



Article

Responses of Biofilm-Forming Halophilic *Calothrix* and *Coelastrella* Strains to Environmental Stressors Associated with Climate Change

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Abstract

Research into the effects of environmental stressors associated with global climate change (GCC) on cyanobacteria and microalgae is scarce, with bloom-forming planktonic cyanobacteria being the exception. This study aimed to address the issue by assessing morphological and biochemical changes in cyanobacterial and microalgal cells exposed to an increased temperature (T), ultraviolet radiation (UVR) and carbon dioxide (CO₂) concentration. The strains selected were *Calothrix* sp. SLM0211 and *Coelastrella* sp. SLM0503, which were isolated from a coastal environment in the central Mediterranean island of Malta. Elevated UVR had a pronounced effect on *Calothrix* sp. filaments, which produced screening compounds and resorted to trichome coiling to enhance self-shading. Enhanced growth was observed in cultures of *Calothrix* sp. grown at an increased CO₂ concentration, which produced significantly high amounts of biomass, chlorophylls and carotenoids. An increased T resulted in stunted growth and low biomass accumulation in both strains. Each strain exhibited a unique response to T and UVR stressors, which stimulated the production of exopolymers (EPS) and mycosporine-like amino acids (MAAs) in cultures of *Calothrix* sp. and lipid production in *Coelastrella* sp. cells. Our findings indicate that the effects of stressors related to GCC on cyanobacterial and microalgal cells are strain-specific, making changes at community and ecosystem levels difficult to predict.

Keywords: cyanobacteria; carbon dioxide; coastal biofilms; halophilic microbes; marine microorganisms; MAA; microalgae; secondary carotenoids; temperature; UV radiation



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1. Introduction

The global environment is currently undergoing change at an unprecedented rate due to global climate variability. Related consequences on living microorganisms are attributed to the rate at which changes in climatic parameters occur and to the adaptive strategies of microbiota. The emission of anthropogenic greenhouse gases, mainly CO₂, is on the increase globally, and this trend is expected to continue due to the demands imposed by unabated population growth [1]. In the meantime, the concentration of global atmospheric CO₂ has increased from 280 ppm during the pre-industrial revolution to an average of 411.28 ppm in October 2020 and 426.48 ppm in November 2025 [2]. Predictions regarding atmospheric CO₂ concentration at the end of this century have been modelled using

different assumptions. The most likely scenario is a two to threefold increase, reaching values from 750 to 1000 ppm by 2100 [3]. Coinciding with this is an increased average global surface temperature (T) of 4.0 °C by 2100, if contributory factors remain unchecked. A concomitant increase in the solar flux of ultraviolet radiation (UVR) has been attributed to the use of chlorofluorocarbons (CFCs), which resulted in the depletion of stratospheric ozone during the 1980s, thus contributing to increased UVR reaching the Earth's surface [4].

Although cyanobacteria and microalgae are crucial to the balance of our ecosystem, research delving into the consequences of T, CO₂ and UVR stressors on their populations is severely lacking, even though they occupy an important niche in both terrestrial and aquatic ecosystems. Until recently, the majority of research into the effects of global climate change (GCC) has centered on bloom-forming planktonic cyanobacteria and their toxicity, while other taxa of microalgae and cyanobacteria have received less attention. Various studies have investigated the optimal environmental conditions for the cultivation of industrial strains. However, studies about the adaptation of microbes to environmental variables associated with climate change in the Mediterranean region are lacking, even though it is known that such variability affects both terrestrial and marine cyanobacteria and microalgae [5], as well as coastal biofilm formation [6].

Since photoautotrophic microorganisms are important primary producers in the marine coastal ecosystem, a change in their population numbers would likely cause a cascading effect through the biocoenosis. This study attempts to answer specific research questions related to the response of coastal cyanobacterial and microalgal cells to environmental stressors associated with GCC.

The strains selected included the filamentous cyanobacterium *Calothrix* sp. SLM0211 and the coccal chlorophyte *Coelastrella* sp. SLM0503 [7], which were isolated from biofilms growing in coastal rock pools on the Maltese shoreline [8]. Such heterogeneous phototrophic biofilms, consisting of a rich biodiversity of species, form in response to environmental stresses to improve the chances of survival of the constituent cyanobacterial and microalgal species [9]. These microorganisms employ various morphological, physiological and molecular strategies to deal with thermal stress, elevated CO₂ levels and exposure to UVR [10–14]. Biochemical adaptations include the production of novel metabolites, but these changes have rarely been described from novel strains of biofilm-forming cyanobacteria and algae [15], resulting in a general lack of understanding of their physiological role and their potential biotechnological application in industry [16].

The aim of this study is to document, evaluate and quantify the effects of environmental parameters on the growth of these microorganisms, their gross and cell morphology, the production of pigments, intracellular and extracellular metabolites, as well as the yield of total biomass. This was achieved by replicating environmental stressors associated with GCC in a laboratory setting. The parameters were based on the 2014 IPCC predictions, which estimate a CO₂ concentration of 1000 ppm and an average 4 °C increase in global surface temperature [3].

2. Materials and Methods

2.1. Selected Strains and Culture Medium

Two phototrophic strains, isolated from biofilms growing in a Maltese coastal environment, were obtained from the Maltese Microalgal Culture Collection (MMCC) [17]. These consisted of the halotolerant *Coelastrella* sp. strain SLM0503 (Figure 1a) and *Calothrix* sp. strain SLM0211 (Figure 1b), which were both characterised microscopically and genetically in a previous study [7]. Stock cultures, grown in SN medium prepared in ultrafiltered seawater at pH 7.0 [18], were incubated at 22 °C and grown at a light intensity of 50 μmol photons m⁻² s⁻¹ and a 10 h photoperiod.

2.2. Experimental Design

The strains were incubated in 0.25 L glass flasks and cultured at 22 °C under cool white light tubes (OSRAM, Munich, Germany) providing photosynthetically active radiation (PAR) at a wavelength of 400 to 700 nm and a light intensity of 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for a 10 h photoperiod. The light conditions remained the same for experiments and controls. The experiments consisted of modifying a single parameter at a time, as follows: an elevated T of 32 °C, a 10 h daily exposure to UV-A and UV-B (8 W, λ_{max} 365, 312 nm) and an increased CO₂ concentration of 1000 ppm (0.1%). The control for the T and UVR experiment was maintained at a T of 22 °C, with no UVR. The control for the CO₂ experiment was maintained at the same T of 22 °C, supplied with 400 ppm (0.04%) CO₂, with no UVR. Filtered CO₂ was supplied continuously for 10 h daily at a flow rate of 2.5 mL/min (0.01 vvm) in each case. Triplicate cultures of each strain were grown as biological replicates for every experiment and control at an initial pH of 7.0 and were maintained in semi-continuous culture for 10 months.

2.3. Growth Assessment

A 2 mL aliquot of *Coelastrella* sp. culture was used to measure the in vivo absorbance of chlorophyll at 680 nm and the optical density at 790 nm using a Shimadzu UV-2501PC spectrophotometer (Shimadzu, Kyoto, Japan). In the case of *Calothrix* sp., growth measurements were based on image analysis, since filaments aggregated in culture. Photographs from the top of open culture flasks were taken under the laminar flow cabinet. Images were analysed using ImageJ 1.53 software (NIH, Bethesda, MD, USA) to calculate area cover and intensity expressed as integrated density. The pH was measured at the same time. Readings were taken bi-weekly during the first two months of treatment, and once monthly thereafter.

