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Horizontal Distribution of the Cell Abundance and Toxicity of *Microcystis* in a Hypereutrophic Moroccan Reservoir

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ABSTRACT

The first results of the horizontal distribution of the cell abundance and toxicity of *Microcystis* in the hypereutrophic Moroccan reservoir Lalla Takerkoust are reported. An unexpected spatio-temporal heterogeneity has been shown between *Microcystis* abundance and microcystins concentrations. The principal determining factors were analyzed in order to identify the most likely sites for the proliferation and/or accumulation of *Microcystis* in this reservoir. The horizontal heterogeneity seems to be mainly influenced by the wind direction and inflows. The results can serve as reference data for monitoring cyanobacterial water blooms and associated cyanotoxins in the lake.

Key words: reservoir, *Microcystis*, Microcystins, spatial heterogeneity, wind, nutrients, inflow of water.

In Morocco, as in many regions of the world, cyanobacteria toxic blooms have received increasing attention over the last few years due to the potential danger for human and animal health [Jochimsen et al., 1998], and deterioration of drinking water quality [Paerl et al., 2001].

Several studies [Loudiki et al., 2002; Oudra et al., 2002; Sabour et al., 2002] have confirmed the occurrence of toxic cyanobacteria blooms

in different aquatic environments. The Lalla-Takerkoust reservoir, which supplies drinking and irrigation water to the Marrakesh area, is the most studied site. This work has revealed hepatoxic *Microcystis* blooms, and characterized microcystins for the first time [Oudra et al., 1998]. While several cyanobacteria species are present in this reservoir, the blooms are mainly dominated by the genus *Microcystis* [Loudiki et al., 2002]. More recently, [El Ghazali et al., 2011] detected, over a year-long cycle, the presence of microcystins in the lake waters. The concentrations of MC-LR often exceed the WHO norms, particularly during the bloom periods. However, the majority of these studies were based on a single sampling location in the lake, usually the most accessible. Yet it is well known that the spatial distribution of *Microcystis* can be heterogeneous on the scale of a site [Pobel et al., 2011]. This heterogeneity can either be due to enhanced growth in preferential zones, or to movement and accumulation of the biomass by the wind. In addition, the potential toxicity of a *Microcystis* bloom can be variable in space and time [Sabart et al., 2010; Pobel et al., 2012].

In order to better understand the horizontal distribution of *Microcystis* in the Lalla-Takerkoust reservoir, and the link between the spatial distribution of the biomass and the concentration of microcystins, we studied the spatial and temporal dynamics of *M. aeruginosa* abundance and toxic potential related to the physico-chemical parameters on the overall of the lake. This work also aims to complement previous work in order to update and strengthen the means of monitoring cyanobacteria and associated cyanotoxins.

MATERIALS AND METHODS

Description of the study site. Lalla Takerkoust reservoir (31°36′ N, 8°2′ W) is one of the oldest Moroccan reservoirs (first flooded in 1935); situated at 600 m, it is around 35 km SSW of Marrakesh (Fig. 1, *a*). Its maximum depth is 25 m, with a total volume of 69×10^6 m^3. The average renewal time for the water in the reservoir is two and a half months, with an average annual inflow of 7.59 m^3/s. The main uses of the reservoir are for irrigation, provision of drinking water and leisure activities.

Sampling locations. Samples have been taken from six points spread along length of the lake: one site in the deep zone (Sp) and five in the shallow, coastal zone (SL1, SL2, SL3, SL4 and SL5) (see Fig. 1, *b*). The choice of these five sites was mainly based on the morphometry of the lake and the activities of the local inhabitants. The samples were taken from February 2008 to March 2009, once a month in the spring and autumn, and twice a month in the summer. The water samples and the phytoplankton were taken from the surface and at different depths using a Van Dorn bottle (2 L capacity). Qualitative samples of the phytoplankton were also taken using plankton net with a 27 μm mesh size. These samples were fixed using a Lugol's solution (10 %).

Physicochemical parameters. At each station, temperature (using the conductivity type WTW LF 318), dissolved oxygen (using the oxygen probe HANNA HI 9142), and pH (using the pH meter type WTW PH 330i) were measured in the water column.

Other chemical-parameters were analyzed in the laboratory. Orthophosphates analyses were performed following the AFNOR norm T90-023. The phosphomolybdic complex obtained was quantified at 700 nm using a spectrophotometer (Cary 50 Scan). Nitrate concentrations were measured with colorimetric assay following the AFNOR norm T90-013. After cadmium column reduction to nitrite, the absorbance was read at 537 nm using a spectrophotometer. The climatic parameters (weather, inflow of water, hydrological data) were provided by the water agency ABHT.

***Microcystis aeruginosa* abundance.** The abundance of *Microcystis* cell was estimated by microscopic cell count. For each sample, 10 ml of water was sonicated (50 kHz for 5 seconds) to disrupt *Microcystis aeruginosa* colonies and not alter cellular integrity [Latour et al., 2004]. The cells were counted using a Mallassez cell with an optical microscope (×400) and the results are expressed as number of cells per liter of water.

