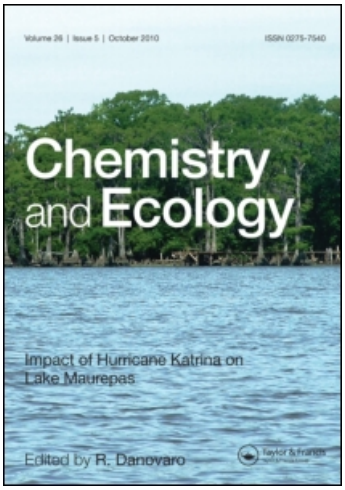

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Effect of light and temperature on the population dynamics of two toxic bloom forming Cyanobacteria – *Microcystis ichthyoblabe* and *Anabaena aphanizomenoides*

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The effect of light and temperature on the growth of *Microcystis ichthyoblabe* and *Anabaena aphanizomenoides*, isolated from the subtropical Oued Mellah lake, Morocco (33°30′N–07°20′W), were investigated in batch culture. Growth rates at 66 light–temperature combinations were determined and fitted with different mathematical models. The results show that the two Cyanobacteria grow at all light intensities and temperatures, except at 10 °C for *A. aphanizomenoides*, where the growth was strongly limited. The μ_{max} of *M. ichthyoblabe* increased with temperature from 0.56 d^{-1} at 10 °C to 1.32 d^{-1} at 35 °C. At all tested temperatures, a relative photoinhibition within the studied range of irradiance was observed and the photosensitivity was thermodependent. For *Anabaena*, the obtained μ_{max} ranged between 0.07 d^{-1} at 10 °C and 1.46 d^{-1} at 35 °C, and a weak photoinhibition was observed at 15 °C. The positive correlation between μ_{max} and I_{opt} ($r^2 \geq 0.93$) indicates a close interaction between light and temperature on the cyanobacteria growth. The results obtained in this work suggest that the growth of these two species is possible under low light and low temperature.

Keywords: Cyanobacteria; *Microcystis ichthyoblabe*; *Anabaena aphanizomenoides*; light–temperature interaction; ecophysiology

1. Introduction

The water-blooms of Cyanobacteria (blue-green algae) are becoming an increasing problem in fresh, brackish and marine waters, where they are responsible for sporadic but recurrent episodes of wild and domestic animal illness and death. They are also implicated in human poisonings from certain municipal and recreational water supplies [1,2]. For the several inventoried cyanobacterial genera with toxin (hepatotoxins and/or neurotoxins) producing strains, *Microcystis* and *Anabaena* are the most commonly distributed world-wide [3]. In Oued Mellah lake (Morocco), *Microcystis ichthyoblabe* and *Anabaena aphanizomenoides* are the most important phytoplankters, where they

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form spectacular toxic blooms [4,5]. This is one reason why an understanding of the conditions influencing their occurrence and dominance is strongly needed for any control and management measures. The experimental investigations dealing with the effect of environmental factors such as temperature, light, photoperiod, nutrient concentration on the physiological properties of the phytoplankton species may lead to better understand some *in situ* observed ecological behaviour. This work presents and discusses the effect of light–temperature interaction, under non nutritional limiting conditions, on the growth of the toxic cyanobacteria *M. ichthyoblabe* and *A. aphanizomenoides*. We fit the experimental results with mathematical models to predict the Cyanobacteria growth.

2. Material and methods

The two strains used in the experiments, *M. ichthyoblabe* (MI) and *A. aphanizomenoides* (AA), were isolated during water-bloom periods in 1999 from the hypertrophic lake Oued Mellah (33°30′N–07°20′W) [5]. A stock of culture for each species was maintained in liquid Z8 medium [6,7] by regular subculturing (every 3 to 5 days). The cyanobacteria were grown at 25 ± 2 °C and suspended by gentle aeration using filtered air. Light was provided by continuous irradiation using cool white fluorescent light (35 μmol photons m^{-2} s^{-1} measured at the culture surface using a flat sensor). *Microcystis* cell density was estimated by measuring 50 colonies and counting the average number of cells per colony. In order to facilitate the measurements of cell density during the experiments, the relationship between cells/trichome density and absorbance at 750 nm were obtained for both strains (Figure 1).

