

# Effects of light and temperature on the growth of *Leptolyngbya* sp., an estuarine Cyanobacterium from Colombia, under Laboratory Conditions

## Efectos de la luz y la temperatura sobre el crecimiento de *Leptolyngbya* sp., una cianobacteria estuarina de Colombia, en condiciones de laboratorio

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### Abstract

Cyanobacteria are groups of microalgae with high ecological importance and have gained relevance due to commercial interest for their nutritional and health value. This research analyzed the growth in strain of *Leptolyngbya* sp. under different combinations of light and temperature conditions. Here, we present an approach of bioprospecting-based study in the Gulf of Urabá, Caribbean Colombia where fifteen different morphologies of cyanobacteria were observed among all collected samples, but after several months of culture and isolation treatment *Leptolyngbya* sp. was detected. Several freshwater and salty culture media both solid and liquid were inoculated by diluting the sample every 15 days of culture, a new set of serial dilutions was done to obtain isolated strains. Results indicated that illumination with a green wavelength provides higher biomass and protein content in culture if it is grown at 28 °C. A temperature of 35 °C was observed to be detrimental to culture, presenting lower biomass (<50%), yields and protein percentages at all wavelengths. According to protein percentage (60%), blue light in cultures grown at 28 °C was disadvantageous, as were all of the other lights in cultures grown at 35 °C. Moreover, results regarding the evaluation of temperature and light effects over *Leptolyngbya* sp. biomass and protein yield revealed that play a role on these responsible variables. These biomolecules found have multiple applications in different fields from bioactive compounds to metabolites with industrial, pharmaceutical and ecological uses. In conclusion, these finding provide insights into optimizing the growth of local cyanobacteria and estuary could become a potential source of protein via microalgae and further investigation is recommended to study the scale-up.

**Keys words:** bioprospecting; *Leptolyngbya* sp.; phycobiliprotein; light spectrum; temperature; Caribbean Colombia

### Resumen

Las cianobacterias son grupos de microalgas con alta importancia ecológica y han ganado relevancia debido al interés comercial por su valor nutricional y para la salud. Esta investigación analizó el crecimiento en una cepa de *Leptolyngbya* sp. bajo diferentes combinaciones de condiciones de luz y temperatura. Aquí presentamos un enfoque de estudio basado en bioprospección en el golfo de Urabá, Caribe colombiano, donde se observaron quince morfologías diferentes de cianobacterias entre todas las muestras recolectadas, pero después de varios meses de cultivo y tratamiento de aislamiento se detectó *Leptolyngbya* sp. Varios medios de cultivo de agua dulce y salada, tanto sólidos como líquidos, fueron inoculados diluyendo la muestra cada 15 días de cultivo. Un nuevo conjunto de diluciones seriadas fue realizado para obtener cepas aisladas. Los resultados indicaron que la iluminación con una longitud de onda verde proporciona mayor biomasa y contenido proteico si el cultivo se mantiene a 28 °C. Una temperatura de 35 °C resultó perjudicial, mostrando una biomasa más baja (<50 %), así como menores rendimientos y porcentajes de proteína en todas las longitudes de onda. De acuerdo con el porcentaje de proteína (60 %), la luz azul en cultivos a 28 °C mostró un comportamiento menos favorable, al igual que todas las luces en cultivos a 35 °C. Además, los resultados relacionados con la evaluación de los efectos de la temperatura y la luz sobre la biomasa y el rendimiento de proteína en *Leptolyngbya* sp. revelaron que estas variables influyen en dichos parámetros. Las biomoléculas encontradas tienen múltiples aplicaciones en diversos campos, desde compuestos bioactivos hasta metabolitos con usos industriales, farmacéuticos y ecológicos. En conclusión, estos hallazgos ofrecen información para optimizar el crecimiento de cianobacterias locales y sugieren que el estuario podría ser una fuente potencial de proteína mediante microalgas.

**Palabras clave:** bioprospección; *Leptolyngbya* sp.; ficobiliproteína; espectro luminoso; temperatura; Caribe colombiano.

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## Introduction

Human activity, especially industrial production, has been the central cause of environmental deterioration (McLaughlin *et al.*, 2013). Even in these times of global biodiversity crisis, it is urgent to incorporate the values of nature into decision-making (Pascual *et al.*, 2023). The biggest challenge in the modern age, in which scientists have an important responsibility, is to develop more sustainable production processes (Schneider *et al.*, 2011). The unmeasured use of natural resources currently generates other economic and social problems. For this reason, new sources and forms of eco-friendly food production are being sought on a global scale.

While 25 % of living species on the planet are found in marine areas, it is estimated that only 10 % of the biodiversity present in the oceans has been documented (Todd, 2018). Regarding microalgae, it is suggested that out of approximately 200,000 species, only about 50,000 have been described (Mobin *et al.*, 2019). This vast diversity of phytoplankton is associated with their dominance in marine ecosystems, although their habitats are as diverse as their species (Córdoba-Mena *et al.*, 2020; Not *et al.*, 2012), and interest in them for various purposes has grown (Tang *et al.*, 2020). They are fast-growing organisms that do not require arable land, are independent of seasonal conditions, and have the potential to transform solar energy into biomass (Khan *et al.*, 2018).

The rich biomass of different microalgal species varies in compounds such as lipids, proteins, and carbohydrates, as well as functional molecules (Tan *et al.*, 2020). For these reasons, microalgae could be used in both human and animal nutrition (Kusmayadi *et al.*, 2021; Sathasivam *et al.*, 2019), and in both cases could contribute to efforts to strengthen global food security. Currently, only a few microalgal strains are widely used for industrial purposes, such as *Spirulina* sp., *Chlorella* sp., *Haematococcus* sp., *Dunaliella* sp., *Botryococcus braunii*, *Phaeodactylum* sp., and *Porphyridium* sp. (Raja *et al.*, 2008). Consequently, expanding our knowledge about understudied microalgae could lead to the discovery of new strains suitable for industrial use, highlighting the need for bioprospecting studies (Sanchez Rizza *et al.*, 2017).

Cyanobacteria are of particular interest for biotechnological applications, including the production of renewable fuels, fatty acids, and phycobiliproteins (Basheva *et al.*, 2018; Domínguez *et al.*, 2018; Kim *et al.*, 2015; Sharma *et al.*, 2014). Phycobiliproteins,

in particular, are water-soluble proteins with blue to red pigmentation and diverse properties, including antioxidant and anti-inflammatory activity (health sector) (Chen *et al.*, 2022); use as pigments in industry (Nascimento *et al.*, 2020); thermostabilizing functions in industrial processes (Puzorjov and McCormick, 2020); and heavy metal binding capabilities (Bellamy-Carter *et al.*, 2022).

From an evolutionary perspective, phycobilisomes are protein complexes that serve as light-harvesting antennae in both cyanobacteria and some eukaryotes. In cyanobacteria, they are more externally located on the thylakoid membrane, whereas in eukaryotes, they are more structurally organized within chloroplasts (Stadnichuk *et al.*, 2023; Zheng *et al.*, 2021). These biomolecules are found only in specific groups of microalgae, such as rhodophytes, cyanobacteria, cryptophytes, and glaucophytes (Rizwan *et al.*, 2018). However, there has been growing interest in novel uses, such as a protein source for food production, in recent years. While studies have shown that environmental conditions, such as pH, nutrient limitation, salinity, and nitrogen supplementation, can affect the production of phycobiliproteins in microalgae (Khatoon *et al.*, 2018), even factors like the intensity and quality of light are among the most influential, with recorded variations in protein content ranging from 0.11 % to 12.7 % of dry weight (Rizwan *et al.*, 2018).

On a related topic, the Caribbean region of Colombia has a rich marine biodiversity distributed across a wide range of ecosystems (Muñoz Sevilla and Le Bail, 2017; Vallejo Toro *et al.*, 2016; Yanes *et al.*, 2019). However, there are still large areas that have not yet been studied in terms of phytoplanktonic abundance (Contreras *et al.*, 2022; Córdoba-Mena *et al.*, 2020; Lozano-Duque *et al.*, 2010). One of these areas is the Gulf of Urabá, considered one of the largest estuaries in the country, yet poorly documented in terms of microalgae diversity (Córdoba-Mena *et al.*, 2020; Contreras-Fernández *et al.*, 2022; García and Sierra, 2007).

Moreover, microbial diversity shows a significant relationship with other prokaryotic communities (such as Cyanobacteria), better explaining the functional diversity of the estuary (Levipan *et al.*, 2024), and serving as a proxy for productivity and accessory pigments such as chlorophyll a (Pacheco *et al.*, 2025).

The aim of the study was to evaluate how temperature and wavelength affect the biomass and protein content of

*Leptolyngbya* sp. In conclusion, these findings provide insights into optimizing the growth of local cyanobacteria, promoting a valuable resource for the development of innovative and sustainable applications. Bioprospecting in the estuary could yield a potential source of protein via microalgae, and further investigation is recommended to study the feasibility of scaling up.