***Microcystins* concentration (MC).** For each sample, 1L of water was filtered on Whattman filter on GF/C and the filter was used for the analysis of intracellular MC.The intracellular MC concentration was extracted twice by sonication (two sets of 5 baths 15 min) of the

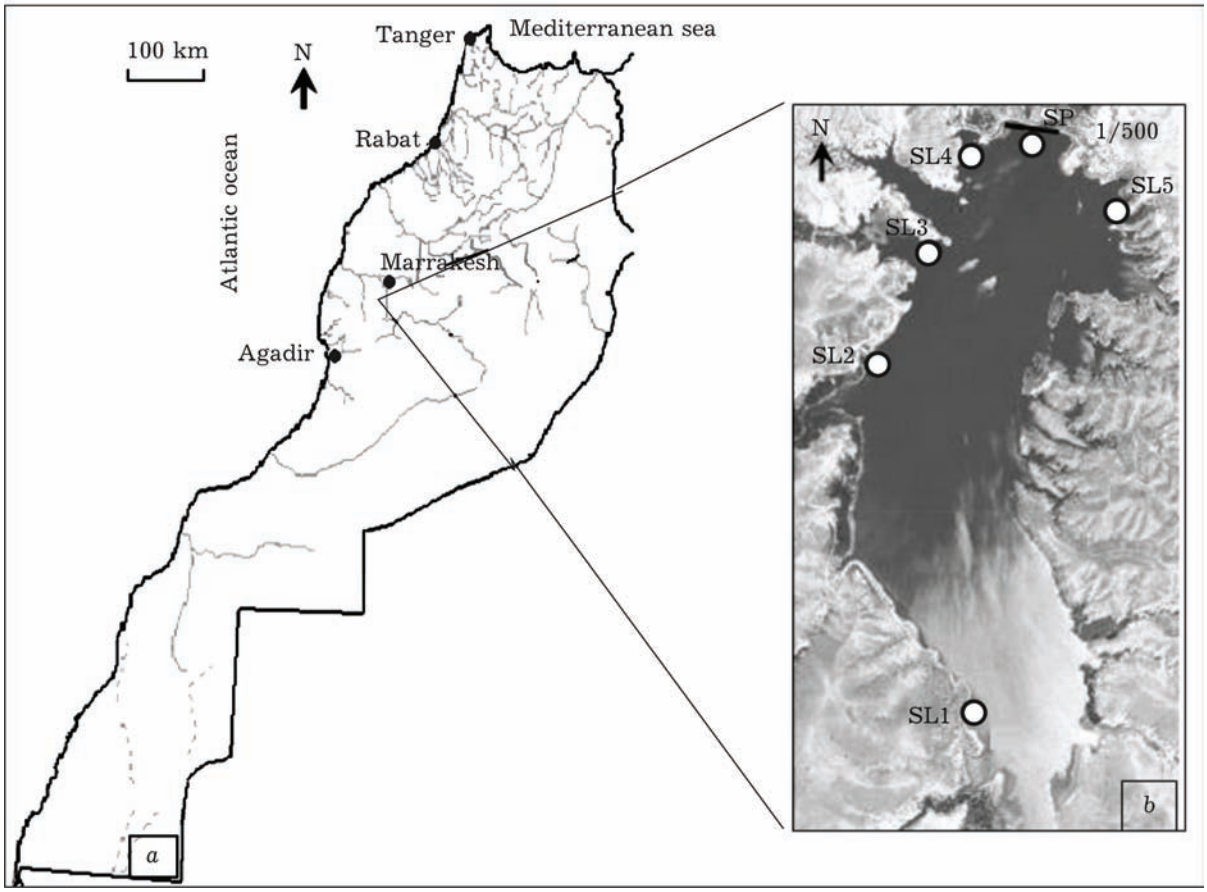

Fig. 1. Geographic location of the LallaTakerkoust reservoir (*a*), and location of the sampling stations (*b*)

filter in 2 ml of 75 % methanol. The lysate was centrifuged at 14 000 rpm/15 min to remove cellular debris then the supernatant was evaporated with a concentrator (Concentrator 5301, Eppendorf, Hamburg, Germany). The extract obtained was dissolved in 200 μL of methanol 20 % and store at −20 °C until analysis.

The intracellular MC concentration was achieved by high-pressure liquid chromatography coupled with photodiode arry detection (HPLC, Agilent Technologies Waghaeusel-Wiesental, Germany). The sample was pushed by a mobile phase consisting of water (*a*) and acetonitrile (*b*) (each containing 0.1 % formic acid). Separation was performed with an C18 (2) column (250 of 4.6 mm, 5-mm particle size; Phenomex Luna) with the following gradient: 0–2 min, 98 % A; 2–12 min, 98–2 % A (linear); and 12–13 min, 2–98 % A. Quality control samples (MC-LR) and blank runs were interspersed between the samples under investigation.

Statistical analysis. Pearson's correlations tests and statistical analysis were performed with XLStats (2015.4.01.20216 version; Addinsoft, Paris, France). The level of significance was set at 5 %. Normality was checked with the Shapiro–Wilk normality test, and variance homoscedasticity was assessed by Fisher's *F*-test. Dynamics of cellular abundance of *Microcystis* and intracellular MC variations were analyzed using repeated measures analysis of variance (ANOVA), and when an overall significant difference was found, multiple comparisons between groups were performed by using Tukey's test.

RESULTS

Spatiotemporal variations in physicochemical and climatic parameters. The temporal evolution of the temperature is similar for all the stations. Two phases can be distinguished: from 27 June, 2008 to 24 September, 2008 the temperature was relatively high (≥ 24 °C at