Cells were viewed using DIC under a PZO Biolar microscope (PZO, Warsaw, Poland) and an Olympus BX 51 photomicroscope equipped with an Olympus DP-71 digital camera (Olympus, Tokyo, Japan). For fluorescence, a Delta Optical Evolution 100 microscope was connected to a 365 nm LED light source and a 400 nm barrier filter (Delta Optical, Warsaw, Poland). Images were taken using a Canon G9X camera (Canon, Tokyo, Japan). Morphological characteristics were recorded, as well as the cell diameter (μm) of *Calothrix* sp. SLM0211 cells and the width (μm) of *Calothrix* sp. SLM0211 filaments.

2.4. Metabolite Assays

For each metabolite, a 2 mL culture aliquot was centrifuged at 14,000 rpm for 15 min. The supernatant was discarded, and the pellet was washed twice with distilled water. Pellets were subjected to two overnight freeze–thaw cycles, sonicated for 15 min at 250 Hz and dried at 55 °C. The pellet dry weight was recorded. No pre-treatment was conducted on pellets used for extracellular metabolites.

The amounts of chlorophylls and carotenoids were quantified for each strain. 0.25 mL of glass beads and 1.5 mL of pure methanol were added to the cell pellet; the tube was vortexed for 15 min and incubated overnight in darkness at 4 °C. The concentration of chlorophyll *a*, chlorophyll *b* and total carotenoids was calculated using equations proposed by Lichtenthaler [19]. Phycobiliprotein (PBP) analysis was also conducted on the cyanobacterial strain using 0.25 mL of glass beads and 1.5 mL of phosphate-buffered saline (0.01 M NaH₂PO₄, 0.15 M NaCl, pH 7). The tubes were vortexed for 15 min and incubated overnight in darkness at 4 °C. The concentrations of phycocyanin (PC), allophycocyanin (AP) and phycoerythrin (PE) were estimated according to established methods [20].

Cultures were also tested for scytonemin and mycosporine-like amino acids (MAAs) at the end of the study using a method adapted from Rastogi and Incharoensakdi [21]. The

extracts were scanned for the presence of typical peaks, between 200 nm and 800 nm, using a Shimadzu UV-2501PC spectrophotometer (Shimadzu, Kyoto, Japan).

Intracellular metabolites were extracted and measured separately from the pellets that sedimented from 2 mL of culture. Carbohydrates were extracted using 4 g L^{-1} KOH as proposed by Schneegurt and colleagues [22] and the quantification was conducted using the anthrone method [23]. Absorbance was measured at 578 nm using a Genesys 10s Vis spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and carbohydrate content was determined from a calibration curve constructed using D-glucose (100 mg L^{-1}) as a standard. Proteins were extracted using 20 g L^{-1} NaOH as proposed by Rausch [24], and concentrations were measured using the microbiuret-method [25] as follows. 0.05 mL of copper sulphate solution was added to 0.1 mL of the protein extract, the absorbance of which was measured at 325 nm. The protein content was determined from a calibration curve constructed using 1 g L^{-1} of BSA. Lipids were extracted and quantified using the method adapted from Chen and Vaidyanathan [26]. The absorbance of the lower organic phase was measured at 260 nm in quartz cuvettes using a Shimadzu UV-2501PC spectrophotometer (Shimadzu, Kyoto, Japan). Total lipid content was determined from a calibration curve constructed using 0.10684 g/L of palmitic acid dissolved in R1 (chloroform: methanol, 2:1 *v/v*) as suggested in the same study.

Extracellular carbohydrates, proteins and lipids were each estimated from three fractions: released metabolites (RM), loosely bound (LB) metabolites and tightly bound (TB) metabolites. The analysed metabolites include capsular exopolymers associated with the cell surface and are referred to here as tightly bound (TB). The loosely bound (LB) substances are usually colloidal and form a slime or matrix outside cells, while the released metabolites (RM) are often low in molecular weight [16].

A 2 mL aliquot of culture was harvested in 50 mL tubes and centrifuged at 4000 rpm at 15°C for 20 min. The carbohydrate and protein content were quantified from one aliquot, whereas lipids were quantified from a separate aliquot. The supernatant was transferred to a microcentrifuge tube and used for RM analysis while the pellet was lyophilised and used for both LB and TB metabolite analysis. The supernatant was first evaporated to $\frac{1}{4}$ of its volume in a drying oven at 60°C and the EPS was precipitated in three volumes of ice-cold ethanol and frozen overnight at -20°C . The extract was then centrifuged at 10,000 rpm for 15 min, the precipitated EPS was washed twice in cold ethanol and the supernatant was discarded. The pellet was resuspended in 1 mL of distilled water to quantify the extracellular carbohydrate and protein as described previously, and in 0.02 mL PBS and 0.98 mL of R1 to measure lipid content as described previously for intracellular metabolites.

LB metabolites were extracted from lyophilised samples prepared for RM extraction using 0.1 mL of tap water and incubating at 30°C for 15 min. The extraction was carried out three times, combining the supernatant into one tube. TB metabolites were extracted from the pellet resulting from LB analysis using 0.1 mL of 33.62 g L^{-1} sodium EDTA and incubating at room temperature for 16 h. The supernatant was transferred to a separate tube. Extracted LB-EPS and TB-EPS were precipitated in cold ethanol and processed for metabolite quantification as described for the RM analysis [27].

2.5. Biomass and Metabolite Yield

The biomass yield for each culture was obtained at the end of the study by freeze-drying and weighing the cell mass produced from a 50 mL volume of culture. 5 mg of the lyophilised biomass was also used for analysis using an IRAffinity-1 Shimadzu Fourier Transform Infrared (FTIR) spectrophotometer, equipped with a Zinc Selenide crystal attenuated total reflectance (ATR). Twenty spectral scans were collected over the wavelength range from 4000 to 400 cm^{-1} at a resolution of 4 cm^{-1} . Each spectrum was an average

of 20 scans obtained using Shimadzu IRsolution software version 1.50. Spectral scans were processed using Spectragryph version 1.2. The transmittance [%] of characteristic bands of the major biochemical compounds, including proteins ($1655\text{--}1540\text{ cm}^{-1}$), carbohydrates ($1174\text{--}980\text{ cm}^{-1}$), lipids ($1745\text{--}1734\text{ cm}^{-1}$) and nucleic acids ($1356\text{--}1191\text{ cm}^{-1}$) was recorded. The following band ratios were calculated from raw data: protein:carbohydrate, lipid:protein, lipid:carbohydrate, and nucleic acid:carbohydrate.

2.6. Statistical Analysis

Statistical analysis was conducted using the Statistical Package for Social Sciences (SPSS) software version 25. Mean values were calculated from triplicate readings from the metabolite assays for each biological replicate. An Independent Samples *t*-test was performed to determine whether the metabolite content of cultures subjected to different growth parameters (T, UVR, and CO₂) varied significantly at a *p*-value lower than 0.05.

3. Results

3.1. Growth in Culture and Biomass Yield

Both strains exhibited a significantly lower cell density and final biomass yield when grown at an increased T (Figure 1). Under enhanced UVR, cell densities of *Coelastrella* sp. were significantly lower than those grown under control conditions, whereas *Calothrix* sp. attained similar cell densities to those of the control, resulting in no significant difference in the final biomass (Figure 1).

At a high CO₂ level, *Calothrix* sp. displayed a higher growth rate and a significantly higher biomass (Figure 1), while on the other hand, no significant difference in cell density and biomass yield was observed in cultures of *Coelastrella* (Figure 1). Further data related to biomass yield are given in Supplementary Materials S1, and the individual growth curves are presented in Supplementary Materials S3. The measured pH was in the range of 6.5–7 for all experiments.