## Materials and methods

### Study area

The northern part of Caribbean Colombia (7.8°–12.5° N and 75.4°–77.5° W) (Figure 1) is a sub-basin of the Caribbean Sea (Beier et al., 2017), where precipitation and river runoff are controlled by the seasonal migration of the Intertropical Convergence Zone (ITCZ) and the trade winds from the northeast and southwest, which determine the timing of the dry and rainy seasons. In the northernmost part of Colombia lies the

country's largest estuary, known as the Gulf of Urabá (7°55' N–8°40' N and 76°53' W–77°23' W; Figure 1), formed by the mixture of Caribbean seawater with the inflows of various rivers, most notably the Atrato River. This river discharges approximately 4,000–5,000 m<sup>3</sup> s<sup>-1</sup> (Escobar and Velásquez, 2018) and influences the coastal hydrodynamics of the Gulf of Urabá (Contreras et al., 2022; Pacheco et al., 2025), phytoplankton dynamics (Córdoba-Mena et al., 2020), and metabolic biodiversity (Levipan et al., 2024).

Other tributaries also contribute significantly to the estuary. The environmental characteristics of many coastal areas of the Gulf of Urabá can be summarized by several factors: high nutrient concentrations (*e.g.*, nitrites: 3–640 µg L<sup>-1</sup>, ammonia: 70–2000 µg L<sup>-1</sup>, nitrates: 100–11,900 µg L<sup>-1</sup>, orthophosphates: values not reported); high levels of suspended solids (9–4600 mg L<sup>-1</sup>); and pH values within the normal range (<8 to 8.1) (Contreras et al., 2022).

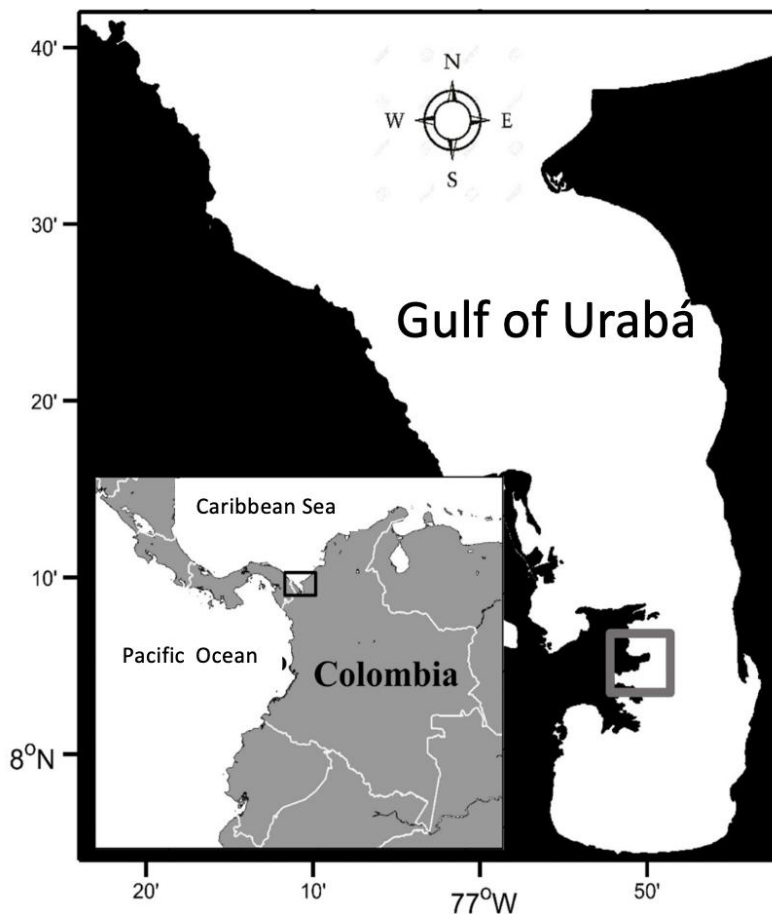


Figure 1. Study area in the Gulf of Urabá, Caribbean region of Colombia.

## Sampling campaign

even sampling campaigns were conducted under the framework contract for access to genetic resources No. 126, May 2016, celebrated between Ministerio Desarrollo y Sostenible de Colombia and Universidad de Antioquia (Colombia). All samples were immediately transferred to the laboratory of the University of Antioquia (Col), biotechnology research group, for further analysis. Samples were collected by horizontal and vertical drag, using nets with different pore diameter sizes (Andersen and Kawachi, 2015; Córdoba-Mena *et al.*, 2020; Miao *et al.*, 2019). The samples were processed immediately after collection, and microphotography was used for morphological organism identification. Several freshwater and salty culture media (Allen and Stanier, 1968), both solid and liquid, were inoculated. By diluting the sample, every 15 days of culture, a new set of serial dilutions was done to obtain isolated strains. Regular observations were made under a microscope to identify phycobiliprotein producers and to monitor for bacterial contamination. Antibiotics (ampicillin, kanamycin, and chloramphenicol: 150, 10, and 17  $\mu\text{g mL}^{-1}$ , respectively), and nitrogen depletion, were used selectively to minimize bacterial growth (Bruckner, 2009).

## Molecular identification

DNA from biomass was obtained using Genomic DNA Mini Kit, Ref. K1820-02, Invitrogen, and it was quantified by colorimetric method using the Picogreen method (Ahn *et al.*, 1996). Deep NGS sequencing of the 16S rDNA gene was developed using variable regions V3 and V4, amplified with the oligonucleotides Bakt\_341F CCTACGGGNGGCWGCAG, Bakt\_805R GACTACHVGGGTATCTAATCC. Paired reads with 300 nucleotides were obtained by Illumina MiSeq sequencing. Only cyanobacterial sequences were filtered, and preliminary quality processing was conducted using MOTHUR software. Homologous sequences for 16S rRNA genes of cyanobacteria, published previously and obtained from NCBI (Foster *et al.*, 2009), were used for phylogenetic tree construction by neighbour-joining with 1000 bootstrap replicates and using MEGA software version 7.

## Effects of light wavelength and temperature on *Leptolyngbya* sp. cultivation

To carry out one of the experiments, one of the samples collected in the estuary was collected using a net in a horizontal

drag, with a porosity of 40  $\mu\text{m}$  pore diameter size net, and after multiple serial dilutions, antibiotic additions, and maintenance in the Aquil culture medium (Sunda *et al.*, 2005), one isolated culture of the cyanobacteria *Leptolyngbya* sp. was obtained. Physical culture conditions were permanent white LED illumination, 80  $\text{W cm}^2$ , orbital agitation at 99 rpm, and 28  $^{\circ}\text{C}$  of temperature.

Secondary cultures were prepared using 0.1 grams of wet biomass, inoculated in 20 mL of Aquil medium, and their cultures were carried out for 22 days with agitation at 99 rpm and daily  $\text{CO}_2$  supply. Two temperatures, 28 and 35  $^{\circ}\text{C}$ , and four different illumination wavelengths were evaluated. The intensity of each color was settled between 50 and 60  $\text{W cm}^2$ . Each replicate was observed at the beginning and end of the experiment using fluorescence and differential interference contrast (DIC) techniques in a Nikon® Eclipse 80i microscope. The specific maximum peak wavelengths of lights (blue, green, red, and white) were determined using a calibrated spectrophotometer (see details in supplemental figure).

## Biomass and phycobiliprotein isolation

At the end of incubation, biomass from each flask was obtained by centrifugation at  $8000 \times g$  for 30 minutes at 4  $^{\circ}\text{C}$ . Supernatants were discarded, and the remaining pellets were transferred to pre-weighed microtubes (weighed before and after centrifugation) and centrifuged again under the same conditions. From each tube, 80 mg of biomass were taken and ground using a mortar and pestle until finely homogenized, with liquid nitrogen applied to maintain a low temperature.

Subsequently, to obtain crude protein extracts, 1 mL of acetate buffer (pH 4.5) and 80 mg of cold glass beads were added to each sample. The mixture was then placed in a Disruptor Genie Digital® and subjected to 10 cycles of 1 minute of disruption followed by 1 minute of rest. During each pause, the samples were immersed in liquid nitrogen to maintain a low temperature. Finally, the samples were centrifuged at  $8000 \times g$  for 20 minutes at 4  $^{\circ}\text{C}$ , and the resulting supernatant was collected and stored at  $-80^{\circ}\text{C}$ .

## Protein characterization

Protein quantification was performed using the 2D-Quant Kit® (BioRad®), and the concentration was determined by interpolation against a BSA standard curve at 562 nm. A 30  $\mu\text{L}$

sample of each protein extract was subjected to SDS-PAGE (12 % gel) at 100V for 1.2 hours, according to the Laemmli method. The gel was stained with Coomassie blue G-250 (BioRad®) (Brunelle and Green, 2014).

Statistical analysis

The assumptions were evaluated and met, therefore there was no need to transform the data. In all cases, the underlying assumptions of the model, normality, homoscedasticity, and independence of the data were verified. Multiple range test via Fisher's least significant difference (LSD) test was used to assess the means statistical differences, and a p-value < 0.05 was considered significant. The spectrophotometric behaviors of crude protein extracts were analyzed by MUMA (metabolic univariate and multivariate analysis) software on the R i386 3.6.2 package (Gaude et al., 2013). Principal component analysis was performed using a vast scaling of dates, and the univariant p-value was selected for MUMA analysis. Statistical analyses were performed using the software StatGraphics XVI version 16.1.17.