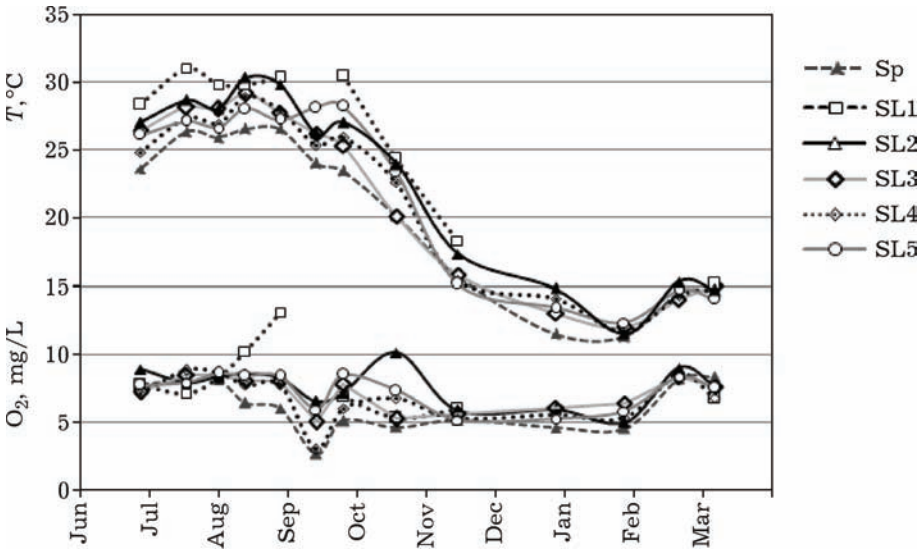

Fig. 2. Spatiotemporal evolution of the temperature and dissolved oxygen

the surface) particularly at the coastal stations; from October the temperature decreased progressively at all the stations (Fig. 2).

The vertical temperature profiles show thermal homogeneity throughout the water column and the absence of a stable vertical stratification in the summer (Fig. 3).

The concentration of dissolved oxygen shows a fairly similar spatio-temporal evolution with variations generally between 7.7 and 8.4 mg/L. However, occasional exceptions are noted in certain stations, notably SL1 (13.1 mg/L on 27 August), SL4 and Sp (3 mg/L and 2.6 mg/L on 12 September) (see Fig. 2).

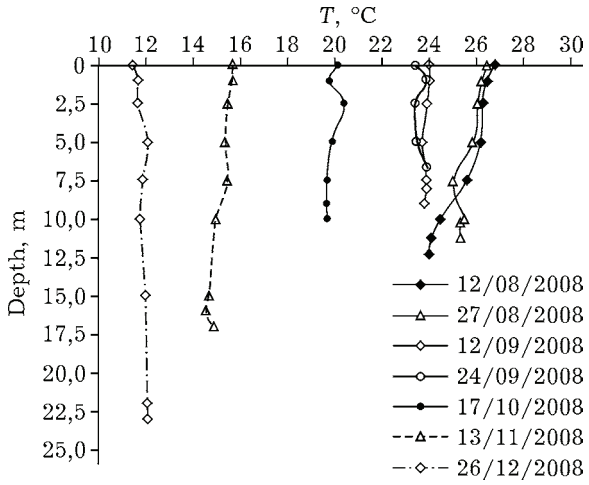

Fig. 3. Vertical profile of the temperature in the water column during summer and autumn (the measurements were taken between 9H-11H)

The water flow was very low during the low water period from 1 June to 1 September (0.34 m^3/s), followed by a first increase recorded on 10 September (6.03 m^3/s). A second peak was recorded on 1 October, 2008 (10.47 m^3/s). A sequence of high water inflows (with a maximum of de 27 m^3/s) was registered from October to November (Fig. 4).

During the study period the average monthly wind speed was fairly low, with a maximum in July 4.72 m/s. The wind speed from August to October was lower, varying between 1.11 m/s and 1.67 m/s. During the period from July-August the prevailing wind was from the north, while in October the prevailing winds were from the north, north-east and east (Fig. 5).

During the study period the nitrate concentrations evolved in a relatively similar way in all the stations. The maximum values were recorded on 31 July (between 1043 μg/L and 1217 μg/L) and on 24 September (1363 μg/L), particularly at the coastal stations. In contrast, the minimum values were recorded at the deep station Sp (235 μg/L on 31 July) (Fig. 6).

The orthophosphate concentrations are generally low, with the exception of isolated increases, particularly at Sp (244.51 μg/L on 31 July, and 88 μg/L on 17 October) (Fig. 7).

Spatiotemporal variations in *Microcystis* abundance. The appearance of the first *Microcystis* colonies in the counted samples for 2008 started in June. At the start of the summer period (27 June to 12 August) the *Micro-*