For the temperature–light interaction experiments, inoculate from the stock cultures of the two strains were used. Batch cultures at exponential growth phase were prepared in autoclaved 2 litre Erlenmeyer flasks containing 1.2 l of Z8 medium, buffered with sodium bicarbonate ($NaHCO_3$) to pH 8.2 and incubated under 15:9 light:dark photoperiod in a temperature controlled incubator. Two replicates for each situation were used. In the first experiment, samples of these high density cultures were placed in the dark to induce synchronisation and to avoid preadaptation to light. After 24 h, the samples were diluted to avoid self-shading and distributed among flasks. Initial

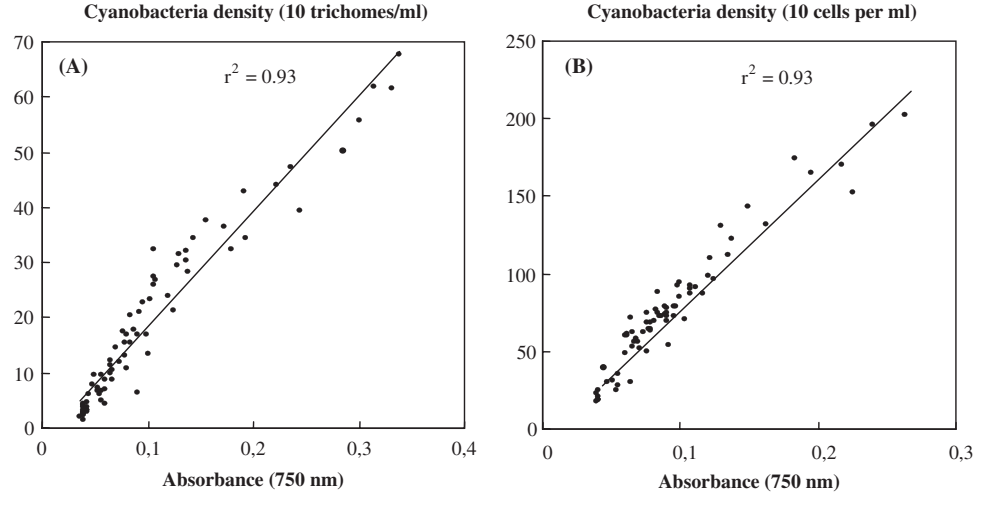

Figure 1. Relations between the absorbance at 750 nm and cyanobacteria density for (A) *A. aphanizomenoides* and (B) *M. ichthyoblabe* cultures.

cell densities were 10^3 trichomes/ml for AA and 10^6 cells/ml for MI. Simultaneously, for a given temperature, cultures were grown in batches with air bubbling (0.5 l air l^{-1} min^{-1}) and exposed to 11 irradiances ranging from 15–450 μmol photons m^{-2} s^{-1} provided by 400 watt Phyto-Claude halogen lamps, which gives a spectrum close to that of daylight. Six incubation temperatures, 10, 15, 20, 25, 30 and 35 °C, were used. These cover the range of water temperatures (24–28 °C) typically observed in Oued Mellah lake during bloom periods of the two studied species.

In preliminary experiments, a high correlation between cyanobacteria density and light absorption at 750 nm ($A_{750\,nm}$) (Figure 1) was found. Later, the growth was followed by measuring $A_{750\,nm}$ using a Secomam UV-VIS S750 spectrophotometer.

The incubations lasted 24 h. After that time, the growth rates (μ, in day^{-1}) were calculated according to the formula:

$$\mu(d^{-1}) = \Delta t^{-1} \ln(A_1/A_0),$$

where Δt is the incubation time, and A_0 and A_1 are, respectively, the 750 nm absorbances at the beginning and end of the incubation time.

To estimate the physiological parameters for growth–light intensity relationship, the models of Steele [8] (Equation 1), Platt and Jassby [9] (Equation 2) and Peeters and Eilers [10] (Equation 3) were fitted to the experimental data. The model that will present the most satisfactory adjustment will be adopted.

- Model of Steele [8]:

$$\mu_{(T,I)} = \mu_{maxT} \times I/I_{optT} \times \exp(1 - I/I_{optT}), \quad (1)$$

  where $\mu_{(T,I)}$ is growth rate at the light intensity I, and μ_{maxT} and I_{optT} are, respectively, the estimated maximal growth rates and optimal light intensity at temperature T.

- Model of Platt and Jassby [9]:

$$\mu_{(T,I)} = \mu_{maxT} \times \mathrm{Tanh}[\alpha \times (I - I_c)/\mu_{maxT}], \quad (2)$$

  where α symbolises the growth efficacy (i.e. initial curve incline), I_c is estimated light intensity without growth ($I_c \geq 0$), and Tanh is the hyperbolic tangential function.