The graphics plotted using Prism 6.0 for Windows, version 6.03A.

Results

Diversity of phytoplankton

The study presented a high diversity of phytoplankton. Some groups were associated with river discharge zones such as Chlorophyta, while the northern zone, characterized by more pronounced oceanic conditions, was rich in Stramenopile and Alveolata (figure 2). Moreover, different morphologies of cyanobacteria were observed among all collected samples. However, *Leptolyngbya* sp. was only detected after several months of culture and isolation treatments. The distance matrix showed a similarity between the obtained sequence and reference sequences of *Leptolyngbya* sp. with distances of 0.019 and 0.027. These results were consistent with the phylogenetic tree, where the target sequence is located as a brother group of *Leptolyngbya* sp. sequences, supported by a bootstrap of 72 % (figure 3).

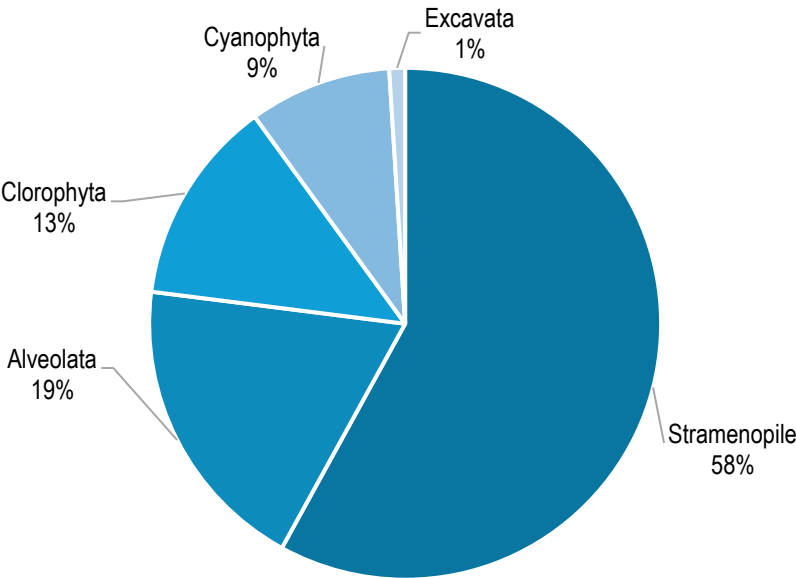


Figure 2. Percentage of species per taxonomic group identified in the samples through morphological analysis.

Effects of light and temperature on the growth of *Leptolyngbya* sp.

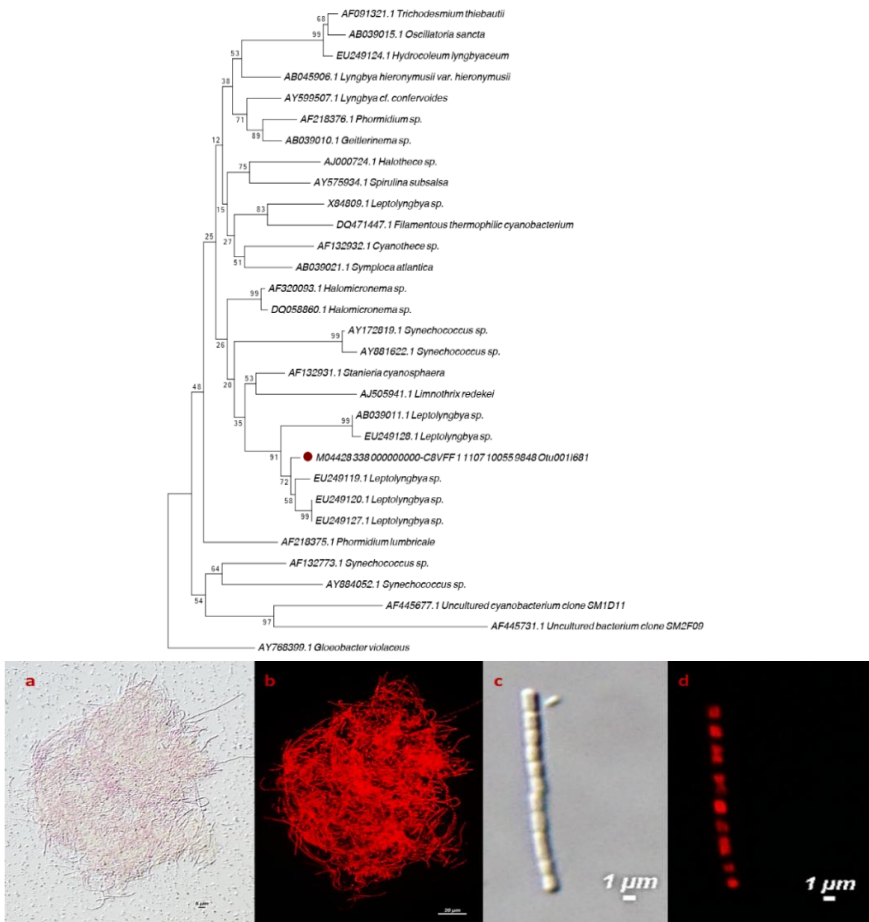


Figure 3. Neighbor joining phylogenetic tree of 16S rRNA cyanobacterial sequences and microscopic appearance of cells. (a) DIC, 40×; (b) fluorescence, 40×, 600 ms exposure, red filter; (c) DIC, 100×.

Effects of light wavelength and temperature on *Leptolyngbya* sp. cultivation

The evaluation of temperature and light effects on *Leptolyngbya*

sp. biomass and protein yield, along with the multifactorial statistical analysis, revealed that both factors had a significant influence on these response variables. Moreover, their interaction also had a statistically significant effect (Tables 1 and 2; figure 4).

Table 1. Summary of the multifactorial analysis of variance (ANOVA) results for each response variable: biomass content and protein percentage. The table shows the comparison of means. Asterisks (\*) indicate statistically significant differences between group conditions ( $p < 0.05$ ;  $n = 3$ ). G: green; W: white wavelengths.

Response	Main effects ( <i>p</i> -value)		Interaction between factor A and B ( <i>p</i> -value)		Higher % Observed for:	
	Factor A: wavelength	Factor B: Temperature	Factor A: wavelength	Factor B: Temperature		
Biomass (mg)	0	0	0	G*		28*
Protein (%)	0	0	0	W and G*		28*

Table 2. Summary of one-way ANOVA results for wet biomass weight and protein percentage under different light wavelengths and two temperature conditions.

	Variance source	Sum squares	df	Mean square	f	(p-value)
Biomass (mg)	Inter groups	185421	7	26489	105,94	0
	Intra groups	4000,44	16	250,03		
	Total	189422	23			
Protein (%)	Inter groups	47,0635	7	6,723	63,94	0
	Intra groups	1,68199	16	0,1051		
	Total	48,7473	23			

The results indicated that illumination with green light promoted higher biomass and protein content in cultures grown at 28 °C. In contrast, cultivation at 35 °C had a detrimental effect, resulting in reduced biomass yield and protein percentage across all light wavelengths. Based on protein content, blue light was particularly unfavorable at 28 °C, and all light treatments were disadvantageous at 35 °C (figure 4).

The absorption spectra of aqueous crude protein extracts revealed that cultures grown at 35 °C generally lacked defined absorption peaks, with the exception of those exposed to blue light, which exhibited a peak near 555 nm. Conversely, all extracts from cultures maintained at 28 °C displayed a more prominent absorption peak between 550 and 570 nm, with the

highest value observed under green light. A second peak was detected around 620 nm in these cultures, where the highest absorption was recorded in extracts from red light treatments. Cultures exposed to blue light at both temperatures exhibited only a weak peak at this wavelength (figure 5a).

Due to insufficient biomass and protein production at 35 °C, only cultures grown at 28 °C were analyzed by SDS-PAGE. The resulting protein gels revealed two prominent bands near 21 kDa in all samples at this temperature (figure 5b). Band intensity corresponded with the protein percentages determined previously, with stronger signals observed in cultures illuminated with green and white light, and weaker signals in those exposed to red light.

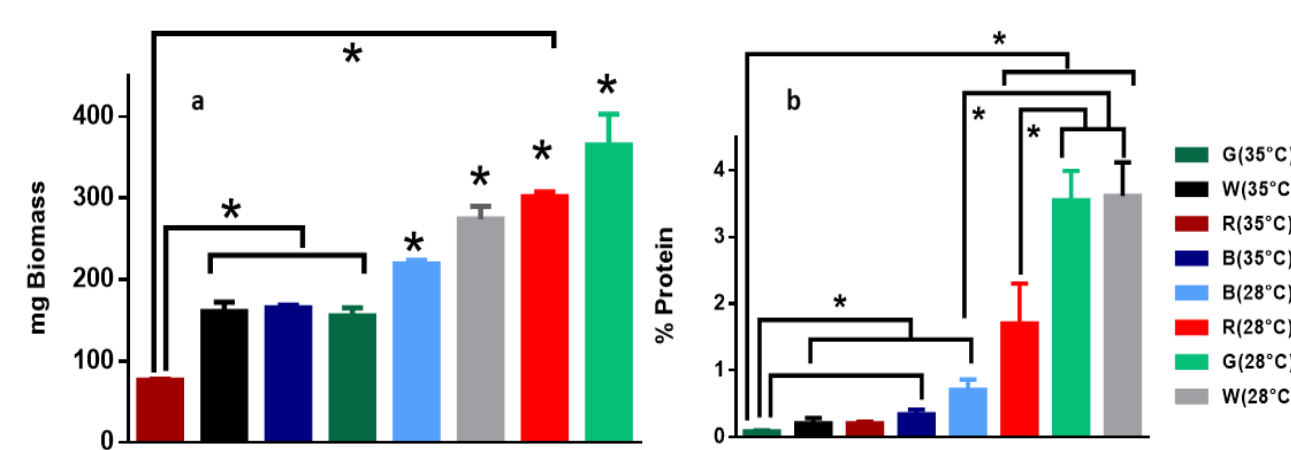


Figure 4. Effect of temperature and light wavelength on *Leptolyngbya* sp. culture. Response variables: (a) wet biomass weight, and (b) protein percentage relative to wet biomass. Light treatments: G (green), W (white), R (red), and B (blue). Asterisks (\*) indicate significant differences according to the LSD test from one-way ANOVA. Graphs generated using GraphPad Prism 6.