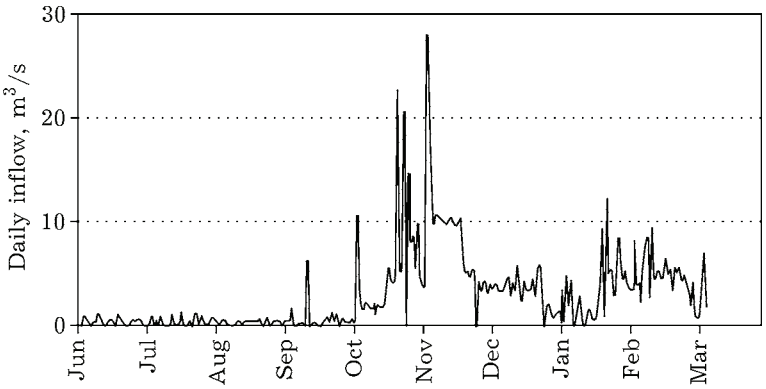

Fig. 4. Change in daily water inflow into the reservoir

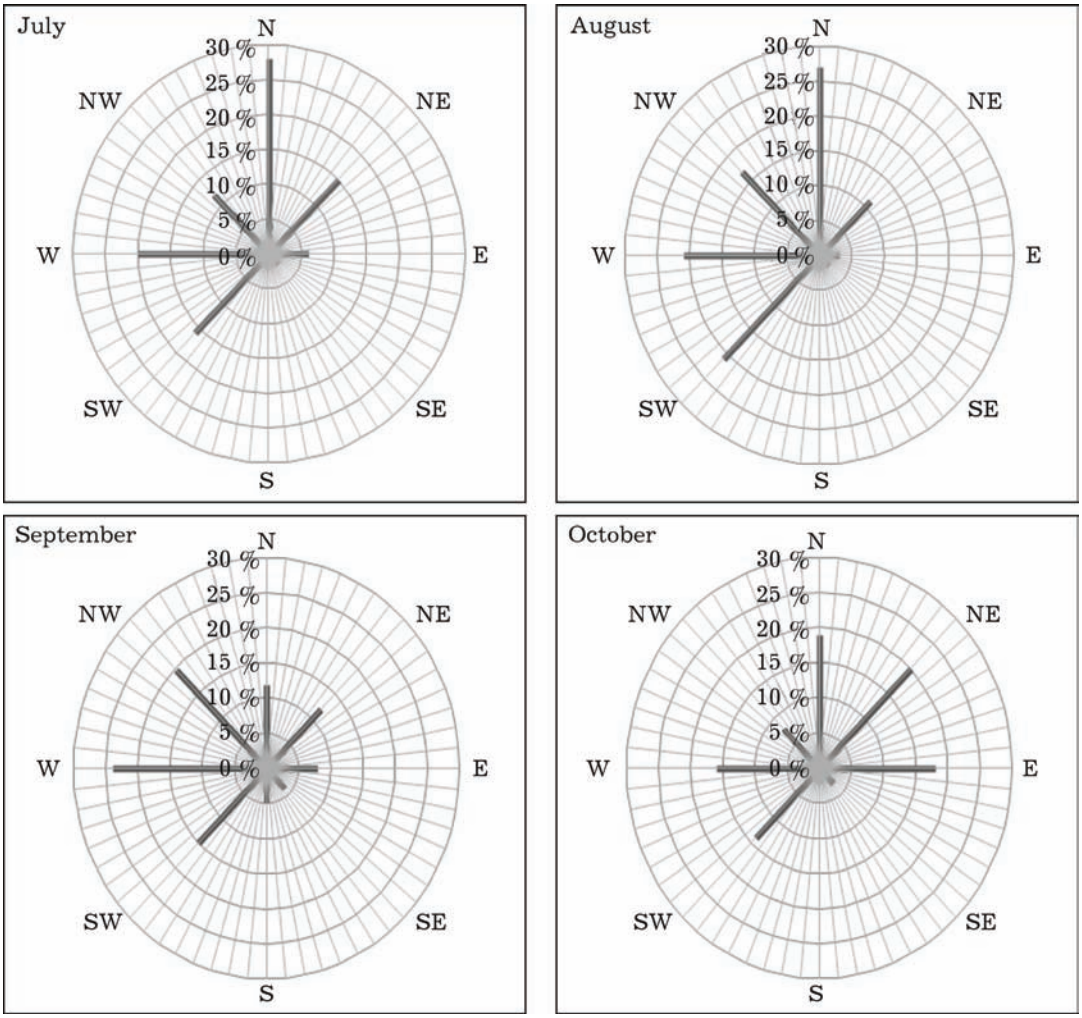

Fig. 5. Wind Rose direction (2008) (Data from the Marrakech/Menara meteorological station)

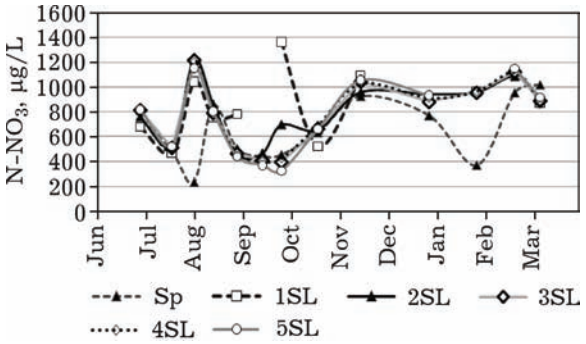

Fig. 6. Spatiotemporal variations in nitrate content

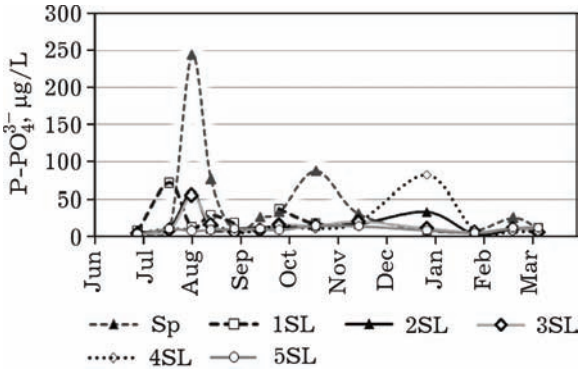

Fig. 7. Spatiotemporal variations in orthophosphate content

cystis cells abundance was low (0.1×10^6 Cel/L to 1.2×10^6 Cel/L) without any significant variations between the stations. In 27th August, the highest levels of *Microcystis* cell abundance were recorded notably at the upstream end of the lake (33.4×10^6 Cel/L at SL1, and 20.8×10^6 Cel/L at SL2) (Fig. 8A). In September cellular abundance decreased across the lake, with densities of less than 15×10^6 Cel/L. On 17th October, a clear increase in cellular abundance was observed at SL2, SP, SL5 stations and SL4 in a lesser extent. (see Fig. 8, *a*). This date showed the highest cellular abundance of the whole sampling period ($p < 0.005$). At the end of November, the proliferation cycle reached the end and the cell densities highly decreased across the whole lake (see Fig. 8, *a*; Fig. 9, *e*, *f*).