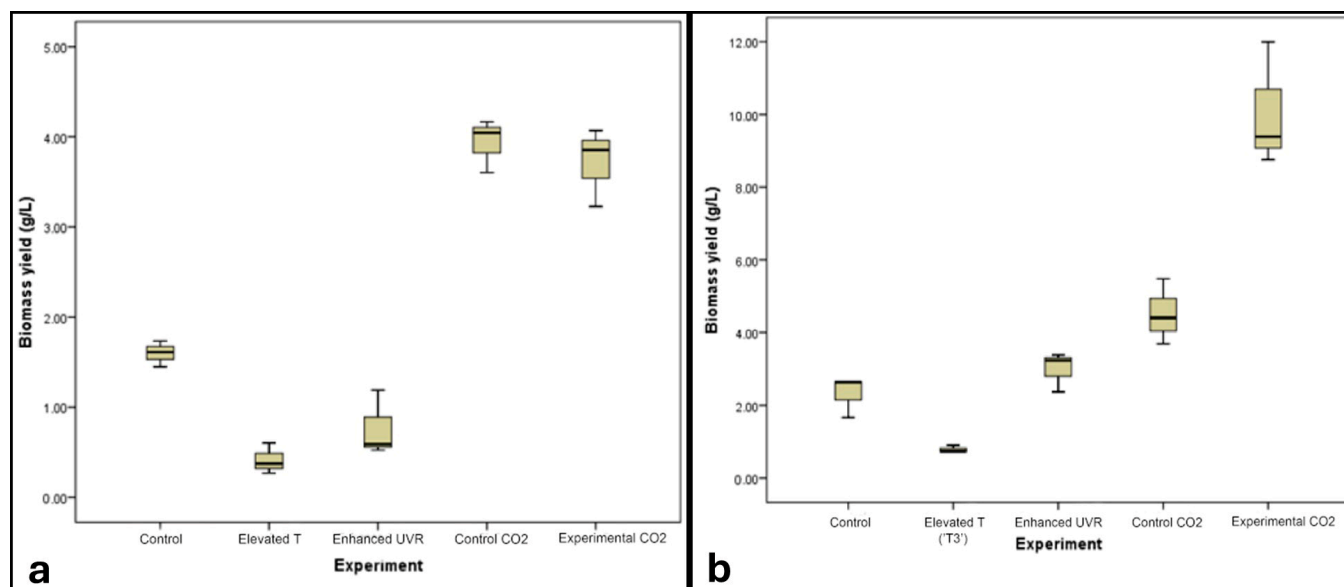


Figure 1. Biomass yield (g/L) of (a) *Coelastrella* sp. SLM0503 cells and (b) *Calothrix* sp. SLM0211 filaments by experiment. Standard deviation is expressed as error bars. The relevant statistical data are given in Supplementary Materials S1.

3.2. Changes in Morphology

At elevated T, *Calothrix* sp. cultures were characterised by the presence of juvenile filaments possessing a thickened sheath surrounding the filament tip (Figure 2). Cells of *Coelastrella* sp. showed a significant reduction in cell diameter and underwent a succession of deteriorative stages, which involved cells that lacked a visible pyrenoid and the production of carotenoid-accumulating aplanospores (Figure 3). Autospores were not observed at high T.

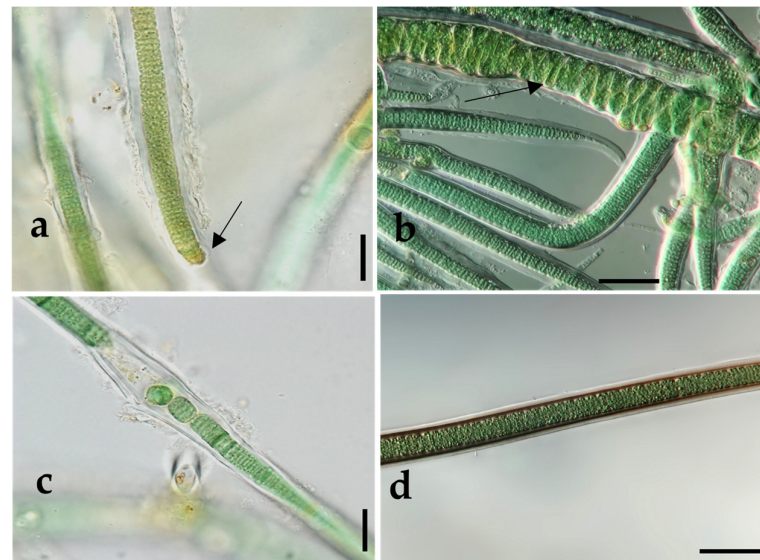


Figure 2. Filaments of *Calothrix* sp. SLM0211 (a) trichome with a basal heterocyte (arrow) enclosed in a thick sheath, (b) coiling (arrow) and branching of tapering filaments, (c) filament breakage to release hormogonia, and (d) brown coloration of the sheath. Scale bars = 20 µm.

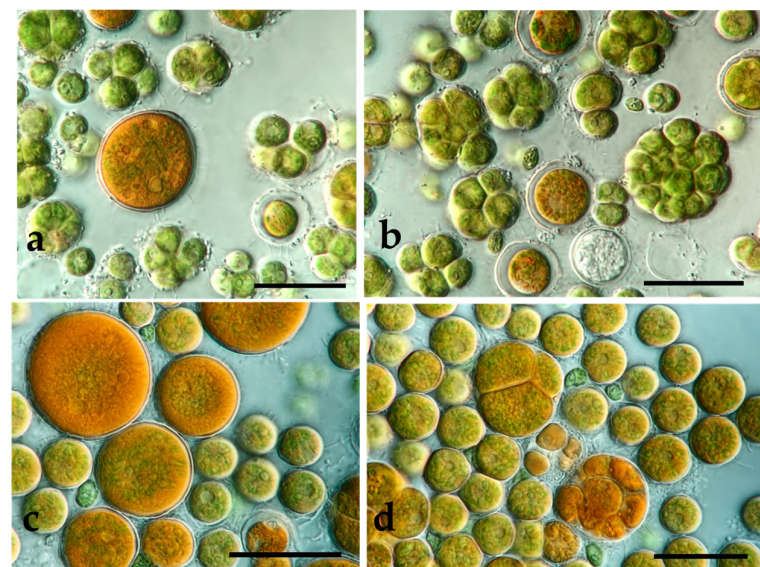


Figure 3. Cells of *Coelastrella* sp. SLM0503 at different physiological stages during the life cycle (a,b) green cultures during the log phase of growth, showing asexual reproduction via the formation of progressively large autosporangia, (c) orange cultures, formed as an adaptive response to environmental stressors, via large cells that accumulate carotenoids and form resting cysts similar to aplanospores, which are observed to divide in turn (d). Scale bars = 20 µm.

Calothrix sp. filaments exhibited frequent trichome coiling (Figures 2 and 4), extensive false branching (Figure 2), filament breakage, and a yellow-brown pigment within the sheath (Figure 2).

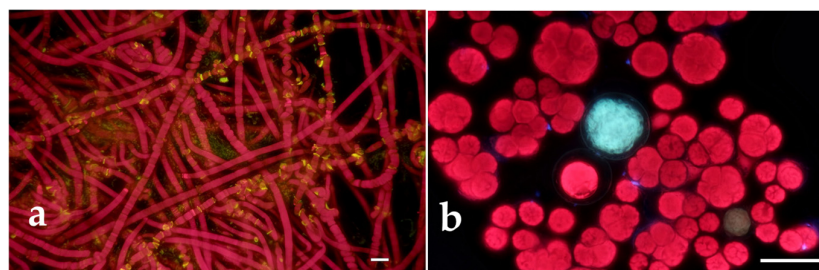


Figure 4. Red autofluorescence of (a) phycocyanin in *Calothrix* sp. SLM0211 filaments and (b) chlorophyll in *Coelastrella* sp. SLM0503 cells. Evident features are (a) the frequent coiling of filaments, and (b) cell division in sporangia forming autospores. Scale bars (in white) = 20 μ m.

