles (Viladrich *et al.*, 2016; Maier *et al.*, 2020). Since gametes are mainly formed in the spring (Coma *et al.*, 1995; Ribes *et al.*, 2007), the observed increase in metabolic expense during accelerated spring warming may reduce the energy available for reproduction. Moreover, since oocyte production has a higher energy cost than spermary sac development, female colonies would be more affected, as has been observed after heatwaves (Linares *et al.*, 2008; Arizmendi-Mejía *et al.*, 2015). This possible reduced investment in reproduction may explain the smaller larvae produced by *P. clavata* in 2011, when there was accelerated spring warming, and their failure in settlement (authors' unpublished data). On the other hand, the observed lower nutritional condition at the end of accelerated spring warming may also increase its vulnerability to a possible subsequent summer heatwave (Garrabou *et al.*, 2009, 2022), when *P. clavata* relies on its energy reserves to cover its metabolism and any extra energy needed to repair the tissue damage caused by oxidative stress (Tignat-Pierre *et al.*, 2022). Indeed, under high temperatures and starvation due to enhanced water column stratification in the summer, gorgonian mortality occurs when the biomass decreases to below 0.026 g DW cm^{-1} of branch length (Coma *et al.*, 2009). We show that this critical threshold can be reached earlier if spring conditions are warmer than usual. Overall, our study provides experimental evidence that spring thermal conditions play a paramount role in shaping gorgonian ecophysiology, population dynamics and vulnerability to summer heatwaves.

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