Spatiotemporal variations in *Microcystins* concentrations (MC). During the summer (27 June to 12 September) the intracellular MC-LR concentrations were relatively low and

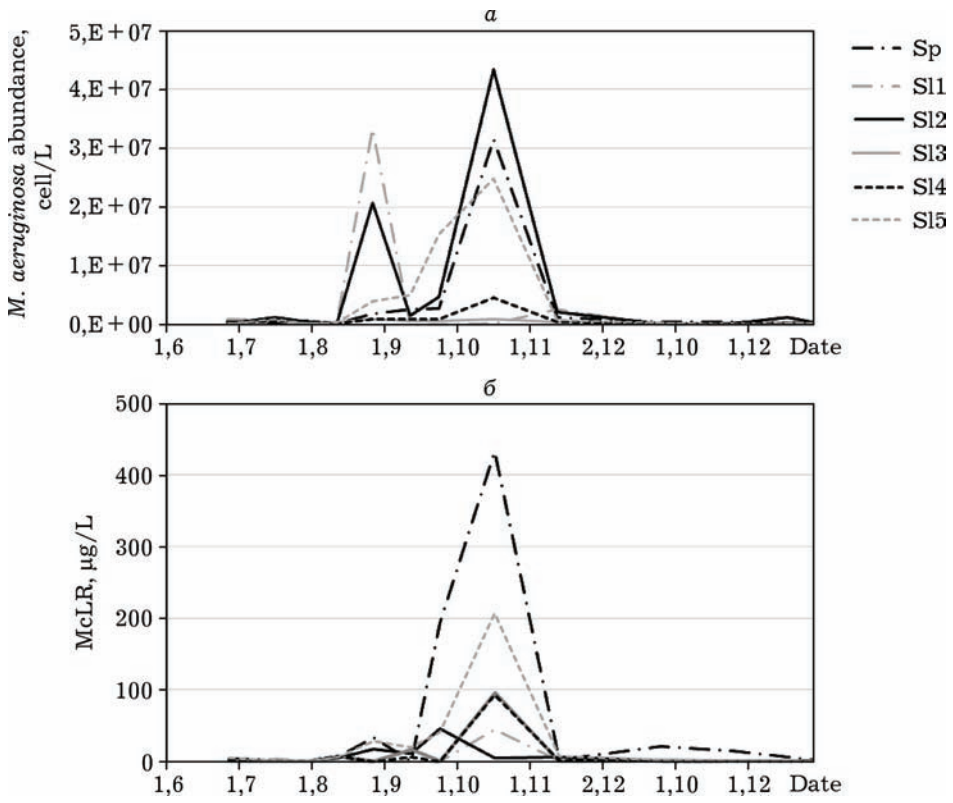

Fig. 8. Spatiotemporal variations in *Microcystis* abundance (*a*) and concentration of MC-LR microcystins (*b*) during summer and autumn 2008

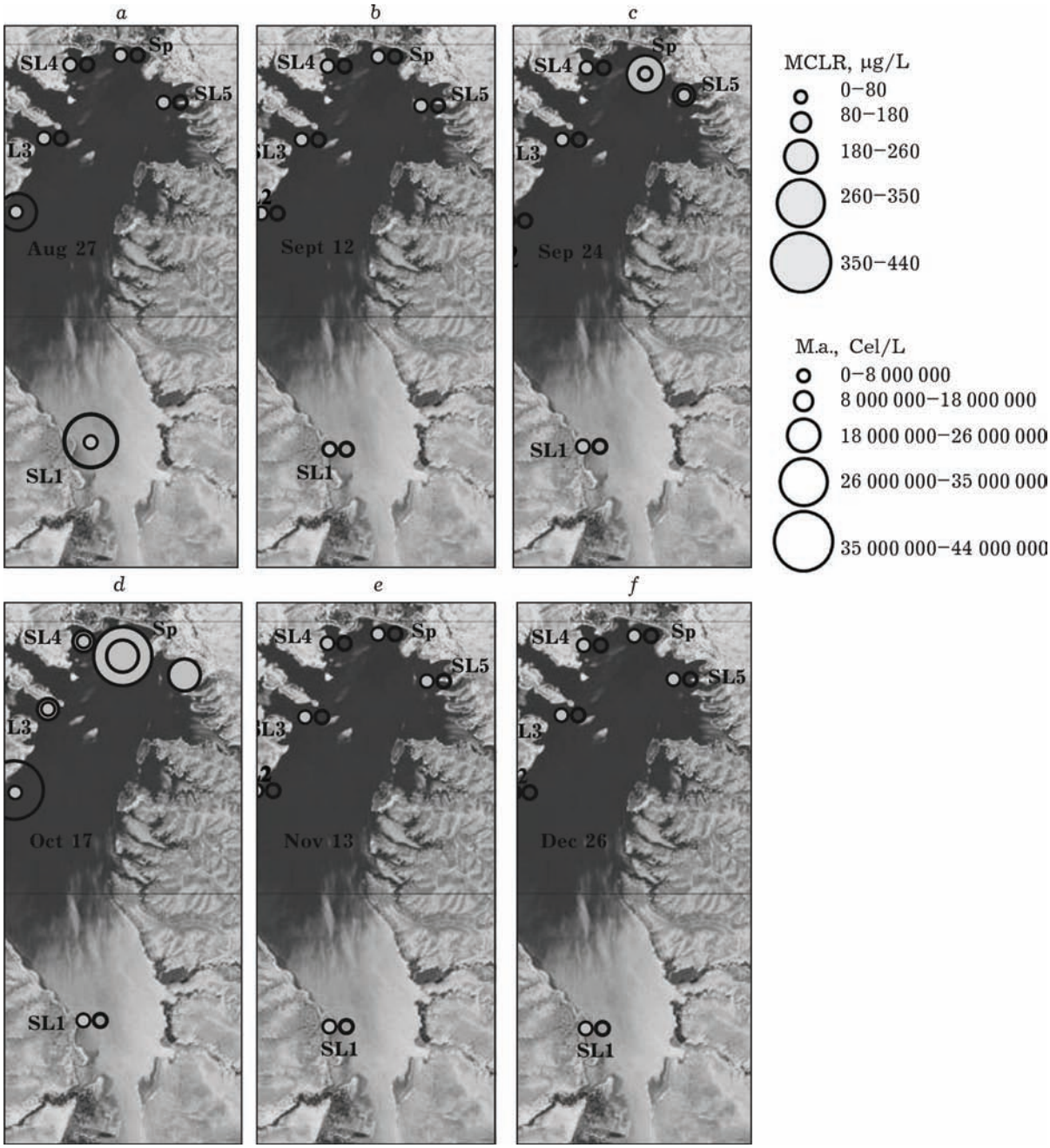

Fig. 9. Map of the *Microcystis* abundance and concentration of MC-LR microcystins during summer and autumn 2008