Coelastrella sp. responded to UVR stress through a succession of cell stages similar to those already described for cultures grown at elevated T; however, in this case, aplanospores were abundant in the decline phase (Figure 3).

At a high CO₂ level, *Calothrix* sp. displayed a larger number of heterocytes in mature filaments and hormogonia. On the other hand, *Coelastrella* sp. cells exhibited significantly larger cell diameters during the log and stationary phases of growth. Data for morphology measurements are given in Supplementary Materials S2.

3.3. Photosynthetic, Accessory and Photoprotective Pigments

Results for the analysis of pigments are presented in Figures 5–7, with the related data presented in Supplementary Materials S4–S6.

In *Calothrix* sp., elevated UVR resulted in a significant increase in the production of chlorophyll *a* (1.29 ± 0.25 mg/g) and carotenoids (1.54 ± 0.38 m/g) (Figure 5). *Calothrix* cells grown at high T produced significantly higher amounts of PC (0.05 ± 0.01 mg/g) and APC (0.04 ± 0.01 mg/g) (Figure 7).

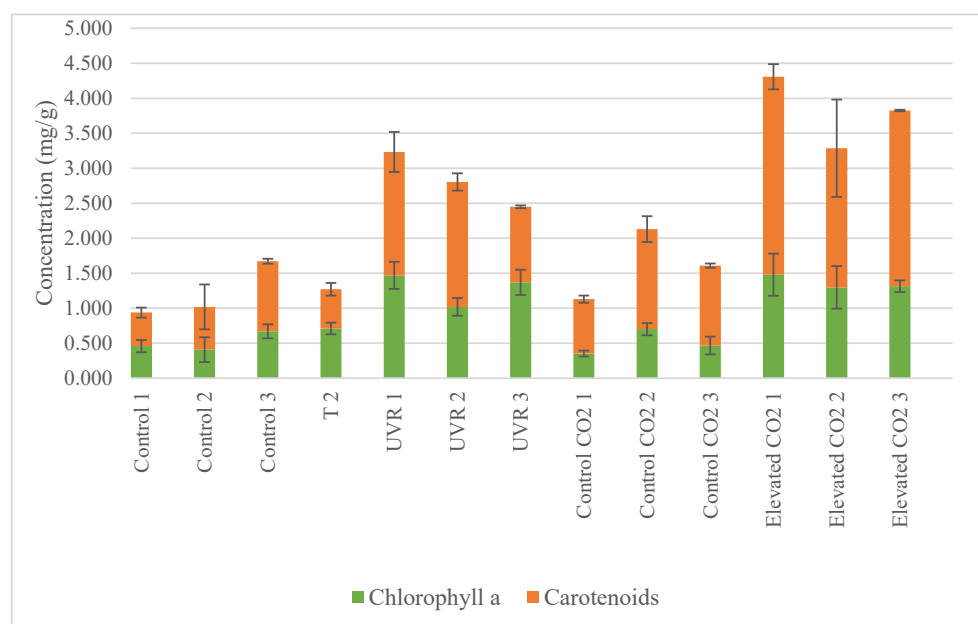


Figure 5. Chlorophyll *a* and total carotenoid content in cells of *Calothrix* sp. SLM0211 according to treatment. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S4.

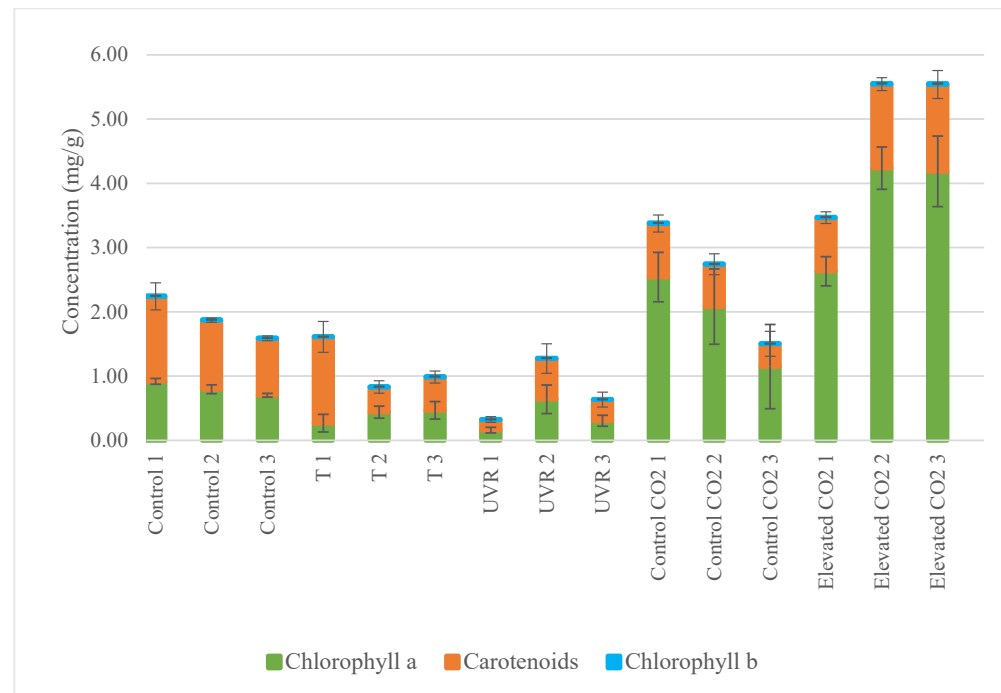


Figure 6. Chlorophyll *a*, chlorophyll *b* and total carotenoid content in cells of *Coelastrella* sp. SLM0503 according to treatment. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S4.

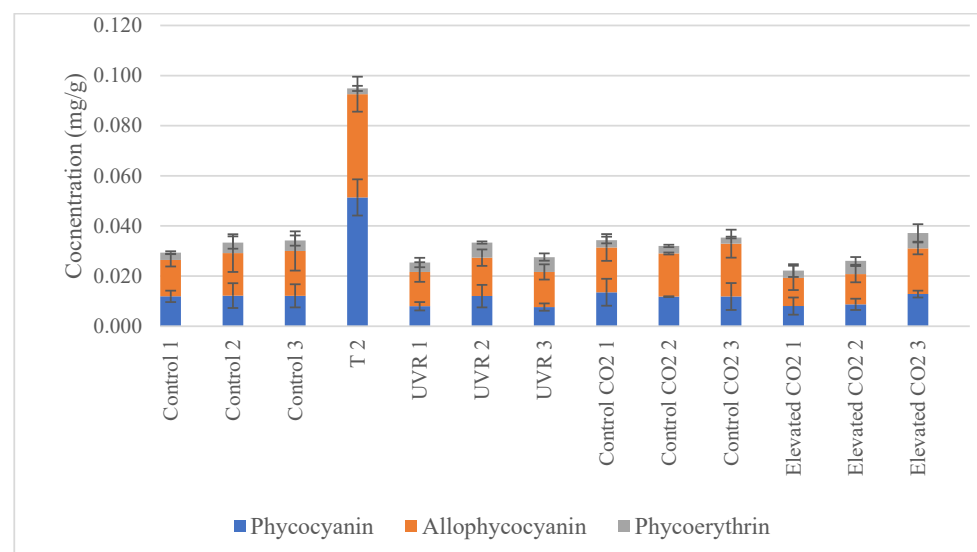


Figure 7. PC, APC and PE concentration in cells of *Calothrix* sp. SLM0211 by treatment and experimental replicate. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S6.