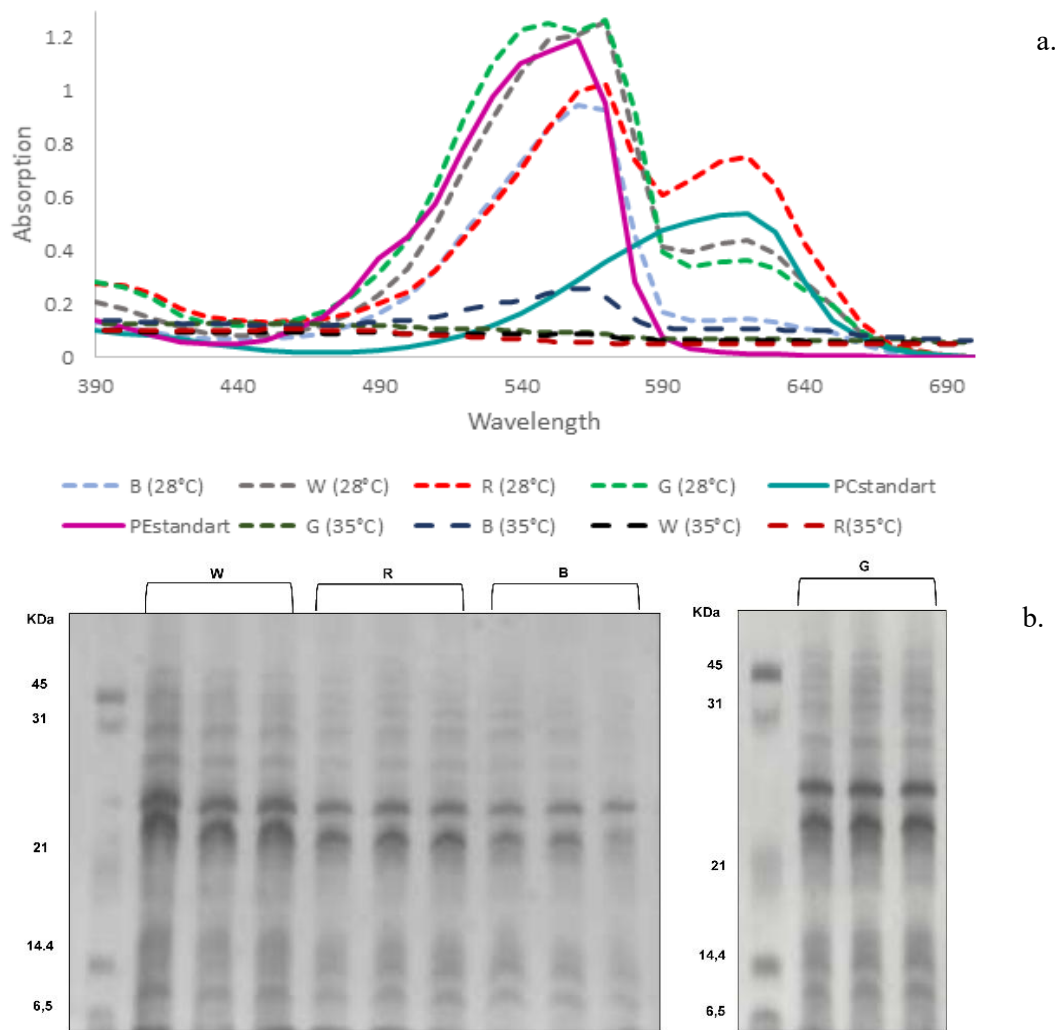


Figure. 5 (a) Absorption spectrum of aqueous protein extracts. Solid lines correspond to commercial phycobiliproteins PE (phycoerythrin) and PC (phycocyanin) spectrum from *Porphyridium cruentum* and *Spirulina*, respectively. Dotted light and dark lines correspond to extracts coming to cultures carried out at 28 and 35°C, respectively. (b) SDS-PAGE of crude protein extracts from *Leptolyngbya* sp. cultures developed at 28°C. (G: Green, W: white, R: red and B: blue source of illuminating light).

PCA results revealed that the first principal component (PC1) accounted for 62.3 % of the variance, while the second component (PC2) explained 28.8 %. The second component clearly separated protein extracts from red-light cultures at 28°C from those cultivated under other wavelengths at the same temperature (figure 6a). Loading and significance of variables in principal component segregation are presented as well, and it can be seen that 370, 490, 500, and 650 nm absorption were the heaviest variables for two components, but only 510 and 520 nm had a significant influence (figure 6b).



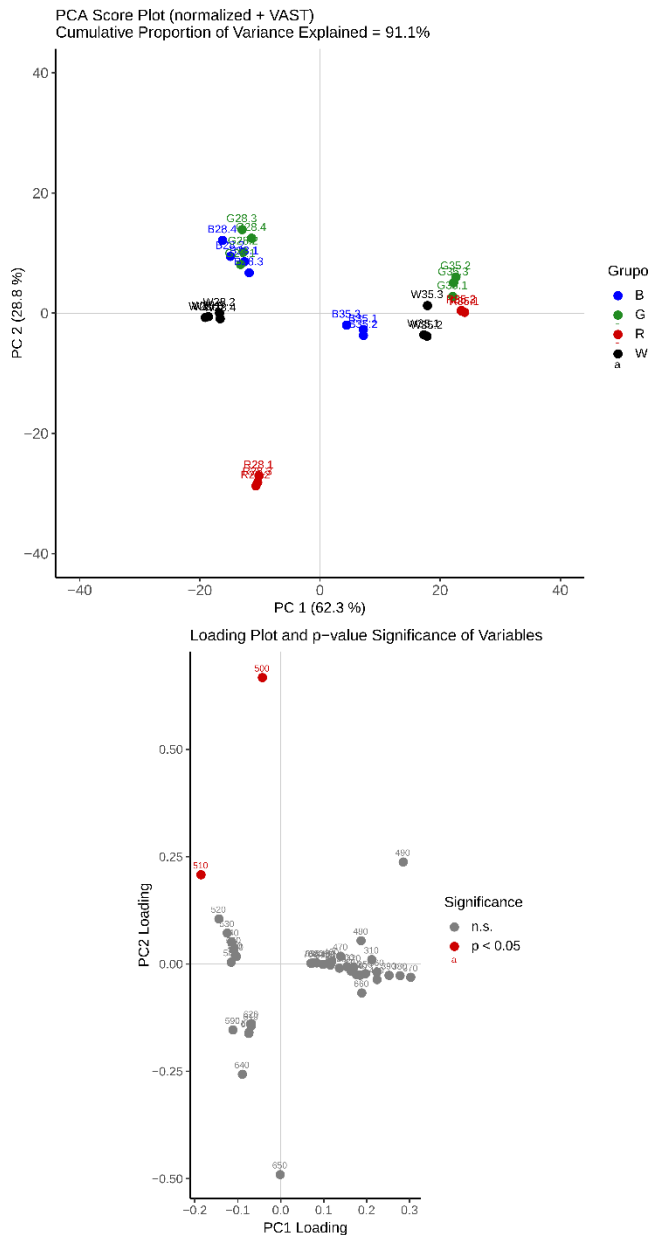


Figure 6. PCA protein extracts visible wavelength absorption. (a) Score Plot (b) Loading and p-value significance of variables. R i386 3.6.2 package.

## Discussion

### Diversity of phytoplankton

The high biodiversity of the Gulf of Urabá, as an estuarine system, can be attributed to the wide variety of interconnected ecosystems. These include continental, estuarine, and coastal marine environments, encompassing forests, mangroves, amphibious vegetation zones, coral reefs, seagrass beds, rocky shorelines, sandy beaches, and sedimentary bottoms (Contreras et al., 2022). The data obtained in this study are consistent with

the expected levels of biodiversity (figure 2) (Córdoba et al., 2020; Contreras et al., 2022; Levipan et al., 2024). It is important to note that species identification was based on simple morphological comparisons of fresh samples, without extended observation periods. Consequently, the actual species richness in the samples may have been underestimated.