- Model of Peeters and Eilers [10]:

$$\mu_{(T,I)} = 2 \times \mu_{maxT} \times (1 + \beta) \times (I/I_{optT})/[(I/I_{optT})^2 + 2 \times (I/I_{optT}) \times \beta + 1], \quad (3)$$

  where β is the attenuation coefficient that allows us to take into account the photoinhibition phenomenon.

In addition, the variations of μ_{max} and the associated I_{opt} versus temperature were adjusted using the expression of Lehman et al. [11] (Equations 4 and 5):

$$\mu_{maxT} = \mu_{max} \times \exp[-2.3 \times (T - T_{opt})^2/B^2], \quad (4)$$

$$I_{optT} = I_{opt} \times \exp[-2.3 \times (T - T_{opt})^2/B^2], \quad (5)$$

with

$$B = T_{sup} - T_{opt} \quad \text{if } T > T_{opt},$$

and

$$B = T_{inf} - T_{opt} \quad \text{if } T < T_{opt}.$$

T_{sup} and T_{inf} are the limit temperatures where $\mu_{maxT} = 0.1 \times \mu_{max}$ and $I_{optT} = 0.1 \times I_{opt}$.

3. Results

The experimental results expressed in growth rates (μ) of the strain *M. ichthyoblabe* at the various light intensity–temperature combinations are shown in Figure 2. The species grow at all tested temperature and light levels. For each temperature, the μ increased versus light until it reached a maximal value (μ_{max}) associated with an optimal light intensity (I_{opt}). Beyond this light intensity, which can be considered as light saturated growth, μ decreased considerably for MI. This expressed the light inhibitory effect (photoinhibition) which occurred at light intensity values from 74 μmol photons $m^{-2}\,s^{-1}$ at 10 °C until 230 μmol photons $m^{-2}\,s^{-1}$ at 35 °C. However, for AA, the relative photoinhibition was only observed at 15 °C and light intensity up to 130 μmol photons $m^{-2}\,s^{-1}$. For temperatures over 15 °C, μ remained almost constant beyond I_{opt}. MI develops faster (μ_{max} between 0.56 and 0.84 d^{-1}) at the low temperatures (10–20 °C) than AA (μ_{max} between 0.07 and 0.78 d^{-1}). However, at the elevated temperatures (30–35 °C) the observed AA μ_{max} (1.27–1.46 d^{-1}) are higher than those of MI (1.25–1.32 d^{-1}). In general, the growth seems to be strongly stimulated at the temperatures over 25 °C with growth rates exceeding 1 day^{-1}.

The adjustment of the experimental data by the mathematical models, described in the material and methods section, are presented in Figure 2. The model of Steele describes well the observed results for $I \leq I_{opt}$, but beyond I_{opt} it underestimates the μ values and consequently emphasises the photoinhibition phenomenon. The Platt and Jassby model seems to be not adequate for two reasons. It provides negative or null values of μ for $I \leq I_c$ while experimental μ are ranged between 0.32 and 0.53 d^{-1} for MI. Moreover, this model did not take into consideration the photoinhibition phenomenon. The inadequate adjustments given by these models seem to be solved by the use of Peeters and Eilers equation. The last model succeeded to predict both the exponential evolution of μ for I until I_{opt}, and the photoinhibition phenomenon particularly observed in MI for $I > I_{opt}$. These observations are confirmed by the significant correlation obtained between observed and calculated growth rates (Figure 3).

The physiological parameters deduced by the equation of Peeters and Eilers at each temperature are presented in Figure 4 with the adjustment of Lehman et al.'s function. This model fits well the relationship of μ_{max} and I_{opt} versus temperature. For the two species, μ_{max} and I_{opt} increase as