In contrast, a significant decrease in the amounts of chlorophyll *a* and carotenoids was recorded for *Coelastrella* sp. cultured at elevated T and UVR (Figure 6).

When grown at an elevated CO₂ concentration, cultures of *Calothrix* and *Coelastrella* spp. produced the highest amounts of carotenoids (10.31 ± 0.93 and 1.16 ± 0.28 mg/g respectively) and chlorophyll *a* (6.18 ± 2.75 and 3.68 ± 0.86 mg/g, respectively) (Figures 5 and 6).

Although a yellow-brown pigment was observed microscopically in the sheath of *Calothrix* sp. cells (Figure 2), the typical peaks of scytonemin at 252, 278, 300 and 386 nm were not detected (Figures 8 and 9). The presence of MAA pigments in *Calothrix* filaments

was confirmed spectrophotometrically (Figures 10 and 11). Under enhanced UVR, the λ_{max} was at 335.5 nm (Figure 10), and at increased CO₂ concentration, the λ_{max} was 333.7 nm (Figure 11).

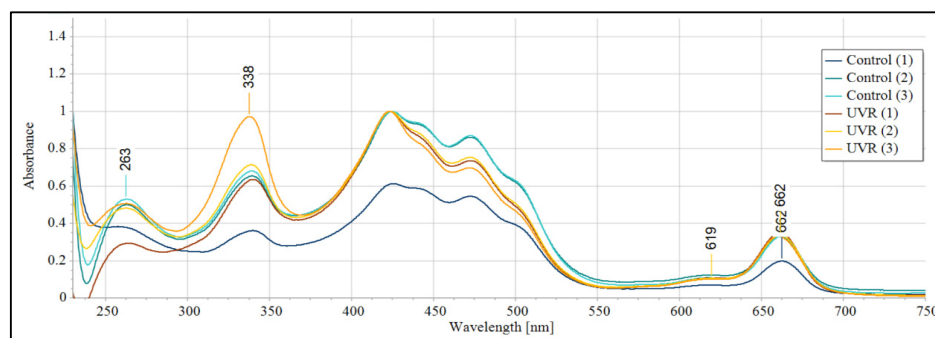


Figure 8. UV/Vis spectra of scytonemin extracts obtained from cultures of *Calothrix* sp. SLM0211 grown under control conditions and enhanced UV-A and UV-B.

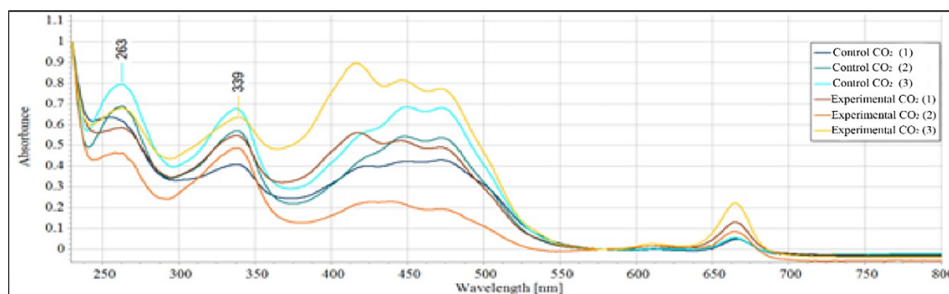


Figure 9. UV/Vis spectra of scytonemin extracts obtained from cultures of *Calothrix* sp. SLM0211 grown with control CO₂ (0.04%) and experimental CO₂ (0.10%).

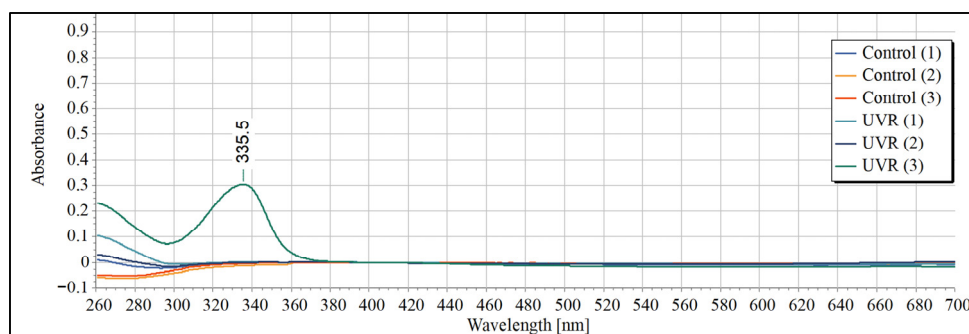


Figure 10. UV/Vis spectra of MAA extracts obtained from cultures of *Calothrix* sp. SLM0211 grown under control conditions and enhanced UVR.

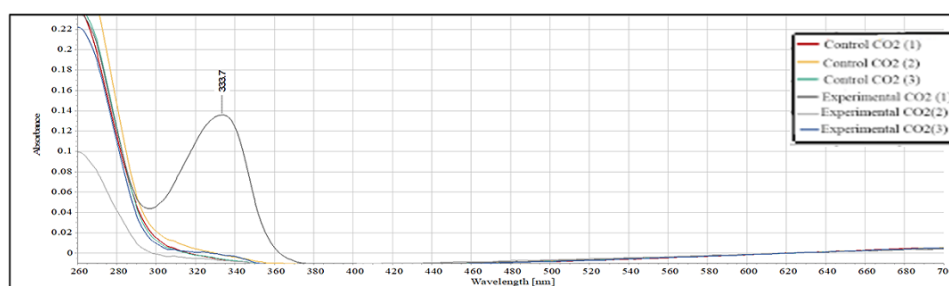


Figure 11. UV/Vis spectra of MAA extracts obtained from cultures of *Calothrix* sp. SLM0211 grown at control CO₂ (0.04%) and experimental CO₂ (0.10%) levels.

3.4. Intracellular and Extracellular Metabolites

Results for the analysis of metabolites are presented in Figures 12–16, with the related data given in Supplementary Materials S7 and S8.

Under enhanced UVR, *Calothrix* sp. produced significantly high amounts of intracellular proteins, carbohydrates and lipids (165.17 ± 72.77 mg/g, 133.21 ± 47.80 mg/g and 15.61 ± 4.93 mg/g, respectively), than the control (79.73 ± 34.66 m g/g, 21.44 ± 6.00 mg/g and 15.61 ± 4.93 mg/g) (Figure 12), as were the released proteins (Figure 15).