Stramenopile organisms dominated the phytoplankton community in the Gulf, with the genus *Chaetoceros* being the most abundant. However, laboratory cultures were primarily dominated by cyanobacteria (figure 3). This discrepancy can

largely be explained by the small size and morphological simplicity of cyanobacteria, which limits microscopic identification in fresh samples. In addition, laboratory conditions may favor the growth of prokaryotes due to their greater tolerance to stressors such as nutrient depletion, osmotic stress, and fluctuations in pH or temperature (Casamatta and Hašler,

### ***Leptolyngbya* sp. a tropical marine cyanobacterium as a study model.**

Cyanobacteria have demonstrated remarkable survival performance across diverse terrestrial and marine ecosystems, which has generated significant interest in their resilience mechanisms (Rastogi *et al.*, 2014), particularly for applications in sustainable production and ecological damage mitigation. Numerous studies have reported the dominance of cyanobacteria in aquatic systems, including the occurrence of harmful algal blooms in various environments, where high cell densities are often observed at temperatures of 28 °C or above (Mobin *et al.*, 2019; Tilahun and Kifle, 2019).

However, not all cyanobacterial strains respond uniformly to elevated temperatures, as their physiological reactions are influenced by the interaction between temperature and UV irradiance (Tables 1 and 2) (Islam *et al.*, 2019; Kłodawska *et al.*, 2019). In our study, exposure to 35 °C resulted in significant cellular damage in cyanobacteria, as evidenced by a marked decline in biomass and protein content in the cultures (figure 4).

Subsequently, among all the growing cultures obtained, one exhibited a distinctive red coloration and demonstrated a strong response to isolation techniques involving antibiotic application, nitrogen depletion, and high salt concentrations. These traits were interpreted as desirable features in organisms intended for biotechnological applications. The cultured organism was identified as *Leptolyngbya* sp. and was further characterized through assessments of its response to light and temperature. The genus *Leptolyngbya* is among the most common cyanobacterial genera, comprising numerous ecotypes. While typically found in soil and freshwater environments, our isolate was collected from a site with greater oceanic influence despite its estuarine characteristics (Albertano *et al.*, 2000; Wall *et al.*, 2014).

Several studies have highlighted the biotechnological potential of this genus as an alternative source of food and bioactive compounds, particularly antioxidants (Ghanbarzadeh *et al.*,

2019). In the case of the strain investigated in this study, recent research by Lee *et al.* (2024) reported that *Leptolyngbya* sp. KIOST-1 shows promise as a protein supplement due to its high protein content and lack of cytotoxicity. However, published information regarding its application in aquaculture remains limited, and further research is needed (Beal *et al.*, 2018).

### **Effects of light wavelength and temperature on *Leptolyngbya* sp. cultivation**

Studies of cultures under controlled conditions have shown that *Leptolyngbya* exhibits diverse growth traits, genetic adaptability and other ecological traits. However, some factors can modulate these characteristics and have consequences for their applications in biotechnology if they are not adequately evaluated (Donkor and Häder, 1996; Li *et al.*, 2020; Sinha *et al.*, 1996, 1997).

On the other hand, several authors have described the influence of light intensity and spectral quality on phycobilin production in cyanobacteria. Given the known biological role of phycobilins as antenna pigments in photosystems, it is clear that light characteristics can significantly affect cyanobacterial growth and metabolism. Previous studies conducted on both freshwater and marine phycocyanin-producing strains reported negative effects of UV light exposure, including impaired carbon and nitrogen fixation, altered phycocyanin spectral properties, and disrupted phycobilisome integrity. These results suggest that UV irradiance limits optimal energy transfer between accessory pigments and chlorophyll, leading to photobleaching (Donkor and Häder, 1996; Sinha *et al.*, 1996, 1997).

Nonetheless, some cyanobacterial species have shown effective adaptive responses to environmental stressors such as UV radiation, high-intensity photosynthetically active radiation (PAR), and elevated temperatures (Moon *et al.*, 2012; Paul, 2008). However, results from studies using different light wavelengths indicate that cyanobacterial responses are not homogeneous. For instance, experiments with *Synechococcus* sp. and *Microcystis aeruginosa* demonstrated higher biomass and phycocyanin productivity under red light, with some studies identifying optimal light intensities around 55  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Choi *et al.*, 2013; Tan *et al.*, 2020). In contrast, *Gloeotheca membranacea* showed lower efficiency in converting red light into biomass, while blue-violet light enhanced its growth rate, and green light maximized chlorophyll-a production in this strain (Mohsenpour *et al.*, 2012).

Other studies have pointed out that improved biomass growth at a particular wavelength does not necessarily translate into higher pigment content. For example, assessments using LED illumination on *Spirulina* sp. cultures showed that blue light at an intensity of  $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$  resulted in the highest phycocyanin yield, while red light supported optimal algal growth (Chen *et al.*, 2010; Park and Dinh, 2019).

To understand the variability in results, it is important to consider that cyanobacteria can grow autotrophically, heterotrophically or mixotrophically; however, these modes are not universal across all species. Growth conditions, along with additional bacterial presence and the type of strain used (wild or domesticated), can significantly influence outcomes in wavelength-based evaluations (Paerl *et al.*, 1985).

Previous bioprospecting studies on *Pseudoanabaena* sp. from the Arctic have indicated that red light enhances phycocyanin production, while green light favors phycoerythrin synthesis. A similar pattern was observed in the present study with cultures grown at 28 °C. Red light produced protein extracts with a higher absorption peak around 620 nm, corresponding to the characteristic absorbance of phycocyanin in *Spirulina* sp., whereas cultures exposed to green light exhibited a more intense absorption peak in the region associated with phycoerythrin from *Porphyridium cruentum*, around 550 nm (figure 5a).

The effect of different wavelengths on the absorption patterns of the extracts appears to have influenced the chromophores contained within the phycobiliproteins in distinct ways. The protein percentage was lower in red-light cultures compared to those irradiated with green light (Khan *et al.*, 2019). In our study, the phycoerythrin absorption peak was higher, suggesting that phycoerythrobilin is likely the preferred chromophore in this strain, consistent with previous reports on *Leptolyngbya* sp.. Additionally, the marked decrease in the phycocyanin absorption peak under blue light resembled patterns previously observed under UV exposure (figure 5a) (Gan *et al.*, 2014; Tilahun and Kifle, 2019).

Under the same blue light condition, the intensity of two prominent protein bands (~21 kDa) observed in the electrophoretic gels was reduced (figure 5b). These bands likely correspond to the  $\alpha$  and  $\beta$  subunits, which are characteristic of most phycobiliproteins. Similarly, previous studies reported two bands at approximately 18 and 21 kDa as phycoerythrin

subunits in *Leptolyngbya* sp. cultures (Pumas *et al.*, 2012). In that study, the maximum absorption peak of phycoerythrin was recorded at 562 nm, suggesting the presence of a single chromophore type. In contrast, our results suggest the presence of two types of chromophores in some extracts, although electrophoretic profiles did not indicate the presence of more than one phycobiliprotein type. This could imply that a single phycobiliprotein may incorporate two chromophores, as reported in other strains (Basheva *et al.*, 2018). Nonetheless, protein sequencing is required to confirm whether only one type of dimeric phycobiliprotein subunit is produced.

Principal Component Analysis (PCA) of the visible spectrum of the protein extracts revealed clear differences based on culture temperature. Moreover, significant variation was also observed among protein extracts from cultures grown at 28 °C. The second principal component distinguished the red-light treatment from all others, primarily influenced by absorption in the 500–650 nm range, with strong loadings around 500 and 650 nm (figure 6). This region encompasses the maximum absorption peaks for both phycoerythrin and phycocyanin, as reported for *Porphyridium cruentum* and *Spirulina*, respectively. This result is consistent with the fact that red light was the only wavelength yielding comparable absorption intensities at both phycobiliprotein peaks.

Contrary to our findings, a *Leptolyngbya* sp. strain isolated from the Arabian Gulf exhibited higher biomass and protein yields at elevated temperatures between 30 °C and 40 °C (Schipper *et al.*, 2019). These differences may be attributed to the environmental conditions of the strain's native habitat. In our study, the maximum in situ temperature recorded at the collection site was 29 °C, which is considerably lower than the 69 °C reported for *Leptolyngbya* sp. from the Gunung Pancar hot spring (Prihantini *et al.*, 2019) and is considered high for some *Leptolyngbya* strains (Neif, 2015).

The optimal growth conditions determined for *Leptolyngbya* sp. in this study were 28 °C and green light at a mean intensity of  $50 \text{ W/cm}^2$ . However, further optimization is required to improve both biomass and protein yields. Despite these limitations, this initial bioprospecting effort represents a valuable step toward the sustainable use of Colombia's underexplored microbial biodiversity. Owing to the wide distribution of the *Leptolyngbya* genus, extensive information is available regarding its genetic and biochemical properties, including successful examples of molecular transformation (El Semary, 2013; Taton *et al.*, 2012; Nakamori *et al.*, 2014). Therefore, the isolated strain may be

suitable for the development of regional biotechnological applications.