showed no significant difference between stations (see Fig. 8, *b*). On contrast, the 17th of October, where *Microcystis* biomass was maximum in the lake, the MC-LR concentrations increased significantly ($p < 0.0001$) and showed a clear spatial disparity with higher level recorded at the SP station ($p < 0.05$) with a maximum of 432.67 µg/L of MC-LR measured (see Fig. 8, *b*). For the rest of the year, from November to December, the MC-LR concentrations returned to very low, homogeneous levels across the lake (see Fig. 9, *e*, *f*). The MC-LR levels are strongly correlated with *M. aeruginosa* biomass in the downstream zone of the lake SP, SL4 and SL5 ($0.89 < r < 0.98$) and low correlated in the upstream stations SL1 and SL2.

DISCUSSION

Although the cyanobacteria *Microcystis* is widely present in a large number of lakes in different parts of the world, very few studies have focused on the spatial and horizontal distribution of MC-LR concentrations, and associated cyanobacterial biomass, within one ecosystem. The identification of the site in the Lalla Takerkoust reservoir which are most conducive to the proliferation and/or accumulation of cyanobacteria would allow the different ecological factors which influence the horizontal distribution of *Microcystis* and associated microcystins to be determined.

Spatiotemporal variations of *Microcystis* cell abundance. At the beginning of the *Microcystis* proliferation (27 August), the highest cell abundances were recorded at the upstream end of the lake. This location could be linked to an input of *M. aeruginosa* from the Yaacoub Al Mansour reservoir, situated 20 km upstream. However, in 2008, when the latter was first flooded, no cyanobacterial proliferations had been yet detected in this new lake [Ait Hammou et al., 2014]. On the other hand, it has been shown in the literature that high concentrations of nutrients can be responsible for the growth of cyanobacteria [Paerl, Huisman, 2008]. On the LallaTakerkoust reservoir, discharges of nutrients, linked to the various human activities in the towns and nearby habitations, could explain a higher proliferation of *M. aeruginosa* locally in the upstream part of the lake. However, nutrient analysis shows lower nutrient concentrations in the upstream zone at the start of the proliferation, so this cannot explain the higher concentrations of *M. aeruginosa* found in this area. In addition, it is also known that the presence of *M. aeruginosa* in the water column is partially linked to benthic recruitment which takes place mainly in the spring [Brunberg, Blomqvist, 2003]. This process, brought about, in part, by an increase in temperature and degree of light [Schöne et al., 2010] is often more intense in the shallow and coastal zones [Rengefors et al., 2004]. Thus higher concentrations of planktonic cyanobacteria might be registered in these shallow, upstream zones. While this process might well contribute to the highest values measured in the upstream zone, it is definitely not the only factor involved, as some of the sample locations in the downstream zone of the lake are also in the shallow, coastal zone, but still have low values of cyanobacterial abundance. According to [Pobel et al., 2011], the wind speed and direction can also affect the distribution of the phytoplankton abundance. *Microcystis* generally form blooms which float freely on the water surface, and are thus liable to be more easily pushed along by the wind than other phytoplankton [Tan et al., 2008]. Many authors have investigated the impact of wind-induced currents on the spatial distribution of phytoplankton [Ishikawa et al., 2002; Kanoshina et al., 2003]. At the start of the *Microcystis* proliferation (July – August 2008), the northerly wind was generally the most consistent and prevailing wind, thus favouring the accumulation of *M. aeruginosa* in the upstream part of the lake which is oriented N-S (see Fig. 1, *b*). Given the low inflow of water into the lake (0.3 m^3/s) during this period, even a wind with a fairly low average speed (of around 4.72 m/s) would be enough to move the colonies and bring about an accumulation of cyanobacteria at the upstream end of the lake. These results are similar to those of [Pobel et al., 2011], where the variations in cyanobacteria abundance are explained by the prevailing wind having blown for a few hours prior to the taking of the samples. In September we noted a spatial homogenization of the *M. aeruginosa* abundances over the whole of the reservoir, probably due to the climatic conditions recorded during this period. In fact, the decrease in temperature, coupled with the first autumn rainfall (20 mm) and a first peak in water inflow (6.09 m^3/s), recorded on the 10 September, probably contributed to the homogenization of the water body and thus the concentrations of cyanobacteria in the upstream zone. This deterioration in weather conditions was accompanied by a reduction in cyanobacterial abundance across the whole reservoir, as noted by [Briand et al., 2008] in their work on the Grangent reservoir. In October, a new accumulation of *M. aeruginosa* was observed, notably in the two downstream sites of Sp and SL5, located close to the dam wall and in an sheltered bay, respectively. This accumulation could be explained by the fact that

these stations are very sheltered from the prevailing winds, and also by the sporadic increase in orthophosphates (probably of internal origin) stimulating *Microcystis* growth. In addition, the highest cell abundances found at SL2, and to a lesser degree at SL3 and SL4, could be explained by the joint effects of the prevailing northerly, north-easterly and easterly winds (19 %, 20 and 18 %, respectively). At the end of the proliferation cycle (November) the drop in *Microcystis* cell density and its complete homogenisation could be explained by the increase in water inflow (27 m^3/s on 2 November) at the entry to the reservoir, leading to mixing of the lake waters.

Overall, the horizontal and temporal distribution of *M. aeruginosa* in the LallaTakerkoust reservoir seems to be mainly determined by the climatic conditions, in particular the wind, the water inflow, and the phosphorous levels.