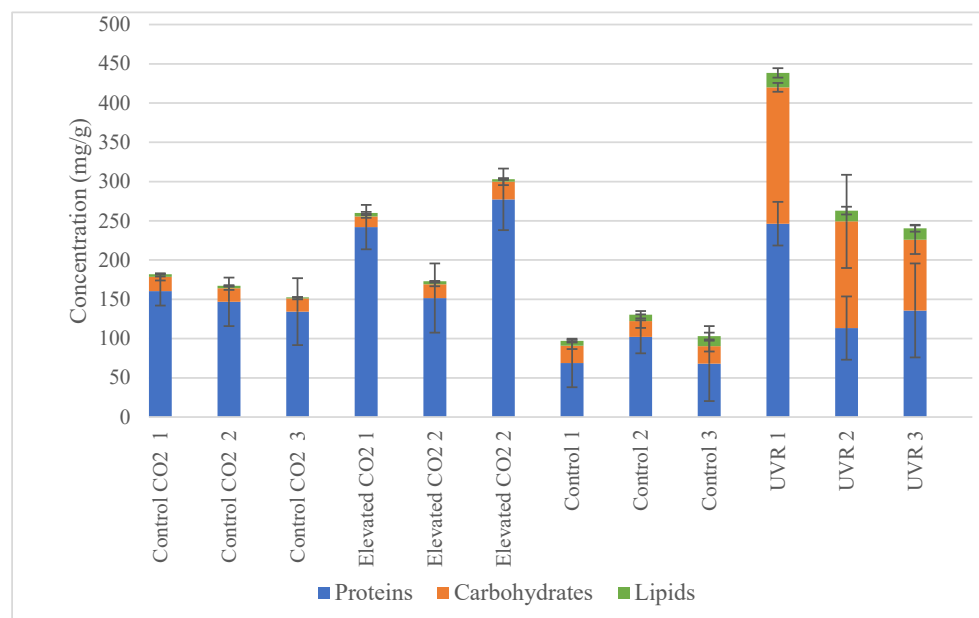


Figure 12. Intracellular metabolites in mg/g from cultures of *Calothrix* sp. SLM0211 by treatment and experimental replicate. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S7.

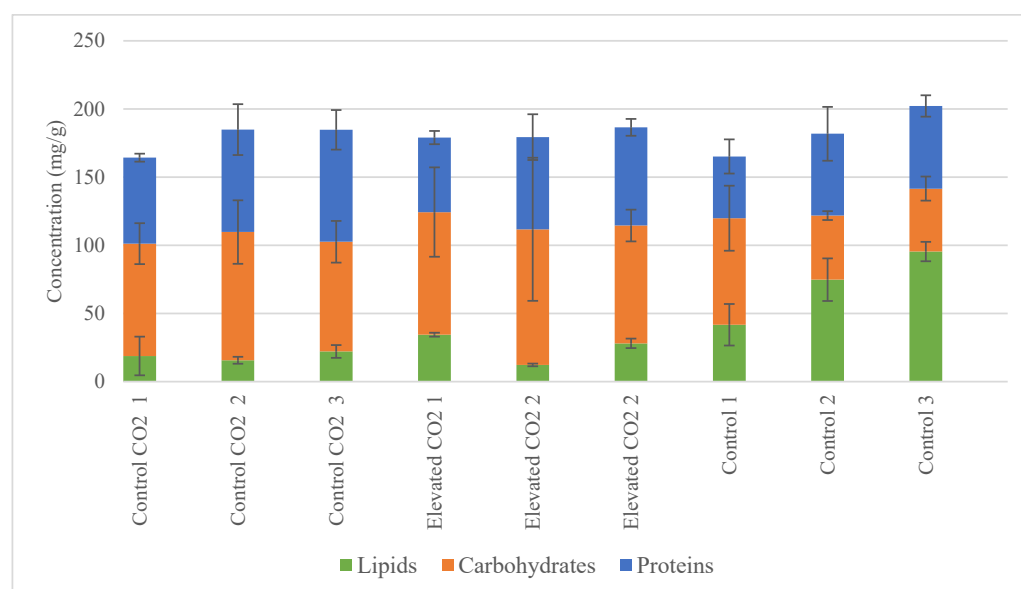


Figure 13. Intracellular metabolites in mg/g of *Coelastrrella* sp. SLM0503 cultures grown at elevated CO₂ levels compared to both controls. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S7.

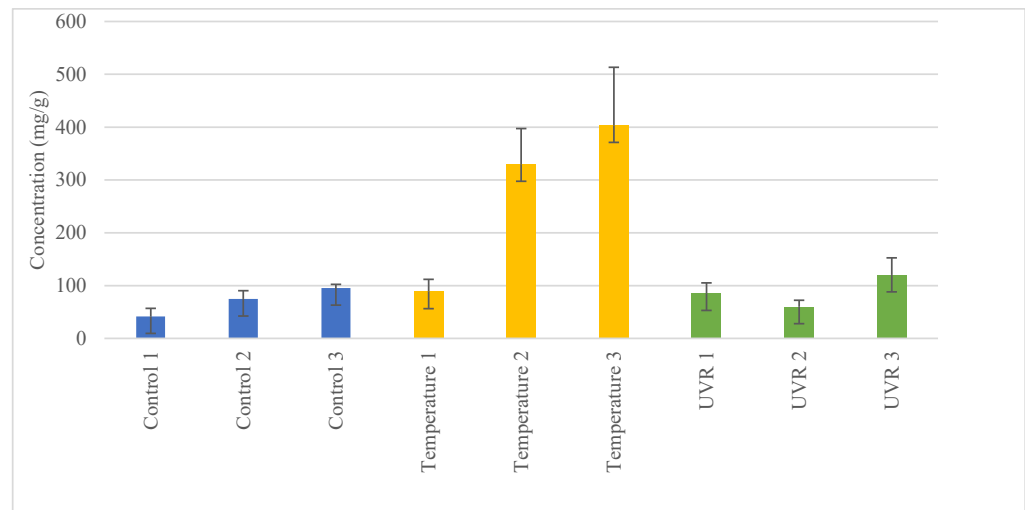


Figure 14. Intracellular lipid content in mg/g from cultures of *Coelastrella* sp. SLM05-03 by treatment and experimental replicate. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S7.

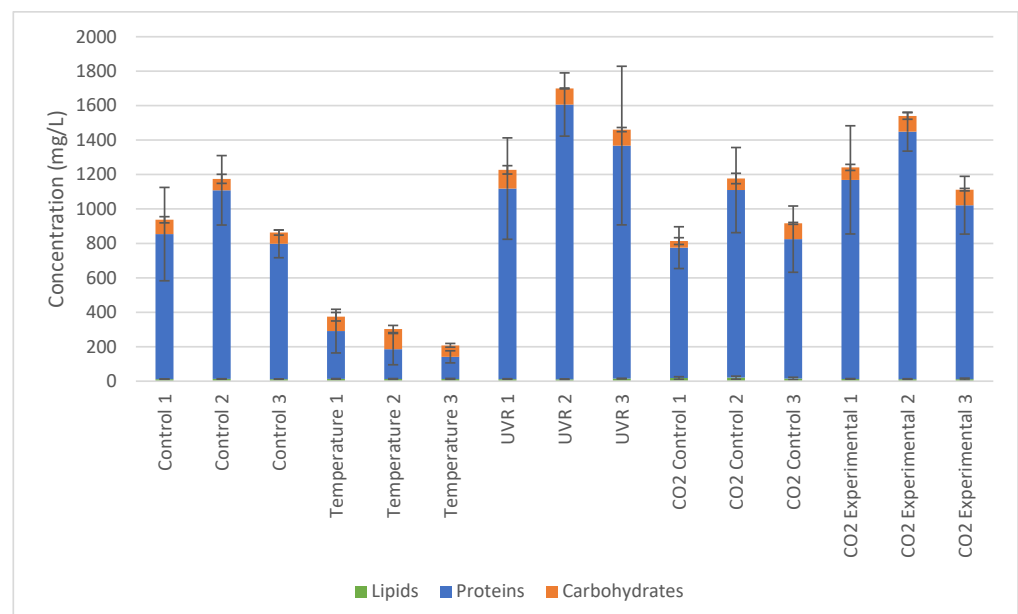


Figure 15. Released metabolites from cultures of *Calothrix* sp. SLM0211 by treatment and experimental replicate. Standard deviation is expressed as error bars. The related statistical data are given in Supplementary Materials S8.