Additionally, the high protein content observed in this species highlights its potential as a nutritional resource for both direct and indirect human consumption. It could also serve as a promising alternative to conventional protein production systems, which are known to have significant environmental impacts and raise concerns about sustainability (Henchion *et al.*, 2017). The ability of this strain to grow under artificial conditions was among the most important findings of this study. *Leptolyngbya* sp. exhibited a positive response to laboratory cultivation, with green light and 28 °C yielding the best results. Nonetheless, the observed productivity was still low, and further optimization is necessary as a next step in the strain development workflow.

On the other hand, cyanobacteria are known to produce a variety of cyanotoxins, which can pose serious risks to human and animal health (Pantelić *et al.*, 2013; Wood, 2016). For this reason, it is essential to evaluate the molecular and biochemical potential for toxin production in this endemic strain before considering its use in food or feed applications.

Finally, the observed temperature response also has ecological implications. Despite the favorable growth performance of *Leptolyngbya* sp. at 28 °C, its low abundance in natural samples suggests that elevated water temperatures in situ may not support the persistence or proliferation of this strain under natural conditions.

### Conflict of interest

The authors declare that they have no conflict of interest.

### Author contributions

Erika Juliana Obando Montoya, Lorenzo Portillo Cogollo, Lennin Flórez-Leiva, Juan Camilo Pulgarín Correa, Pedro Pablo Pérez Jaramillo y Lucia Atehortua Garcés: performed the experiments, analyzed the data and wrote this manuscript.

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### References

- Ahn, S. J., Costa, J. and Emanuel, J. R. (1996). PicoGreen quantitation of DNA: Effective evaluation of samples pre- or post-PCR. *Nucleic Acids Research*, 24(13), 2623–2625. <https://doi.org/10.1093/nar/24.13.2623>
- Albertano, P., Barsanti, L., Passarelli, V. and Gualtieri, P. (2000). A complex photoreceptive structure in the cyanobacterium *Leptolyngbya* sp. *Micron*, 31(1), 27–34. [https://doi.org/10.1016/S0968-4328\(99\)00063-3](https://doi.org/10.1016/S0968-4328(99)00063-3)
- Allen, M. M. and Stanier, R. Y. (1968). Growth and division of some unicellular blue-green algae. *Journal of General Microbiology*, 51(2), 199–202. <https://doi.org/10.1099/00221287-51-2-199>
- Andersen, R. A. and Kawachi, M. (2015). Traditional microalgae isolation techniques. In R. A. Andersen (Ed.), *Algal culturing techniques* (pp. 83–100). Elsevier.
- Basheva, D., Moten, D., Stoyanov, P., Belkinova, D., Mladenov, R. and Teneva, I. (2018). Content of phycoerythrin, phycocyanin, allophycocyanin and phycoerythrocyanin in some cyanobacterial strains: Applications. *Engineering in Life Sciences*, 18(11), 861–866. <https://doi.org/10.1002/elsc.201800035>
- Beal, C. M., Gerber, L. N., Thongrod, S., Phromkunthong, W., Kiron, V., Granados, J., Archibald, I., Greene, C. H., and Huntley, M. E. (2018). Marine microalgae commercial production improves sustainability of global fisheries and aquaculture. *Scientific Reports*, 8, 15064. <https://doi.org/10.1038/s41598-018-33504-w>
- Beier, E., Bernal, G., Ruiz-Ochoa, M. and Barton, E. D. (2017). Freshwater exchanges and surface salinity in the Colombian basin, Caribbean Sea. *PLOS ONE*, 12(8), e0182116. <https://doi.org/10.1371/journal.pone.0182116>
- Bellamy-Carter, J., Sound, J. and Leney, A. (2022). Probing heavy metal binding to phycobiliproteins. *The Febs Journal*, 289, 4646 - 4656. <https://doi.org/10.1111/febs.16396>
- Bruckner, C. G. and Kroth, P. G. (2009). Protocols for the removal of

- bacteria from freshwater benthic diatom cultures. *Journal of Phycology*, 45(5), 981–986. <https://doi.org/10.1111/j.1529-8817.2009.00708.x>
- Brunelle, J. L. and Green, R. (2014). One-dimensional SDS-polyacrylamide gel electrophoresis (1D SDS-PAGE). In J. Lorsch (Ed.), *Methods in enzymology* (pp. 151–159). Academic Press. <https://doi.org/10.1016/B978-0-12-420119-4.00012-4>
- Casamatta, D. A. and Hašler, P. (2016). Blue-green algae (cyanobacteria) in rivers. In N. Orlando Jr. (Ed.), *River algae* (pp. 5–34). Springer International Publishing. [https://doi.org/10.1007/978-3-319-31984-1\\_2](https://doi.org/10.1007/978-3-319-31984-1_2)
- Chen, H. B., Wu, J. Y., Wang, C. F., Fu, C. C., Shieh, C. J., Chen, C. I., Contreras-Fernández, S., Florez-Leiva, L., Bernal-Sánchez, M. C., Pacheco-Paternina, W., Bedoya-Valestt, S. and Portillo-Cogollo, L. (2022). Gulf of Urabá (Caribbean Colombia), a tropical estuary: A review with some general lessons about how it works. *Ocean Science Journal*, 57(4), 359–378. <https://doi.org/10.1007/s12601-022-00093-9>
- Chen, H., Qi, H. and Xiong, P. (2022). Phycobiliproteins—A Family of Algae-Derived Biliproteins: Productions, Characterization and Pharmaceutical Potentials. *Marine Drugs*, 20. <https://doi.org/10.3390/md20070450>
- Choi, C. Y., Kim, N. N., Shin, H. S., Park, H. G., Cheon, S. G. and Kil, G. S. (2013). The effect of various wavelengths of light from light-emitting diodes on the antioxidant system of marine cyanobacteria, *Synechococcus* sp. *Molecular and Cellular Toxicology*, 9, 295–302. <https://doi.org/10.1007/s13273-013-0037-9>
- Domínguez, G. D., Suárez, V. M., Lázaro, O. and Pérez, V. (2018). Principales propiedades de las ficobiliproteínas: C-ficocianina. *Revista Cubana de Hematología, Inmunología y Hemoterapia*, 32(1), 1–10.
- Donkor, V. A. and Häder, D. P. (1996). Effects of ultraviolet irradiation on photosynthetic pigments in some filamentous cyanobacteria. *Aquatic Microbial Ecology*, 11, 143–149. <https://doi.org/10.3354/ame011143>
- El Sema, N. A. (2013). Microscopic, molecular, and biochemical investigations to characterize a benthic cyanoprokaryote *Leptolyngbya* strain from Egypt. *Microscopy Research and Technique*, 76(3), 249–257. <https://doi.org/10.1002/jemt.22160>
- Wang, C. Y., and Liu, Y. C. (2010). Modeling on chlorophyll and phycocyanin production by *Spirulina platensis* under various light-emitting diodes. *Biochemical Engineering Journal*, 53, 52–56. <https://doi.org/10.1016/j.bej.2010.09.004>
- Choi, C.Y., Kim, N.N., Shin, H.S., Park, H.G., Cheon, S.G., Kil, G.S., 2013. The effect of various wavelengths of light from light-emitting diodes on the antioxidant system of marine cyanobacteria, *Synechococcus* sp. *Molecular and Cellular Toxicology* 9, 295–302. <https://doi.org/10.1007/s13273-013-0037-9>
- Córdoba-Mena, N., Florez-Leiva, L., Atehortúa, L., and Obando, E. (2020). Changes in phytoplankton communities in a tropical estuary in the Colombian Caribbean Sea. *Estuaries and Coasts*, 43, 2106–2127. <https://doi.org/10.1007/s12237-020-00750-z>
- Escobar, C. A., and Velásquez-Montoya, L. (2018). Modeling the sediment dynamics in the gulf of Urabá, colombian Caribbean sea. *Ocean Engineering*, 147, 476–487. <https://doi.org/10.1016/j.oceaneng.2017.10.055>
- Foster, J. S., Green, S. J., Ahrendt, S. R., Golubic, S., Reid, R. P., Hetherington, K. L. and Bebout, L. (2009). Molecular and morphological characterization of cyanobacterial diversity in the stromatolites of Highborne Cay, Bahamas. *ISME Journal*, 3, 573–587. <https://doi.org/10.1038/ismej.2008.129>
- Gaude, E., Chignola, F., Spiliotopoulos, D., Spitaleri, A., Ghitti, M. M., Garcia-Manteiga, J., Mari, S. and Musco, G. (2013). muma, an R package for metabolomics univariate and multivariate statistical analysis. *Current Metabolomics*, 1(3), 180–189.
- Gan, F., Zhang, S., Rockwell, N. C., Martin, S. S., Lagarias, J. C. and Bryant, D. A. (2014). Extensive remodeling of a cyanobacterial photosynthetic apparatus in far-red light. *Science*, 345(6202), 1312–1317. <https://doi.org/10.1126/science.1256963>
- García V., C. and Sierra C., P. C. (2007). Un golfo en el Caribe colombiano. En Atlas del golfo de Urabá: Una mirada al Caribe de Antioquia y Chocó (pp. 15–21). INVEMAR.
- Ghanbarzadeh, M., Niknam, V., Soltani, N. and Ebrahimzadeh, H. (2019). *Leptolyngbya fragilis* ISC 108 is the most effective strain for dodecane biodegradation in contaminated soils. *International Journal of Phytoremediation*, 21(9), 908–920. <https://doi.org/10.1080/15226514.2019.1583635>
- Henchion, M., Hayes, M., Mullen, A., Fenelon, M., and Tiwari, B. (2017). Future protein supply and demand: Strategies and factors