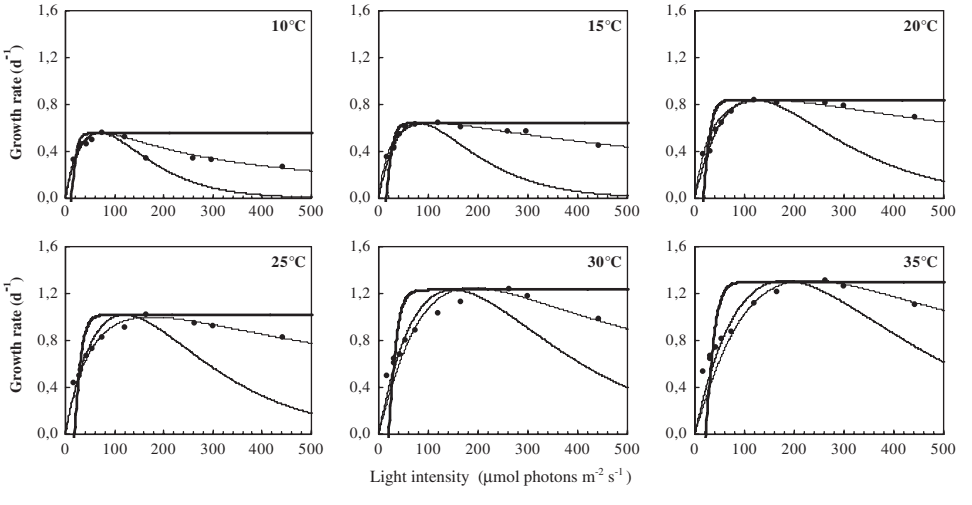

Figure 2. Growth rates of *M. ichthyoblabe* as a function of light intensity at different temperatures. The observed data (•) are fitted with the functions of Steele (1965) (——), Platt and Jassby (1976) (——) and Peeters and Eilers (1978) (——).

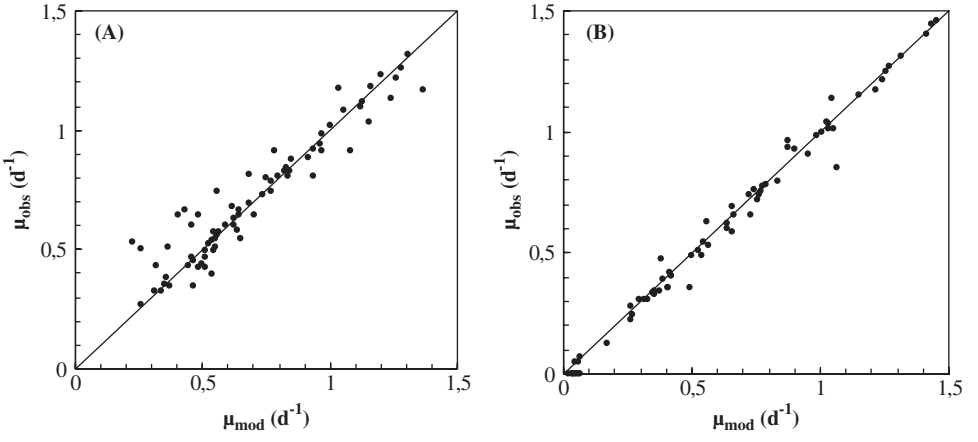

Figure 3. Correlation between observed growth rate (μ_{obs}) and fitted growth rate (μ_{mod}) by Peeters and Eilers (1978) model for (A) *M. ichthyoblabe*, and (B) *A. aphanizomenoides*.

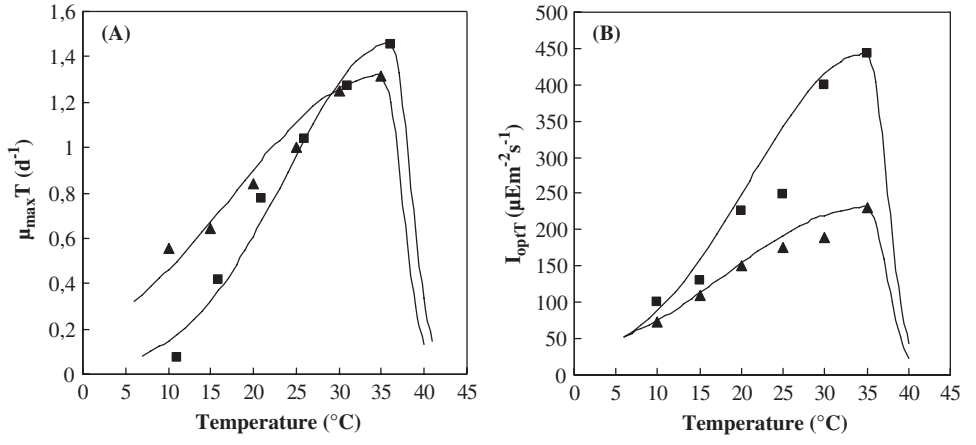

Figure 4. Maximum growth rate (μ_{maxT}) (A) and optimal light intensity (I_{optT}) (B) of *M. ichthyoblabe* (▲) and *A. aphanizomenoides* (■) in relation to temperature fitted with the function of Lehman et al. (1975).