At an elevated T, *Calothrix* sp. produced significantly high amounts of TB carbohydrates (23.34 ± 6.98 mg/g) when compared to the control (4.74 ± 1.67 mg/g), but significantly lower amounts of released proteins (193.24 ± 103.69 mg/L) (Figure 15) when compared to control cultures (907.30 ± 224.69 mg/L). Under the same conditions, the intracellular lipid content of *Coelastrella* sp. was significantly higher (273.93 ± 56.90 mg/g) than that of control cultures (70.64 ± 26.11 mg/g) (Figure 14). The growth of *Coelastrella* sp. cells at increased T and enhanced UVR, on the other hand, was so limited that intracellular proteins, carbohydrates and extracellular metabolites could not be quantified.

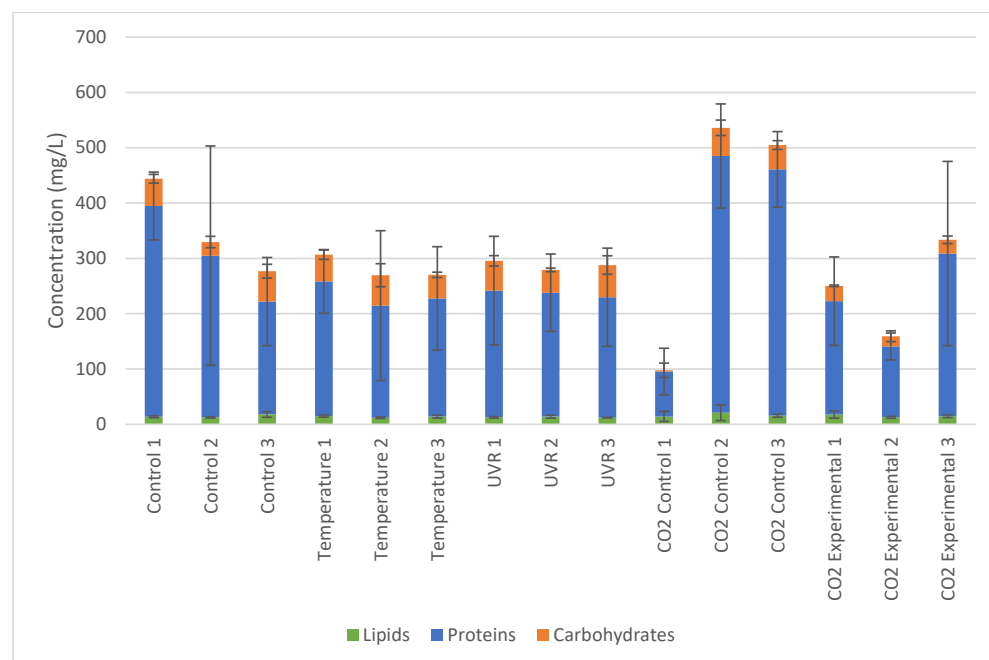


Figure 16. Released metabolites from cultures of *Coelastrella* sp. SLM0503 by treatment and experimental replicate. Standard deviation is expressed as error bars. Related statistical data are given in Supplementary Materials S8.

At a high level of CO₂, *Calothrix* sp. cultures produced significantly high amounts of intracellular proteins and lipids (223.63 ± 65.01 mg/g and 3.93 ± 1.04 mg/g, respectively), as well as TB carbohydrates, proteins and lipids. LB proteins and carbohydrates of *Calothrix* sp. cells (39.60 ± 15.69 mg/g, 5.04 ± 2.49 mg/g) were significantly higher, as were the released proteins (1200.48 ± 265.14 mg/L).

On the other hand, elevated CO₂ levels resulted in no significant difference in their intracellular (Figure 13) or released (Figure 16) metabolites of *Coelastrella* sp. cells.

Band assignments for FTIR are given in Table 1, while the spectra and associated data are presented in Supplementary Materials S9. The protein:carbohydrate and lipid:protein ratios were found to be significantly higher in cultures of *Coelastrella* sp. grown at an increased T. On the other hand, an elevated CO₂ concentration resulted in a significantly higher lipid: carbohydrate ratio. For *Calothrix* cultures, no significant differences were recorded between experiments and controls.

Table 1. Band assignment in FTIR spectra of both strains is based on [28–30].

Band Number	Wavenumber Range (cm ⁻¹)	Band Assignment	Major Molecule(s)
1	3400–3300	ν (O-H) stretching	Water
2	1745–1734	ν (C=O) of ester functional groups	Lipids
3	1655–1638	ν (C=O) stretching of amides	Proteins
4	1545–1540	δ (N-H) of amides (Amide II band)	Proteins
5	1191–1356	ν_{as} (>P=O)	Nucleic acids (and other phosphate-containing compounds).
6	1174–980	ν (C-O-C) of polysaccharides	Carbohydrates
7			

4. Discussion

4.1. The Effects of Elevated T

Data provided by the MET Office at Malta International Airport indicate that the Maltese islands have experienced persistently high temperatures in recent years, with maximum summer values consistently reaching 30 °C for seawater and 35 °C or more for air and ground temperature

The halophilic microbial strains utilised in this study are capable of surviving in coastal rock pools during summer [8], and thus these environmental parameters were employed as the baseline. The T was thus based on the average T of the rock pool water during sampling, which was confirmed via T readings obtained from satellite data (28 °C). This T was incremented by the projected rise of 4 °C, to arrive at an experimental T of 32 °C.

Thermal stress had the highest detrimental effect on the growth of *Calothrix* and *Coelastrella* spp. cells in culture, as shown by the growth curves and final biomass yields (Figure 1). An elevated T of 32 °C proved to be outside the optimal growth range for these microbial strains and exceeded their functional threshold.

Changes in morphological features included a decrease in the overall cell size of *Coelastrella* sp. as an adaptation to dissipate heat generated from an increased metabolic rate. In contrast, *Calothrix* sp. filaments were observed to fragment and release propagules (Figure 2).

In contrast, sciophilous strains belonging to *Nostoc* and *Jenufa* spp., which grow at lower temperatures, attained a higher biomass when grown at an elevated T of 24 °C, suggesting that this was still within their optimal growth range and these cells were able to adapt [31].

At an elevated T, *Calothrix* sp. cells accumulated PC and APC (Figure 7), since phycoobiliproteins maintain photosynthetic efficiency and prevent oxidative damage via their tetrapyrrole structure, which is thermally stable [32]. Greater amounts of EPS were produced, measured as TB and LB carbohydrates or polysaccharides, which could also be observed as a cloudy slime layer forming around the cultured cells and microscopically as a thick sheath surrounding the filaments (Figure 2). Cells benefit from this production of EPS, which prevents oxidative damage and protects them from desiccation [33].

The *Coelastrella* sp. cells produced carotenoids (Figure 3) both at a moderate (22 °C) and at an elevated T (32 °C) (Figure 6), and these cultures attained an orange colouration. *Coelastrella* spp. known to accumulate secondary carotenoids include *C. aeroterrestica*, *C. terrestris*, *C. oocystiformis* and *C. rubescens* [34]. Another microalga that has been observed to accumulate carotenoids when subjected to heat stress is *Dunaliella salina* [35].