Spatiotemporal variations in MC-LR. Different physico-chemical and biological factors are known to influence the synthesis of microcystins: light intensity [Kim et al., 2005], the presence of predators such as zooplankton [Jang et al., 2007], the temperature [Rapala et al., 1997], the phosphorous content [Kuniyoshi et al., 2013] and the azote concentration [Vézie et al., 2002]. Our results indicate a major spatiotemporal variation in MC-LR on the scale of the Lalla Takerkoust reservoir. The variations of the concentrations of MC-LR in the lake did not always coincide with the dynamics of *M. aeruginosa* biomass as it has already been observed in other studies [Duong et al., 2012]. The dynamics of *Microcystis*, which is the main cyanobacteria in the reservoir able to produce the MCs, could partly be linked to changes in the relative proportions of toxic and non-toxic strains. However, several studies have shown that there is no direct relation between the proportion of toxic strains and the MC concentration [Hotto et al., 2008; Sabart et al., 2010]. As a result, the variation in toxic strains alone is not enough to explain the variation in MC concentrations. Nevertheless, the highest MC-LR concentrations were recorded during the maximum cellular abundance of *Microcystis* in the downstream stations. This seems indicate that favorable environmental conditions for growth can also promote the production of MC-LR. During this period (24 September – 17 October) the relatively high phosphorous concentrations at the downstream end, probably following external (watershed-derived) and internal (recycling of plankton and sediment) input, could explain, in part, the highest MC concentrations. This period corresponds also to a range of temperatures (between 20 to 24 °C) that are known to favor the production of MC. Indeed, according to [Van der Westhuizen, Eloff, 1985], the MC contents of *M. aeruginosa* cultivated *in vitro* at 20 °C is higher than that measured at 15, 28 and 38 °C.

The intracellular MC-LR concentrations recorded in this study are in agreement with the study carried out by [Sinang et al., 2012] and [Sitoki et al., 2012], in which the concentrations of total MC are in the range of 122.3 μg/L and 200 μg/L. However, the high MC concentrations in the Lalla Takerkoust reservoir are well above the WHO guidelines for drinking water. Therefore it is important to highlight the potential risk to the health of the surrounding human and animal populations, particularly those who use the lake water directly, with no prior treatment. Moreover, as the MC concentrations did not always fit with the cyanobacterial abundance, regular surveillance of the cyanobacteria and their associated toxins is vital in this reservoir and more globally in all eutrophic and contaminated lakes.

CONCLUSION

Mapping of The spatial and temporal distribution of the abundance of *M. aeruginosa* and MC-LR in the LallaTakerkoust reservoir over a one year cycle is the first study of this kind in Morocco. The results obtained allow us to identify the sites prone to the most marked accumulation of cyanobacterial biomass and MC concentrations, and to establish the determining factors affecting their horizontal distribution in the lake.

The principal factors affecting the spatiotemporal distribution of *M. aeruginosa* in this lake are the wind, the water inflow at the entry, and the nutrient contents. The cell abundances and MC-LR concentrations showed strong spatiotemporal variations on the scale

of the reservoir. High *Microcystis* and MC-LR concentrations appear to be closely linked to the trophic state (phosphorous content) of the lake, and highlight the potential risk for human and animal health in the surrounding population.

Given the large spatial and temporal variations in the abundance and toxicity of the cyanobacterial proliferations, regular and frequent surveillance of these proliferations and the associated cyanotoxins in the lake is necessary in order to limit the risks and consequences for those using the water.

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REFERENES

Ait Hammou H., Latour D., Sabart M., Samoudi S., Mouhri Kh., Robin J., Loudiki M. Temporal evolution and vertical stratification of *Microcystis* toxic potential during a first bloom event // Aquat. Ecol. 2014. Vol. 48. P. 219–228.

Briand E., Escoffier N., Straub C., Sabart M., Quiblier C., Humbert J. F. Spatiotemporal changes in the genetic diversity of a bloom-forming *Microcystis aeruginosa* (cyanobacteria) population // ISME J. 2008. Vol. 3. P. 419–429.

Brunberg A. K., Blomqvist P. Recruitment of *Microcystis* (Cyanophyceae) from lake sediments: the importance of coastal inocula // J. Phycol. 2003. Vol. 39. P. 58–63.

Duong T.-T., Quynh Le T.-P., Dao T.-S., Pflugmacher S., Rochelle-Newall E., Hoang T.-K., Vu T.-N., Ho C.-T., Dang D. K. Seasonal variation of cyanobacteria and microcystines in the Nui Coc Reservoir, Northern Vietnam // J. Appl. Phycol. 2012. DOI 10.1007/s10811-012-9919-9.

El Ghazali I., Saqrane S., Saker M., Ouahid Y., Oudra B., Vasconcelos V., Delcampo F. F. Caractérisation biochimique et moléculaire d'efflorescences a cyanobactéries toxiques dans le réservoir Lalla Takerkoust (Maroc) // J. Water Sci. 2011. Vol. 24, N 2. P. 117–128.

Hotto A. M., Satchwell M. F., Berry D. L., Gobler C. J., Boyer G. L. Spatial and temporal diversity of microcystins and microcystin-producing genotypes in Oneida Lake. N.Y.: Harmful Algae, 2008. Vol. 7. P. 671–681.

Ishikawa K., Kumagai M., Vincent W. F., Tsujimura S., Nakahara H. Transport and accumulation of bloom-forming cyanobacteria in a large, mid-latitude lake: the gyre-*Microcystis* hypothesis // Limnol. 2002. Vol. 3. P. 87–96.

Jang M. H., Jung J. M., Takamura N. Changes in microcystin production in cyanobacteria exposed to zooplancton at different densities and infochemical concentrations // Limnol. Oceanogr. 2007. Vol. 52. P. 1454–1466.