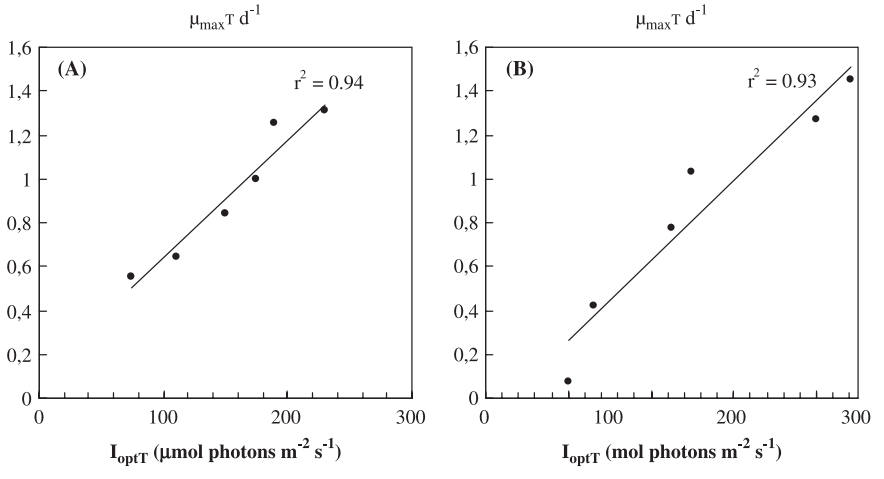

Figure 5. Relation between μ_{maxT} and I_{optT} for (A) *M. ichthyoblabe*, and (B) *A. aphanizomenoides*.

function of temperature until the applied maximal temperature (35 °C) considered then as optimal. The results show also that AA requires higher heliothermal conditions for maximal growth than MI. In addition, the obtained μ_{max} and I_{opt} show a strong positive correlation ($r^2 \geq 0.93$) (Figure 5).

4. Discussion

Strains of the bloom forming Cyanobacteria species, *M. ichthyoblabe* and *A. aphanizomenoides*, were isolated for the first time in Morocco from the brackish Oued Mellah lake. We have previously shown that these blooms occur in late spring and summer and the toxicity assessment by mice gives values of intraperitoneal LD_{50} ranging between 254 and 1924 mg_{DW}/kg and according to HPLC analysis, 4 to 11 microcystin (hepatotoxin) variants were separated [4,5]. The present work provides information on the growth response of these Cyanobacteria strains to the simultaneous variation of light and temperature under non nutritional limiting conditions. The growth of the Cyanobacteria under plentiful availability of nutrients, supplied in Z8 medium, becomes a function of light and temperature from which the ecological effects are inseparable [12]. Under optimal heliothermal conditions, MI and AA obtain their highest μ_{max} which are respectively 1.32 and 1.46 d^{-1}. Compared with other Cyanobacteria (Table 1), these studied strains could be considered as fast growth organisms. Among species, the μ_{max} differences observed owed to the specific growth performances or to the culture conditions. MI and AA appear eurythermal, with growth activity between 10 and 35 °C. The two species obtain their highest growth rates at 35 °C but the μ_{maxT} exceed already 1 day^{-1} from 25 °C. This is in agreement with the literature data, which show that the thermal optimum for Cyanobacteria has been described as being around 25 °C or higher [13–16]. In addition, elevated water temperature seems to be critical for the formation of cyanobacterial blooms in Oued Mellah lake [4,5]. Prior to the bloom event, an increase in water temperature to between 24 and 25 °C (May–June) for MI and between 25 and 28 °C (July–September) for AA was recorded [4,5]. The Cyanobacteria optimum temperatures are higher than for diatoms and green algae and that might be why cyanobacterial blooms usually occur during the warmer months [17]. The temperature affects growth of Cyanobacteria by changing the rates of enzymatic reactions, the molecular configuration of cellular constituents and other physiological phenomena [18]. However, whilst a general relationship of accelerated cyanobacterial growth with elevated temperature is often observed, temperature alone is unlikely to be the most important environmental variable [19].