- influencing a sustainable equilibrium. *Foods*, 6(7), 53. <https://doi.org/10.3390/foods6070053>
- Islam, M.A., Beardall, J., Cook, P., 2019. Intra-strain Variability in the Effects of Temperature on UV-B Sensitivity of Cyanobacteria. *Photochemistry and Photobiology*, 95, 306–314. <https://doi.org/10.1111/php.13014>
- Khan, M. I., Shin, J. H., and Kim, J. D. (2018). The promising future of microalgae: Current status, challenges, and optimization of a sustainable and renewable industry for biofuels, feed, and other products. *Microbial Cell Factories*, 17, 2-21. <https://doi.org/10.1186/s12934-018-0879-x>
- Khan, Z., Wan Maznah, W. O., Faradina Merican, M. S. M., Convey, P., Najimudin, N. and Alias, S. A. (2019). A comparative study of phycobilliprotein production in two strains of *Pseudanabaena* isolated from Arctic and tropical regions in relation to different light wavelengths and photoperiods. *Polar Science*, 20, 3–8. <https://doi.org/10.1016/j.polar.2018.10.002>
- Khatoon, H., Kok Leong, L., Abdu Rahman, N., Mian, S., Begum, H., Banerjee, S., and Endut, A. (2018). Effects of different light source and media on growth and production of phycobilliprotein from freshwater cyanobacteria. *Bioresource Technology*, 249, 652–658. <https://doi.org/10.1016/j.biortech.2017.10.052>
- Kim, J. H., Choi, W., Jeon, S.-M., Kim, T., Park, A., Kim, J., Heo, S.-J., Oh, C., Shim, W.-B., and Kang, D.-H. (2015). Isolation and characterization of *Leptolyngbya* sp. KIOST-1, a basophilic and euryhaline filamentous cyanobacterium from an open paddle-wheel raceway *Arthrospira* culture pond in Korea. *Journal of Applied Microbiology*, 119, 1597–1612. <https://doi.org/10.1111/jam.12961>
- Kusmayadi, A., Leong, Y., Yen, H., Huang, C. and Chang, J. (2021). Microalgae as sustainable food and feed sources for animals and humans - Biotechnological and environmental aspects. *Chemosphere*, 271, 129800. <https://doi.org/10.1016/j.chemosphere.2021.129800>
- Kłodawska, K., Bujas, A., Turos-Cabal, M., Żbik, P., Fu, P. and Malec, P. (2019). Effect of growth temperature on biosynthesis and accumulation of carotenoids in cyanobacterium *Anabaena* sp. PCC 7120 under diazotrophic conditions. *Microbiological Research*, 226, 34-40. <https://doi.org/10.1016/j.micres.2019.05.003>
- Lee, W.-K., Ryu, Y.-K., Kim, T., Park, A., Lee, Y.-J., Lee, Y., Kim, J. H., Oh, C., Kang, D.-H. and Choi, W.-Y. (2024). Optimization of industrial-scale cultivation conditions to enhance the nutritional composition of nontoxic cyanobacterium *Leptolyngbya* sp. KIOST-1. *Applied Sciences*, 14(1), 282. <https://doi.org/10.3390/app14010282>
- Levipan, H. A., Opazo, L. F., Arenas-Urbe, S., Wicki, H., Marchant, F., Florez-Leiva, L. and Avendaño-Herrera, R. (2024). Estimating taxonomic and functional structure along a tropical estuary: Linking metabolic traits and aspects of ecosystem functioning. *Microbiology Spectrum*, 12(1), e03886-23. <https://doi.org/10.1128/spectrum.03886-23>
- Lee, Y.; Kim, J.H.; Oh, C.; Kang, D.-H.; Choi, W.-Y. Optimization of Industrial-Scale Cultivation Conditions to Enhance the Nutritional Composition of Nontoxic Cyanobacterium *Leptolyngbya* sp. KIOST-1. *Applied Sciences*, 14, 282. <https://doi.org/10.3390/app14010282>
- Li, Y., Naman, C. B., Alexander, K. L., Guan, H., and Gerwick, W. H. (2020). The chemistry, biochemistry and pharmacology of marine natural products from *Leptolyngbya*, a chemically endowed genus of cyanobacteria. *Marine Drugs*, 18(10), 508. <https://doi.org/10.3390/md18100508>
- Lozano-Duque, Y., Vidal, L. A. and Navas, G. R. (2010). La comunidad fitoplanctónica en el mar Caribe colombiano. En INVEMAR (Ed.), *Biodiversidad del margen continental del Caribe colombiano* (pp. 87–104). Serie de Publicaciones Especiales. INVEMAR.
- McLaughlin, Ó. B., Emmerson, M. C., and O’Gorman, E. J. (2013). Habitat isolation reduces the temporal stability of island ecosystems in the face of flood disturbance. *Advances in Ecological Research*, 48, 225–284. <https://doi.org/10.1016/B978-0-12-417199-2.00004-5>
- Miao, X., Wang, S., Liu, M., Ma, J., Hu, J., Li, T. and Chen, L. (2019). Changes in the phytoplankton community structure of the Backshore Wetland of Expo Garden, Shanghai from 2009 to 2010. *Aquaculture and Fisheries*, 4, 198–204. <https://doi.org/10.1016/j.aaf.2019.02.004>
- Mobin, S. M. A., Chowdhury, H., and Alam, F. (2019). Commercially important bioproducts from microalgae and their current applications – A review. *Energy Procedia*, 160, 752–760. <https://doi.org/10.1016/j.egypro.2019.02.183>
- Mohsenpour, S. F., Richards, B. and Willoughby, N. (2012). Spectral conversion of light for enhanced microalgae growth rates and photosynthetic pigment production. *Bioresource Technology*, 125, 75–81. <https://doi.org/10.1016/j.biortech.2012.08.072>



Moon, Y.J., Kim, S. Il and Chung, Y.H., 2012. Sensing and Responding to UV-A in Cyanobacteria. *International Journal of Molecular Sciences* 13, 16303–16332. <https://doi.org/10.3390/ijms131216303>

Muñoz Sevilla, N. P., and Le Bail, M. (2017). Latin American and Caribbean regional perspective on ecosystem-based management (EBM) of Large Marine Ecosystems goods and services. *Environmental Development*, 22, 9–17. <https://doi.org/10.1016/j.envdev.2017.01.006>

Nascimento, S., Santos, V., Watanabe, É. and Ferreira, J. (2020). Assessment of the purification of phycobiliproteins in cyanobacteria through aqueous two-phase systems with different proportions of PEG/salt. *Food and Bioproducts Processing*, 119, 345–349. <https://doi.org/10.1016/j.fbp.2019.11.020>

Nakamori, H., Yatabe, T., Yoon, K. S., and Ogo, S. (2014). Purification and characterization of an oxygen-evolving photosystem II from *Leptolyngbya* sp. strain O-77. *Journal of Bioscience and Bioengineering*, 118(1), 119–124. <https://doi.org/10.1016/j.jbiosc.2014.01.009>

Detalles de adaptación: Neif, E. M. (2015). Efeito dos fatores ambientais e das mudanças climáticas sobre a comunidade perifítica em lagos rasos de água doce [Tese doctoral, Universidade Estadual de Maringá]. Repositório da UEM. <http://hdl.handle.net/1834/10091>

Not, F., Siano, R., Kooistra, W. H. C. F., Simon, N., Vaulot, D. and Probert, I. (2012). Diversity and ecology of eukaryotic marine phytoplankton. In G. Piganeau (Ed.), *Advances in botanical research* (Vol. 64, pp. 1–53). Academic Press. <https://doi.org/10.1016/B978-0-12-391499-6.00001-3>

Pacheco, W., Florez-Leiva, L., Correa, M., Montoya-Sánchez, R. and Ricaurte-Villota, C. (2025). Potential drivers for chlorophyll-a variability in the southwestern Caribbean of Colombia. *Regional Studies in Marine Science*, 82, 104032. <https://doi.org/10.1016/j.rsma.2025.104032>

Paerl, H. W., Bland, P. T., Bowles, N. D., and Haibach, M. E. (1985). Adaptation to high-intensity, low-wavelength light among surface blooms of the cyanobacterium *Microcystis aeruginosa*. *Applied and Environmental Microbiology*, 49(5), 1046–1052. <https://doi.org/10.1128/AEM.49.5.1046-1052.1985>

Pantelić, D., Svirčev, Z., Simeunović, J., Vidović, M., and Trajković, I.