Jochimsen E. M., Carmichael W. W., An J., Cardo D. M., Cookson S. T., Holmes C. E., Antunes M. B., Melo-Filho D. A., Lyra T. M., Barreto V. S., Azevedo S. M., Jarvis W. R. Liver failure and death following exposure to microcystin toxins at a hemodialysis center in Brazil // New Engl. Journ. Med. 1998. Vol. 36. P. 373–378.

Kanoshina I., Lips U., Leppänen J. M. The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea) // Harmful Algae. 2003. Vol. 2. P. 29–41.

Kim H. R., Kim C. K., Ahn T. S., Yoo S. A., Lee D. H. Effects of temperature and light on microcystinsynthetase gene transcription in *Microcystis aeruginosa* // Key Eng. Mater. 2005. P. 606–611.

Kuniyoshi T. M., Sevilla E., Bes M. T., Fillat M. F., Peleato M. L. Phosphate deficiency (N/P 40:1) induces mcyD transcription and microcystin synthesis in *Microcystisaeruginosa* PCC7806 // Plant Physiol. Biochem. 2013.

Latour D., Sabido O., Salencon M. J., Giraudet H. Dynamics and metabolic activity of the benthic cyanobacterium *Microcystis aeruginosa* in the Grangent reservoir (France) // J. Plankton Res. 2004. Vol. 26. P. 1–8.

Loudiki M., Oudra B., Sabour B., Sbiyyaa B., Vasconcelos V. Taxonomy and geographic distribution of potential toxic cyanobacterial strains in Morocco // Int. Journ. Limnol. 2002. Vol. 38, N 2. P. 101–108.

Oudra B., Loudiki M., Sabour B., Sbiyyaa, B., Vasconcelos V. Etude des blooms à cyanobactéries dans trois lacs réservoirs du Maroc // Revue des sciences de l'eau. 2002. Vol. 15. P. 301–313.

Oudra B., Loudiki M., Sbiyyaa B. et al. Occurrence of hepatotoxic *Microcystisaeruginosa* blooms in eutrophic Moroccan lake reservoir // Harmful Algae / eds. B. Reguera, J. Blonco, M. L. Fernandez, T. Wyatt); Xunta de Galicia & Intergovernmental Oceanographic Commission (IOC) of UNESCO, Santiago de Compostela, Spain, 1998. P. 29–31.

Paerl H. W., Fulton R. S., Moisander P. H., Dyble J. Harmful freshwater algal blooms with an emphasis on cyanobacteria // Sci. World. 2001. Vol. 1. P. 76–113.

Paerl H. W., Huisman J. Blooms like it hot // Science. 2008. Vol. 320. P. 57–58.

Pobel D., Godon J. J., Humbert J. F. et al. High-frequency monitoring of the genetic diversity and the potential toxicity of a *Microcystis aeruginosa* bloom in a French shallow lake // FEMS Microbiol. Ecol. 2012. Vol. 79. P. 132–141. DOI:10.1111/ j.1574-6941.2011.01203.x

Pobel D., Robin J., Humbert J.-F. Influence of sampling strategies on the monitoring of cyanobacteria in shallow lakes: lessons from a case study in France // Water Res. 2011. Vol. 45. P. 1005–1014.

Rapala J., Sivonen K., Lyraand C., Niemela S. Variation of microcystins, cyanobacterialhepatotoxins, in *Anabaena* spp. As a function of growth stimuli // Appl. Environ. Microbiol. 1997. Vol. 63. P. 2206–2212.

Rengefors K., Gustafsson S., Sthal-Delbanco A. Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from coastal and profundal sediments // Aquat. Microb. Ecol. 2004. Vol. 36. P. 213–226.

Sabart M., Pobel D., Briand E., Combourieu B., Salencon M. J., Humbert J. F., Latour D. Spatiotemporal variations in microcystin concentrations and in the proportions of microcystin-producing cells in several *Microcystisaeruginosa* populations // Appl. Environ. Microbiol. 2010. Vol. 76. P. 4750–4759.

Sabour B., Loudiki M., Oudra B., Vasconcelos V., Martins R., Oubraim S., Fawzi B. Toxicology of a *Microcystisichthyoblabe* waterbloom from lake Oued Mellah (Morocco) // Environ. Toxicol. 2002. Vol. 17, N 1. P. 24–31.

Schöne K., Jähnichen, S., Ihle T. Arriving in better shape: Benthic *Microcystis* as inoculum for pelagic growth // Harm. Algae. 2010. Vol. 9. P. 494–503.

Sinang S. C., Reichwaldt E. S., Ghadouani A. Spatial and temporal variability in the relationship between cyanobacterial biomass and microcystins // Environ. Monit Assess. 2012. DOI 10.1007/s10661-012-3031-0.

Sitoki L., Kurmayer R., Rott. E. Spatial variation of phytoplankton composition, biovolume, and resulting microcystin concentrations in the Nyanza Gulf (Lake Victoria, Kenya) // Hydrobiologia. 2012. Vol. 691. P. 109–122.

Tan X., Kong F. X., Zeng Q., Cao H. S., Qian S., Zhang M. Seasonal variation of *Microcystis* in Lake Taihu and its relationships with environmental factors // J. Environ. Sci. 2008. Vol. 21. P. 892–899.

Van der Westhuizen A. J., Eloff J. N. Effect of temperature and light on the toxicity and growth of the bluegreen alga *Microcystis aeruginosa* (UV-006) // Planta. 1985. Vol. 163. P. 55–59.

Vézie C., Rappala J., Vaitomaa J., Seitsonen J, Sivonen K. Effect of nitrogen and phosphorus on growth of toxic and non toxic*Microcystis* strains and on intracellular microcystin concentration // Microb. Ecol. 2002. Vol. 43. P. 443–454.