As they are primarily photoautotrophs, Cyanobacteria depend closely on irradiance – only some Cyanobacteria exhibit a heterotrophic mode of metabolism but some are able to be both dark-heterotrophic and/photoheterotrophic and therefore able to survive in conditions of low irradiance [20]. In general, the Cyanobacteria seem to have similar light requirements to other

Table 1. Comparison of maximum growth rates and culture conditions of different strains of Microcystis and Anabaena species.

Strain	μ_{max} (d^{-1})	Culture conditions	Reference
M. ichthyoblabe	1.32	35 °C; 230 $\mu E\, m^{-2}\, s^{-1}$; 15:9 L:D	Present work
M. aeruginosa	1.28	30 °C; 220 $\mu E\, m^{-2}\, s^{-1}$; 15:9 L:D	[14]
M. aeruginosa	0.62	35 °C; 190 $\mu E\, m^{-2}\, s^{-1}$; 15:9 L:D	[24]
M. aeruginosa	0.48	23 °C; C.S.I.*	[9]
A. aphanizomenoides	1.46	35 °C; 442 $\mu E\, m^{-2}\, s^{-1}$; 15:9 L:D	Present work
A. cylindrica	1.56	25 °C; C.S.I.	[13]
A. flos-aquae	0.78	20 °C; C.S.I.	[31]
A. flos-aquae	0.35	20 °C; S.I.; 6:18 L:D	[31]

Notes: *C.S.I., continuous saturating illumination; S.I., saturating illumination.

phytoplankters, although the level at which photosynthesis becomes light-limited is lower for Cyanobacteria than for other algae. This is due to the accessory photopigments phycocyanin and phycoerythrin [21]. Our results show that MI and AA can grow at weak irradiance ($\geq$15 μmol photons m^{-2} s^{-1}). That is in agreement with field observations, where irradiance is strongly reduced by water turbidity, Cyanobacteria have a significant competitive advantage over other phytoplankton due to their low growth constant [22]. The regular increase of I_{opt} according to the temperature (from 74 to 230 μmol photons m^{-2} s^{-1} in MI and from 100 to 442 μmol photons m^{-2} s^{-1} in AA) demonstrates that these two parameters are interdependent. Beyond the optimal light intensity, the growth seems to be limited by the photoinhibition in MI. The same result has been observed by other authors [23–28] in Cyanobacteria and in other algal groups. The absence of this phenomenon and the elevated values of I_{opt} calculated for AA indicate that this strain requires more irradiance in order to reach its maximal growth and may explain its massive proliferation during late summer when the solar irradiance is maximal. The values of I_{opt} for these Cyanobacteria species are, nevertheless, very weak compared to the irradiance recorded at the surface of Oued Mellah lake during bloom periods. The *in situ* values of incident light are in the ranges of 796–1991 and 1500–1912 μmol photons m^{-2} s^{-1}, respectively, during MI and AA *M. ichthyoblabe* and *A. aphanizomenoides* blooms. However, because of the light reflection at the surface and the water turbidity (maximal depth of the Secchi disk visibility between 0.1 and 0.38 m), light attenuates quickly and then the limit of euphotic zone does not exceed 1 m. To defeat this limitation and due to the presence of gas vacuoles in their cells, the two species float at the surface and form scum. These results suggests also that in the lake, where the temperature is generally higher than 25 °C after the end of spring, the two studied species endowed of buoyancy ecostrategy, can proliferate in suboptimal to optimal heliothermal growth conditions. On the other hand, it is known that at the surface of water bodies, Cyanobacteria are frequently exposed to high or excessive light intensities which can lead to surface scum undergoing photo-oxidation and subsequent death [14,29]. However, at least for *Microcystis*, the photo-oxidation can be avoided by the production of protective carotenoid pigments [30]. Other strategies utilised by Cyanobacteria against the intense light intensity include controlling buoyancy and vertical migration to areas of more optimal light intensity. In conclusion, the growth responses of Cyanobacteria to a wide range of light intensities are important for their survival and competitiveness.

The physiological parameters determined for MI and AA using mathematical models, constitute a source of new data about the adaptation capacities to different heliothermal conditions. However, to understand the physiology of these species forming toxic blooms, and to predict their occurrence under various environmental conditions, the used methodology must be generalised to other abiotic factors (N, P, C) and the models must be developed and improved to integrate simultaneously various factors and phenomena. These results show that more ecological data are needed using different Cyanobacteria species so as to better understand the occurrence of Cyanobacteria blooms. These data are the first to study *Microcystis ichthyoblabe* and *Anabaena aphanizomenoides* population dynamics in controlled laboratory conditions.

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