(2013). Cyanotoxins: Characteristics, production and degradation routes in drinking water treatment with reference to the situation in Serbia. *Chemosphere*, 91(3), 421–441. <https://doi.org/10.1016/j.chemosphere.2013.01.003>

Park, J., and Dinh, T. B. (2019). Contrasting effects of monochromatic LED lighting on growth, pigments and photosynthesis in the commercially important cyanobacterium *Arthrospira maxima*. *Bioresource Technology*, 291, 121846. <https://doi.org/10.1016/j.biortech.2019.121846>

Pascual, U., Balvanera, P., Anderson, C. B., Chaplin-Kramer, R., Christie, M., González-Jiménez, D., Martin, A., Raymond, C. M., Termansen, M., Vatn, A., Athayde, S., Baptiste, B., Barton, D. N., Jacobs, S., Kelemen, E., Kumar, R., Lazos, E., Mwampamba, T. H., Nakangu, B., ... Zent, E. (2023). Diverse values of nature for sustainability. *Nature*, 620, 813–823. <https://doi.org/10.1038/s41586-023-06406-9>

Paul, V.J., 2008. Global warming and cyanobacterial harmful algal blooms. *Advances in experimental medicine and biology*, 619, 239–257. [https://doi.org/10.1007/978-0-387-75865-7\\_11](https://doi.org/10.1007/978-0-387-75865-7_11)

Prihantini, N. B., Pertiwi, Z. D., Yuniati, R., Sjamsuridzal, W., and Putrika, A. (2019). The effect of temperature variation on the growth of *Leptolyngbya* (cyanobacteria) HS-16 and HS-36 to biomass weight in BG-11 medium. *Biocatalysis and Agricultural Biotechnology*, 19, 2–6. <https://doi.org/10.1016/j.bcab.2019.101105>

Puzorjov, A. and McCormick, A. (2020). Phycobiliproteins from extreme environments and their potential applications. *Journal of Experimental Botany*, 13, 3827–3842. <https://doi.org/10.1093/jxb/eraa139>

Pumas, C., Peerapornpisal, Y., Vacharapiyasophon, P., Leelapornpisid, P., Boonchum, W., Ishii, M. and Khanongnuch, C. (2012). Purification and characterization of a thermostable phycoerythrin from hot spring cyanobacterium *Leptolyngbya* sp. KC45. *International Journal of Agriculture and Biology*, 14, 121–125.

Raja, R., Hemaiswarya, S., Kumar, N. A., Sridhar, S. and Rengasamy, R. (2008). A perspective on the biotechnological potential of microalgae. *Critical Reviews in Microbiology*, 34(2), 77–88. <https://doi.org/10.1080/10408410802086783>

Rastogi, R.P., Sinha, R.P., Moh, S.H., Lee, T.K., Kottuparambil, S., Kim, Y.J., Rhee, J.S., Choi, E.M., Brown, M.T., Häder, D.P. and Han, T., 2014. Ultraviolet radiation and cyanobacteria. *Journal of Photochemistry*

and Photobiology B: *Biology*, 141, 154–169.  
<https://doi.org/10.1016/j.jphotobiol.2014.09.020>

Rizwan, M., Mujtaba, G., Memon, S. A., Lee, K., and Rashid, N. (2018). Exploring the potential of microalgae for new biotechnology applications and beyond: A review. *Renewable and Sustainable Energy Reviews*, 92, 394–404.  
<https://doi.org/10.1016/j.rser.2018.04.034>

Sanchez Rizza, L., Sanz Smachetti, M. E., Do Nascimento, M., Salerno, G. L. and Curatti, L. (2017). Bioprospecting for native microalgae as an alternative source of sugars for the production of bioethanol. *Algal Research*, 22, 140–147.  
<https://doi.org/10.1016/j.algal.2016.12.021>

Sathasivam, R., Radhakrishnan, R., Hashem, A. and Abd\_Allah, E. F. (2019). Microalgae metabolites: A rich source for food and medicine. *Saudi Journal of Biological Sciences*, 26(4), 709–722.  
<https://doi.org/10.1016/j.sjbs.2017.11.003>

Schipper, K., Al Muraikhi, M., Alghasal, G. S. H. S., Saadaoui, I., Bounnit, T., Rasheed, R., Dalgamouni, T., Al Jabri, H. M. S. J., Wijffels, R. H. and Barbosa, M. J. (2019). Potential of novel desert microalgae and cyanobacteria for commercial applications and CO<sub>2</sub> sequestration. *Journal of Applied Phycology*, 31, 2231–2243.  
<https://doi.org/10.1007/s10811-019-01763-3>

Schneider, U. A., Havlík, P., Schmid, E., Valin, H., Mosnier, A., Obersteiner, M., Böttcher, H., Skalský, R., Balkovič, J., Sauer, T. and Fritz, S. (2011). Impacts of population growth, economic development, and technical change on global food production and consumption. *Agricultural Systems*, 104(3), 204–215.  
<https://doi.org/10.1016/j.agsy.2010.11.003>

Sharma, N. K., Rai, A. K. and Stal, L. J. (2014). *Cyanobacteria: An economic perspective*. Chennai: Wiley-Blackwell.

Sinha, R. P., Singh, N., Kumar, A., Kumar, H. D. and Häder, D. P. (1997). Impacts of ultraviolet-B irradiation on nitrogen-fixing cyanobacteria of rice paddy fields. *Journal of Plant Physiology*, 150(1), 188–193. [https://doi.org/10.1016/S0176-1617\(97\)80201-5](https://doi.org/10.1016/S0176-1617(97)80201-5)

Sinha, R. P., Singh, N., Kumar, A., Kumar, H. D., Häder, M. and Häder, D. P. (1996). Effects of UV irradiation on certain physiological and biochemical processes in cyanobacteria. *Journal of Photochemistry and Photobiology B: Biology*, 32(2–3), 107–113.

[https://doi.org/10.1016/1011-1344\(95\)07205-5](https://doi.org/10.1016/1011-1344(95)07205-5)

Stadnichuk, I. and Kusnetsov, V. (2023). Phycobilisomes and Phycobiliproteins in the Pigment Apparatus of Oxygenic Photosynthetic: From Cyanobacteria to Tertiary Endosymbiosis. *International Journal of Molecular Sciences*, 24.  
<https://doi.org/10.3390/ijms24032290>

Sunda, W. G., Price, N. M. and Morel, F. M. M. (2005). Trace metal ion buffers and their use in culture studies. In R. A. Andersen (Ed.), *Algal culturing techniques* (pp. 35–63). Elsevier.  
<https://doi.org/10.1016/b978-012088426-1/50005-6>

Tan, X., Zhang, D., Duan, Z., Parajuli, K. and Hu, J. (2020). Effects of light color on interspecific competition between *Microcystis aeruginosa* and *Chlorella pyrenoidosa* in batch experiment. *Environmental Science and Pollution Research*, 27, 344–352.  
<https://doi.org/10.1007/s11356-019-06650-5>

Tang, D. Y. Y., Khoo, K. S., Chew, K. W., Tao, Y., Ho, S.-H. and Show, P. L. (2020). Potential utilization of bioproducts from microalgae for the quality enhancement of natural products. *Bioresource Technology*, 122997, 1–53.  
<https://doi.org/10.1016/j.biortech.2020.122997>

Taton, A., Lis, E., Adin, D. M., Dong, G., Cookson, S., Kay, S. A., Golden, S. S., and Golden, J. W. (2012). Gene transfer in *Leptolyngbya* sp. strain BL0902, a cyanobacterium suitable for production of biomass and bioproducts. *PLoS ONE*, 7(1), e30901.  
<https://doi.org/10.1371/journal.pone.0030901>

Tilahun, S., and Kifle, D. (2019). The influence of El Niño-induced drought on cyanobacterial community structure in a shallow tropical reservoir (Koka Reservoir, Ethiopia). *Aquatic Ecology*, 53, 61–77. <https://doi.org/10.1007/s10452-019-09673-9>

Todd, S. K. (2018). Life in the world's oceans [Online course]. The Great Courses. <http://www.thegreatcoursesplus.com/life-in-the-worlds-oceans>

Vallejo Toro, P. P., Vásquez Bedoya, L. F., Correa, I. D., Bernal Franco, G. R., Alcántara-Carrió, J. and Palacio Baena, J. A. (2016). Impact of terrestrial mining and intensive agriculture in pollution of estuarine surface sediments: Spatial distribution of trace metals in the Gulf of Urabá, Colombia. *Marine Pollution Bulletin*, 111(1–2), 311–320.  
<https://doi.org/10.1016/j.marpolbul.2016.06.093>



- Wall, J., Wood, S., Orlovich, D., Rhodes, L. and Summerfield, T. (2014). Characterisation of freshwater and marine cyanobacteria in the Hokianga region, Northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 48(2), 177–193. <https://doi.org/10.1080/00288330.2013.854814>
- Wood, R. (2016). Acute animal and human poisonings from cyanotoxin exposure — A review of the literature. *Environment International*, 91, 276–282. <https://doi.org/10.1016/j.envint.2016.02.026>
- Yanes, A., Botero, C. M., Arrizabalaga, M. and Vásquez, J. G. (2019). Methodological proposal for ecological risk assessment of the coastal zone of Antioquia, Colombia. *Ecological Engineering*, 130, 242–251. <https://doi.org/10.1016/j.ecoleng.2017.12.010>
- Zheng, L., Zheng, Z., Li, X., Wang, G., Zhang, K., Wei, P., Zhao, J. and Gao, N. (2021). Structural insight into the mechanism of energy transfer in cyanobacterial phycobilisomes. *Nature Communications*, 12. <https://doi.org/10.1038/s41467-021-25813-y>.