For *Coelastrella*, the lipid to protein ratios of cultures grown at an elevated T were higher than for those grown under control conditions. Biochemical pathways for the production and accumulation of lipids are dependent on enzymes that function at a higher rate and have been found to be species-specific [36]. In fact, *Coelastrella* sp. cells accumulated intracellular lipids at elevated T (Figure 14). Intracellular lipids, primarily triacylglycerols, form in microalgae under heat stress as an adaptive mechanism to protect the cell against oxidative damage and metabolic imbalance. When exposed to temperatures above their optimal range, microalgal cells redirect the carbon flow to energy storage as lipids to survive the unfavourable conditions. A significant decrease in the chlorophyll *a* content was recorded at the end of the study. In fact, chlorophylls are prone to photo-oxidative damage, due to the production of superoxide and hydrogen peroxide within chloroplasts when cells are under environmental stress [37].

4.2. The Influence of Enhanced UVR

Microalgae may employ a range of mechanisms that allow them to tolerate or avoid exposure to UVR. Even though both strains adopt a biofilm mode of life in their natural habitat as an adaptive mechanism, this was not observed in culture, probably since these were unialgal cultures. Changes in cellular morphology in *Calothrix* sp. included heavy trichome coiling (Figures 2 and 4), which imparted a self-shading effect from UVR. Such adaptive mechanisms enabled the cells to produce a high final biomass yield. In a separate study, *Jenufa* sp. cells produced thicker cell walls, while filaments of *Nostoc* sp. became aggregated to form compact clusters surrounded by thickened extracellular sheaths, in which the outer filaments sheltered inner ones from UVR stress [31].

Although a yellow-brown pigment was observed microscopically in the sheath of *Calothrix* sp. cells (Figure 2), the typical absorption maxima of scytonemin at 252, 278, 300 and 386 nm were not detected (Figures 8 and 9). On the other hand, an MAA was identified, as in other *Calothrix* sp. strains [38]. However, its absorption maximum of 335.5 nm suggests the presence of a new photoprotective pigment in cyanobacteria.

At increased UVR, *Calothrix* sp. cells produced significantly higher amounts of carotenoids and chlorophyll *a*. Secondary carotenoids are known to provide protection and shielding from UVR [39]. As a result, *Calothrix* sp. cells produced significantly higher amounts of intracellular carbohydrate, protein and lipid (Figure 12), which in turn promoted the production of UVR-absorbing compounds. UV-B specifically was found to increase carotenoid production in four cyanobacterial species, namely, *Scytonema javanicum*, *Nostoc muscorum*, *Aphanothece naegeli*, and *Synechococcus elongatesv* [40]. And in a study of *Nostoc commune*, UVR was also found to significantly increase the synthesis of both polysaccharides and phycobiliproteins [41].

In contrast, *Coelastrrella* sp. produced a lower amount of chlorophyll, a fact which may be attributed to direct UV-B damage to photosynthetic processes, particularly the electron transport system, PSII and pigment bleaching [42]. This damage resulted in a decrease in overall photosynthetic activity and a significantly lower final biomass yield (Figure 1).

Towards the end of the study, *Coelastrrella* sp. cells had accumulated secondary carotenoids, which largely prevented chlorophyll degradation and in fact, the chlorophyll *a* content was unaffected. On the other hand, cultures that did not accumulate carotenoids produced a significantly lower amount of chlorophyll *a*. The response to UV-A was found to be highly strain-specific in microalgae and two MAAs with photoprotective properties, called Coelastrin A and Coelastrin B, have recently been described from *Coelastrrella rubescens* [43].

4.3. The Effect of Increased CO₂ Concentration

The supply of CO₂ helped maintain the pH of the culture medium in a favourable range, between 6.5 and 7. As the cells photosynthesized and consumed CO₂, the pH tended to rise, but the controlled addition of CO₂ countered this, preventing the formation of less bioavailable inorganic carbon species such as carbonate ions (CO₃²⁻).

Both *Calothrix* and *Coelastrrella* spp. cells produced the highest amount of biomass when grown at elevated CO₂ levels (Figure 1). Both strains produced significantly higher amounts of chlorophylls and carotenoids. This is consistent with other studies, which suggest that chlorophyll accumulates with increasing CO₂ concentrations [44]. However, the increased amounts of pigments were not accompanied by a parallel increase in biomass production in *Coelastrrella* sp., confirming that nutrients became depleted in culture due to the high growth rate, thus prohibiting biomass accumulation at this stage.

Cultures of *Calothrix* sp. cells also produced significantly high amounts of intracellular proteins and lipids, EPS, secreted proteins and an MAA with an absorption maximum

at 333.7 nm. The latter is a novel finding, and further analyses are required to determine its structural and functional properties. Different MAAs with an absorption maximum at 334 nm have been identified in other genera of cyanobacteria, and these include shi-norine, porphyra-334 and mycosporine-2-glycine. The production of MAAs is induced by exposure to UVR, high light intensities and salt stress, due to their photoprotective and osmoprotectant roles. This has been demonstrated in other halotolerant cyanobacteria, including *Aphanothece halophytica* [45] and *Euhaltece* spp. [46,47].

The accumulation of secondary carotenoids in *Calothrix* and *Coelastrella* spp. cells is not connected to photosynthesis but is rather in reaction to, and as a protective mechanism against, different environmental stressors. Even though secondary carotenoids act as powerful antioxidants, such properties have not been demonstrated actively in algal cells. It is likely that they are not involved in the scavenging of reactive oxygen species within the photosynthetic apparatus, because they are not associated with it. Thus, they most probably act as light filters or sunscreens in extreme conditions, decreasing the absorbance of excess energy and the risk of photodamage [34].

5. Conclusions

Apart from morphological adaptations, both *Calothrix* sp. and *Coelastrella* sp. cells accumulated protective metabolites to counteract the damage caused by environmental stressors associated with global climate change. These compounds warrant further investigation since some are likely to possess novel molecular structures, especially since these microbial strains have never been previously studied. These microorganisms inhabit coastal rock pools in the central Mediterranean, extreme habitats that are characterized by combined adverse abiotic factors, such as extreme solar irradiation, high temperature fluctuations, and seasonal drying, which they survive by forming complex microbial communities in biofilms and microbial mats.

Our collective results demonstrate that the effects of GCC parameters on the growth of cyanobacteria and microalgae in culture are significant and strain-specific. The environmental stressors tested individually on the *Calothrix* sp. and *Coelastrella* cells resulted in significant growth inhibition. Their combined effect, while difficult to predict, is likely to be even more harmful on cyanobacterial and microalgal communities growing in situ. The effect would all depend on the rate of change of environmental parameters, as microbial communities might be able to adapt to small fluctuations. This is especially true for biofilm and biomat-forming microorganisms, such as the *Calothrix* sp. and *Coelastrella* sp. strains studied here, in which the production of an EPS matrix and secondary metabolites impart protection to the coastal microbial community as a whole.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/microorganisms14020487/s1>, Supplementary Materials S1: Biomass yield; Supplementary Materials S2: Morphology measurements; Supplementary Materials S3: Growth curves; Supplementary Materials S4: Pigments; Supplementary Materials S5: Carotenoid absorption spectra; Supplementary Materials S6: Phycobiliproteins; Supplementary Materials S7: Intracellular metabolites; Supplementary Materials S8: Extracellular metabolites; Supplementary Materials S9: FTIR Spectra and Metabolite Band Ratios.

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Abbreviations

The following abbreviations are used in this manuscript:

GCC	Global Climate Change
T	Temperature
UVR	Ultraviolet Radiation
CO ₂	Carbon Dioxide Concentration
EPS	Exopolymeric Substances
PC	Phycocyanin
APC	Allophycocyanin
PE	Phycoerythrin
MAA	Mycosporine-like Amino Acids
RM	Released Metabolites
LB	Loosely Bound Metabolites
TB	Tightly Bound Metabolites

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